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PREY SELECTION BY THE ATLANTIC ANGEL SHARK *SQUATINA DUMERIL* IN THE NORTHEASTERN GULF OF MEXICO

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ABSTRACT

Atlantic angel sharks *Squatina dumeril* (Lesueur, 1818) were collected for stomach content analysis from a trawl fishery in northeastern Florida in the winter (n = 50) and spring (n = 59) of 2005. The trawl catch was also sampled to describe the potential prey items in the environment in relation to stomach contents of angel sharks. Angel sharks consumed teleost fishes most often (62% and 75% numerical abundance), with squid (24% and 12% numerical abundance) and crustaceans (13% and 14% numerical abundance) also important in their diet in the winter and spring, respectively. On both occasions, the samples from the trawl catch showed that jacks (Carangidae, mostly *Trachurus lathami* Nichols, 1920) were the most frequently caught group of fishes, followed by porgies (Sparidae, mostly *Stenotomus caprinus* Jordan and Gilbert, 1882), with goatfishes (Mullidae) and butterfishes (Stromateidae) also commonly caught. Angel sharks collected in the winter and spring both showed prey selection for squids, while those collected in the spring also showed selection for scorpionfishes (Scorpaenidae), hakes (Phycidae), and croakers (Sciaenidae). The sizes of prey items from stomach contents were skewed toward smaller fish than those in the trawl catch, however, sizes of prey items were not significantly different from those in the trawl. This study provides the first quantification of diet for the Atlantic angel shark.

Prey selection by top predators, such as marine mammals and sharks, is hypothesized to be a key factor in shaping community structure of marine ecosystems, and the removal of top predators may have cascading effects on other species (Yodiz, 1994). Conversely, the removal of key prey species from an environment also may affect the predators that rely upon them (Hambright, 1994). Dietary selection of predators is dependent on factors such as morphology, prey behavior, and habitat, and can be indicative of how a predator might respond to changes in its prey base.

Though a relatively simple concept, prey selection can be difficult to measure due to the obstacles of measuring prey abundance, especially in marine environments. These difficulties stem mostly from inadequate sampling methods. Highly mobile predators may have a diverse and widely dispersed prey base, and a single sampling method is rarely sufficient to describe prey abundance (Bethea et al., 2004) and to collect the predator for diet analysis.

Angel sharks are a marine, benthic, deep-water elasmobranch occurring in waters of the Atlantic and Pacific Oceans (Compagno, 1984). Due to heavy trawling activities, angel sharks (specifically *Squatina squatina* Linnaeus, 1758) are globally assessed as “critically endangered”, are considered extinct in the North Sea, and are considered extirpated from areas of the Mediterranean Sea (IUCN, 2006). The smoothback *Squatina oculata* (Bonaparte, 1840) and sawback *Squatina aculeata* (Cuvier, 1829) angel sharks are also listed as “critically endangered” in the Mediterranean and “endangered” globally (IUCN, 2006). In the United States, a commercial fishery for the Pacific angel shark *Squatina californica* (Ayres, 1859) was established in California in the late 1970s, and the Pacific angel shark was the most common shark species caught for food in California for the years 1985–1986 (CDFG, 2001). Atlantic angel sharks, *Squatina dumeril* (Lesueur, 1818), are currently only caught as bycatch in trawl fisheries in the Gulf of Mexico but are listed as prohibited (no commercial landings allowed) because of a lack of available information and the precautionary approach to fisheries management (NMFS, 1993). Quantitatively describing the diet and foraging ecology 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 biological and ecological information be gathered to aid in the assessing and monitoring of elasmobranch populations and their prey. Our objectives in this study were to describe and quantify the diet and prey selectivity for Atlantic angel sharks in the northeastern Gulf of Mexico.

Methods

Angel Shark and Prey Collections.—Atlantic angel sharks were caught as bycatch in the Gulf of Mexico butterfish *Peprilus burti* (Fowler, 1944) bottom trawl fishery in winter (11 February) and spring (29 April) of 2005. Trawl vessels targeting butterfish only actively trawl in the daylight hours along the 200 m contour in the northeastern Gulf of Mexico, between Pensacola and Port St. Joe, Florida. In contrast to many other trawl fisheries in which bycatch is discarded at sea, the entire catch in the butterfish trawl fishery is retained and frozen onboard the vessels. For this study, butterfish trawl boats unloaded their frozen catch at local fish houses, where the catch was then moved to a large, water-filled hold and then to a conveyor belt. Workers manually sorted the catch by removing commercially important species such as butterfish, rough scad *Trachurus lathami* Nichols, 1920, and longfin squid *Loligo pealeii* (Lesueur, 1821). Species that were not removed during the sorting process were packaged into 25 kg boxes, hence called "bycatch." We sampled angel sharks by removing them from the conveyor belt as the catch was processed, then transferred them to coolers and transported them back to the laboratory for later processing.

The bycatch portion of the trawl catch was sampled using a stratified random design to collect potential prey for estimates of relative abundance and sizes. One box of bycatch per hour was randomly selected during the sorting process, kept on ice during transport, and then frozen. Subsampling continued for the duration of the offloading process (3–5 hrs) because Atlantic angel sharks were observed to be distributed throughout the entire catch. Packaged boxes of sorted butterfish, "goggle-eye jacks" (rough scad), and squid were purchased and then frozen until processed at the laboratory. Virtually all butterfish captured in the trawl were sorted out of the catch for individual sale, as were large goggle eye jacks and squid. The smaller goggle eye jacks and squid, however, were left in the catch and processed, packaged, and quantified as bycatch along with the other bycatch species.

A subset of other commercially important fish was measured and weighed at the fish house. All animals were identified using several keys, specifically for fish (Robins and Carleton, 1986; McEachran and Fechhelm, 1998, 2005), for squid (FAO, 2002), and for crustaceans (Williams, 1984). In addition, preserved fish and otolith reference collections were assembled from identified fish. Crustaceans were rare in the trawl catches and therefore no reference collection was assembled.

To determine the sizes of potential fish prey, individuals were measured for morphological features, including total length (TL), fork length (FL), standard length (SL), length of the vertebral column (from the base of the skull to the beginning of the caudal fin rays) (VC), body depth (BD) (nearest mm), and total weight (g). Sagittal otoliths were removed from all fish sampled, rinsed and allowed to dry, weighed, and then measured for total length and height with the use of a digital imaging system (Motic®). Squid were weighed and measured for TL, mantle length (ML), pen length (PL), upper and lower beak length (UL and BL), and upper and lower beak height (UH and BH). Lengths and weights of the whole fish or squid were then regressed as a function of each of these morphological features to estimate the whole size of fish or squid prey from partial remains in angel shark stomach contents as appropriate (Murie, 1995; Scharf et al., 1998; Bethea et al., 2004). Morphometric regressions were not developed for crustaceans because they were rare in the trawl catches.

Catch Quantification and Prey Abundance.—Trip tickets, which give the total weight of each species (e.g., butterfish or goggle eyes) or group of species (e.g., bycatch) landed were used to calculate the total number of boxes of each species that were packaged from all trips. The number of each species was averaged for randomly selected boxes of "bycatch", and the average number of each species per box was multiplied by the total number of boxes of bycatch processed at the fish house. The numbers of commercially important species were calculated in the same manner based on randomly selected boxes of butterfish, squid, and goggle eyes, and these averages were added to the bycatch estimate to give the total number of each species in the entire catch. Change in the catch composition between sampling trips was measured with Morisita's (1959) index of similarity (C_λ) (Krebs, 1999a,b). Morisita's index uses count data rather than proportions and ranges from zero (no overlap or similarity) to slightly greater than one (high overlap). Because the number of species encountered was very high (> 60 species), the catch was summarized by family.

Diet Analysis.—For angel shark diet analysis, stomach contents were identified to the lowest possible taxonomic level using the reference keys and collection, then assigned a reference number, wet blotted, weighed, and lengths were taken when possible. When prey items were not intact, partial prey measurements, such as standard (SL) and vertebral column (VC) lengths were taken. Liquid and mucus from the stomachs were placed in a 500 mL beaker, and a small flow of water was used to create a "gravity sieve" in which hard or dense parts, such as otoliths, remained on the bottom of the beaker while lighter material flowed out of the beaker (Murie and Lavigne, 1985). Intact otoliths removed from the digesta were used to identify the prey species, were rinsed and dried, and were later measured for otolith length, height, and weight. Whole squid were measured for mantle length (ML) and weighed with beaks intact, otherwise squid beaks found separately from other squid remains were weighed, measured for upper beak height (UH) and length (UL), and bottom beak height (BH) and length (BL), and were stored dry. Morphometrics of the various prey were then used to back-calculate both the length and weight of the prey when initially ingested (Murie, 1995). Because morphometric regressions were not developed for crustaceans, back-calculated weights of identifiable crustaceans were estimated from comparably-sized whole prey items found in other angel shark stomachs when possible (I. Baremore, NOAA Fisheries, unpubl. data).

Digestion codes were assigned to prey items on a scale from zero to nine, with zero representing nearly whole items with little to no discernable degradation (0–10%), and increasing incrementally to nine (> 90%, or nearly completely digested and mostly unidentifiable) (Cortés and Gruber, 1990; Berens, 2005). Prey items assigned a digestion code of nine were not included in the diet analysis because they were most likely left over in the stomach from a previous feeding event (Jobling and Breiby, 1986). Additionally, prey items coded zero were excluded from diet analyses to reduce bias from possible feeding events while within the trawl (Bethea et al., 2004). To minimize the possibility of bias due to retention of squid beaks in the stomachs, only squid remains with flesh or beaks with no signs of digestion were included in the diet analysis.

Cumulative prey curves were generated to assess the adequacy of the sample size (Ferry and Cailliet, 1996). To generate these curves, a computer program (A. Dutton, unpubl.) was utilized to randomize the order in which stomachs were examined 10 times and to count the number of new prey items in each stomach per randomization. The total number of stomachs was plotted versus the average number of new prey items found in each stomach and the diet was considered to be well described, and an adequate number of stomachs analyzed, when the curve reached an asymptote (Ferry and Cailliet, 1996).

Indices of diet composition determined were percent by occurrence (%O), percent by number (%N), percent by weight (%W) (Hyslop, 1980), and percent by back-calculated weight

(%WBC) (Murie, 1995). Occurrence is the total number of stomachs containing that prey item divided by the total number of stomachs containing food, %N is the number of one prey type in all the stomachs divided by the total number of prey items in all stomachs, and %W is the pooled weight of one prey type in all the stomachs divided by the total weight of all prey types in all stomachs. Since %W was calculated using digested stomach contents, which may be biased by differential digestion rates of prey and time of collection, %WBC was also calculated as the pooled back-calculated weight of one prey type in all stomachs divided by the total back-calculated weight of all prey items (Murie, 1995). These indices were used to calculate the index of relative importance (IRI), which is the sum of %N and %W, multiplied by %O (Pinkas et al., 1971). The IRI was calculated using both the digested weights of prey items in stomachs (IRI) and also with back-calculated whole weights of prey (IRIBC) for comparison. The IRI for each prey type was divided by the total IRI of all prey types in order to get the IRI in percent form (%IRI, %IRIBC), which limits the biases of the individual components of diet analysis and facilitates comparisons among other diet studies (Cortés, 1997). The IRI for each prey category (e.g., teleosts) was calculated with the overall %O, therefore the values are not equal to the sum of the %IRI values for each prey type because %O is not an additive index. If prey items could not be identified by species, then indices were calculated by the taxonomic level to which they were identified.

Niche Breadth and Overlap.—All measures of niche breadth and overlap of the diet of angel sharks were calculated with %N because %W and %IRI could not be calculated for all prey items, and %O does not account for multiple prey items of the same type in individual stomachs. Prey items were summarized by family to simplify comparisons, and crustaceans and unidentified teleosts were excluded from these analyses.

Niche breadth between two sampling time periods was calculated with Levin's standardized index (B_A) (Krebs, 1999b). The standardized index is expressed on a scale from zero (minimum niche breadth) to one (maximum niche breadth), which facilitates comparisons among species (Krebs, 1999a). Diet overlap of angel sharks collected was calculated with Morisita's index of similarity (Morisita, 1959) because it gives almost no bias according to sample size and number of resources (Smith and Zaret, 1982). Variation for these parameters (i.e., B_A and Morisita's index of similarity) was estimated through bootstrapping. The original diet sample prey distributions from each sampling trip were resampled with replacement based on the frequency of prey categories for each sampling trip. The original sample was repeated 10,000 times using Monte Carlo simulation and each unique prey category was bootstrapped within the sample 200 times with replacement. All simulations were run in Microsoft Excel equipped with risk analysis and matrix algebra software and Microsoft Visual Basic for Applications (Crystal Ball; Decisioneering Inc.).

Dietary Selection.—Two selection indices were employed to describe prey selection of the Atlantic angel shark. Manly's α (α_i) (Krebs, 1999a,b) was used to assess selection because it offers a simple measure of selection by comparing the probabilities of encounter and capture:

$$\alpha_i = r_i / n_i * \left(1 / \sum (r_j / n_j)\right)$$

where r_i or r_j is the proportion of prey type i or j in the diet, and n_i or n_j is the proportion of prey type i or j in the environment. The α values are normalized so that all α values sum to 1, and selective feeding occurs when α_i is greater than m, where m = 1/(total number of prey types). For those values that were greater than the selection threshold (m), a one sample Student's t-test was used to compare those α_i values to the value representing random selection. Variation for the α_i values were estimated through bootstrapping similar to that completed for the estimates of niche breadth and Morisita's index.

The rank preference index (t_i) (Johnson, 1980) was also calculated:

$$t_i = r_i - s_i$$

where r_i is the rank of usage of resource type i, and s_i is the rank of availability of resource type i. This index ranks both the utilization and availability of resources, and it is not generally affected by the addition or omission of rare food items in the diet (Johnson, 1980).

Prey Size Selection.—Prey size selection by angel sharks, or the sizes of prey items consumed versus the sizes of prey items in the environment, was investigated using a Mann-Whitney U-test to test for differences between means, and with a Kolmogorov-Smirnov D statistic to test for skewness in size frequency distributions between prey items in stomachs compared to potential prey items collected in trawls. Because the trawl contained animals that were too large to be consumed by angel sharks and because there was no evidence of angel sharks consuming parts of larger prey items, the comparison was restricted to trawl-caught fish < 250 mm TL. This size limit was established based on the largest prey items found in angel shark stomachs of similar sizes (Baremore, 2007). Regression equations developed from the sampled catch were used to back-calculate TL and body depth for prey items that were not recovered whole. Squid were not used in size selection analyses due to their soft bodies, and crustaceans were also excluded because few were found whole in stomachs. For prey items that were not prevalent enough to calculate regressions, weights were back-calculated using a species of similar size and shape or were estimated from another individual of the same species and similar size.

Results

Angel Shark Collections and Sampling of Potential Prey.—A total of 50 and 59 angel sharks were caught in the winter and spring of 2005, respectively, in butterfish trawls and all were retained for stomach content analysis. Atlantic angel sharks in the trawls ranged in size from 190 to 970 mm TL (Fig. 1). In the winter, five out of a total of 716 boxes of bycatch were sampled (0.7% of total bycatch caught by weight). Three boxes of bycatch (0.8% of total bycatch caught), 11 kg of butterfish (0.8% of total butterfish caught), 11 kg of rough scad (0.3% of total rough scad caught), and 5 kg of squid (3.4% of total squid) were collected in the spring sampling. Regressions relating lengths and weights of whole prey fish and squid to dimensions measurable in partial prey remains were significant and most were adequately predictive with $r^2 > 0.80$ (Table 1). Regression equations were only provided for species found in angel shark stomachs; a more comprehensive list of morphometric relationships for species caught in the trawl can be found in Baremore (2007).

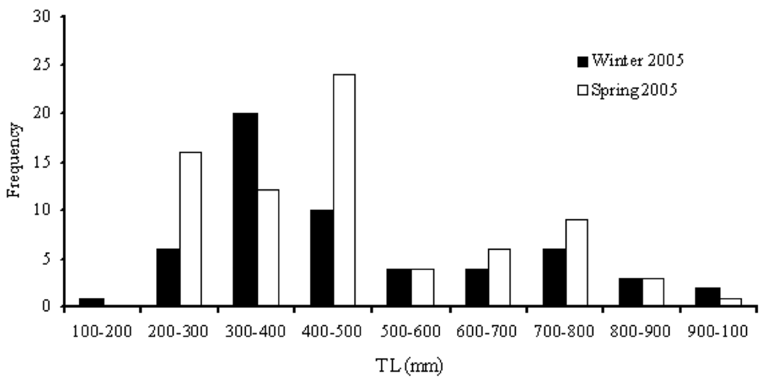

Figure 1. Size frequency of Atlantic angel sharks collected in winter and spring of 2005.

Table 1. Regression equations used to back-calculate lengths and weights of partially digested prey items. W = weight (g), SL = standard length (mm), VC = length of vertebral column (mm), TL = total length (mm), BD = body depth (mm), and UL = length of upper squid beak (mm). Ranges of x values are listed from minimum to maximum. All regressions were significant at $P \leq 0.05$.

Prey species	Regression equation	r^2	n	Min (x)	Max (x)
Atlantic croaker	$W = 0.03SL^{3.09}$	0.96	64	121	210
Micropogonias undulatus	$W = -134.80 + 1.92VC$	0.93	33	86	167
	$W = 1 \times 10^{-06}TL^{3.41}$	0.97	64	155	255
	$TL = 55.967 + 1.22VC$	0.91	33	86	167
	$TL = 1.14SL + 15.58$	0.99	64	121	210
Dwarf goatfish	$W = 0.03SL^{3.18}$	0.97	55	80	160
Upeneus parvus	$W = 0.04VC^{3.05}$	0.91	36	58	115
	$W = 2 \times 10^{-06}TL^{3.36}$	0.98	55	101	200
	$TL = 1.28SL - 1.62$	0.99	55	80	160
	$TL = 1.67VC + 3.55$	0.96	36	58	115
	$BD = 0.21TL - 3.98$	0.89	54	101	200
Longfin squid	$W = 3.399UL^{1.625}$	0.88	22	190	415
Loligo pealeii					
Longspine porgy	$W = -114.32 + 1.53SL$	0.97	77	86	173
Stenotomus caprinus	$W = 0.05VC^{2.93}$	0.93	57	61	120
	$W = 7 \times 10^{-05}TL^{2.72}$	0.97	57	104	225
	$TL = 1.29SL + 1.90$	0.98	77	86	173
	$TL = 1.87VC - 1.18$	0.91	57	61	120
	$BD = 0.37TL + 5.09$	0.93	77	104	225
Red goatfish	$W = 0.03SL^{2.97}$	0.87	60	116	170
Mullus auratus	$W = 0.04VC^{3.05}$	0.90	30	91	125
	$W = 1 \times 10^{-05}TL^{2.93}$	0.87	60	154	215
	$TL = 1.21SL + 11.83$	0.98	60	116	170
	$TL = 1.55VC + 18.1$	0.87	30	91	125
Rough scad	$W = 1 \times 10^{-05}SL^{3.09}$	0.99	76	52	194
Trachurus lathami	$W = 3 \times 10^{-05}VC^{3.07}$	0.97	69	36	131
	$W = 8 \times 10^{-06}TL^{3.01}$	0.99	76	64	237
	$TL = 1.11SL^{1.02}$	0.99	76	52	194
	$TL = 1.60VC^{1.02}$	0.98	69	36	131
	$BD = 0.20TL - 0.60$	0.94	76	64	237
Wenchman	$W = 0.03SL^{3.05}$	0.98	76	56	210
Pristipomoides aquilonaris	$W = 0.04VC^{3.11}$	0.97	64	38	145
	$W = 6 \times 10^{-06}TL^{3.12}$	0.99	76	76	282
	$TL = 1.33SL + 0.01$	0.99	76	56	210
	$TL = 1.89VC + 1.46$	0.98	64	38	145
	$BD = 0.28TL - 1.65$	0.97	76	76	282

Catch Quantification and Prey Abundance.—In total, 28,204 and 14,227 kg of fish were landed by the butterfish trawlers in the winter and spring, respectively. Of those landings, fishes in the family Carangidae (jacks) were the most abundant in the trawl catches on both dates, making up 31.1% and 27.7% of the total catch by number (Fig. 2). The vast majority of carangids in the catch were rough scad. Porgies (Sparidae) were the second most abundant family on both sampling dates, with the longspine porgy *Stenotomus caprinus* Jordan and Gilbert, 1882 as the dominant species. Other common families in the winter catch were Stromateidae (butterfishes),

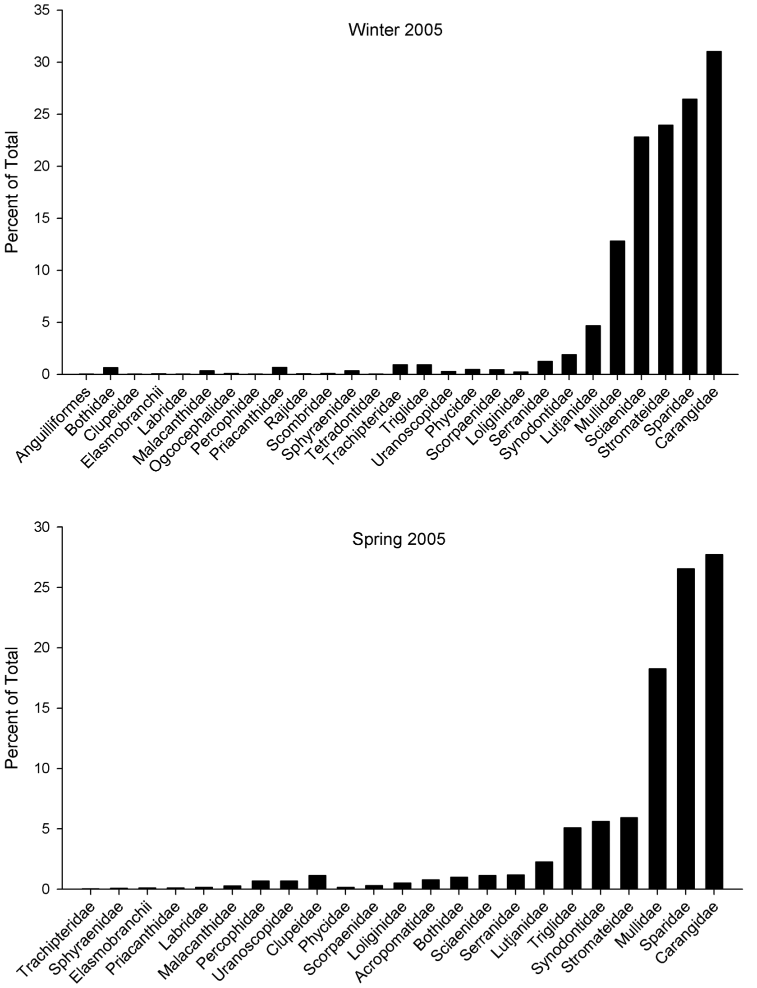

Figure 2. Composition of the trawl catches by numerical abundance in winter and spring of 2005, summarized by family.

Sciaenidae (croakers), and Mullidae (goatfishes), in descending order of abundance. The third most common family from the spring catch was Mullidae, followed by Stromateidae, and Synodontidae (lizardfishes). Morisita's index of similarity was high between sampling trips, with a value of 0.87.

Diet Analysis.—Of the 50 angel shark stomachs collected in the winter, six (12%) were completely empty, while 25 (50%) contained prey items that were assigned a digestion code other than zero or nine and were therefore used in diet analyses. Of the 59 angel sharks collected in the spring, none had empty stomachs and 32 stomachs (54%) contained prey items that were not coded zero or nine. Cumulative prey curves showed that the diets were relatively well described for angel sharks (Fig. 3). Diets of angel sharks were similar between seasons (i.e., winter and spring), with teleosts being the most often encountered prey by occurrence (64% and 84%) and numerical abundance (62% and 75%) for winter and spring, respectively (Table 2). Teleosts were also important on a weight basis in the diet of angel sharks, with red goatfish, dwarf

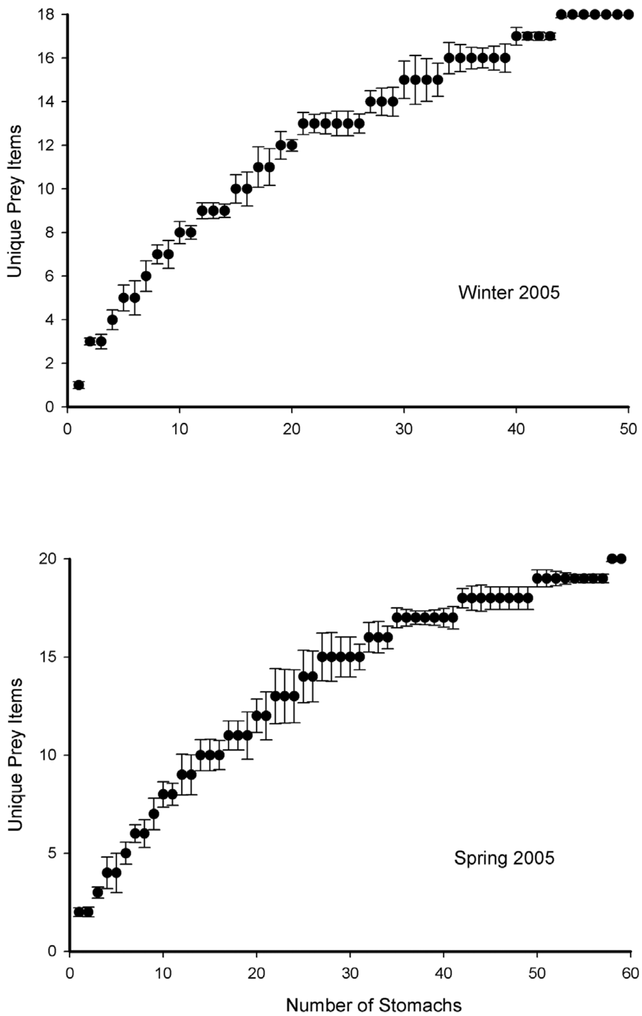

Figure 3. Cumulative prey curves for stomach contents of all angel sharks collected in winter and spring of 2005. Asymptotes in the curves indicate that the diets were relatively well described for each sampling trip. Error bars represent standard error.

goatfish, and Atlantic croaker all being > 10% of the diet based on both %W and %WBC. Squid occurred most commonly of any single species, with 24% and 16% occurrence for winter and spring trips, respectively, followed by Atlantic croaker (16% and 12% occurrence), and red goatfish *Mullus auratus* Jordan and Gilbert, 1882 (8% and 12% occurrence) (Table 2). Squid were also important based on back-calculated weight, especially in the winter where it represented 26% of the diet by %WBC and to a lesser extent in the spring (6% WBC). This differed substantially from the importance of squid based on weights recovered directly from digested food items in the stomachs of angel sharks where squid represented < 1% by weight (Table 2). Crustaceans were found in 16% and 25% of angel shark stomachs in winter and spring, respectively. Although they represented 13% and 14% numerical abundance of stomach content items, they were < 5% by both digested and estimated whole weight. With

Table 2. Occurrence (%O), numerical abundance (%N), weight (%W), back-calculated weight (%WBC), Index of Relative Importance (%IRI), and IRI calculated with %WBC (%IRIBC) for prey sampled from stomach contents of angel sharks collected in the northeastern Gulf of Mexico in the winter and spring of 2005. Values in bold represent the indices calculated for overall prey categories.

	Winter 2005						Spring 2005					
Prey identification	%O	%N	%W	%WBC	%IRI	%IRI BC	%O	%N	%W	%WBC	%IRI	%IRI BC
Teleosts	**64.0**	**62.2**	**95.9**	**69.0**	**92.1**	**84.8**	**84.4**	**74.6**	**97.4**	**91.6**	**96.2**	**95.4**
F. Acropmatidae: *Synagrops bellus*							3.1	1.7	1.1	0.7	0.3	0.5
F. Bothidae							3.1	1.7	1.0	6.4	0.3	1.7
F. Carangidae: *Trachurus lathami*							3.1	1.7	9.1	6.2	1.0	1.7
F. Lutjanidae: *Pristipomoides aquilonaris*	4.0	2.2	0.4	5.4	0.5	1.2						
F. Mullidae												
Mullus auratus	8.0	6.7	20.1	12.7	9.0	6.2	12.5	6.8	25.0	24.3	11.7	26.8
Upeneus parvus							6.3	5.1	20.0	13.6	4.6	8.0
F. Ophidiidae	8.0	6.7	10.2	7.2	5.7	4.4						
F. Phycidae	4.0	2.2	1.5	1.0	0.6	0.5	3.1	1.7	0.3	0.2	0.2	0.4
F. Sciaenidae												
Micropogonias undulatus	16.0	8.9	27.0	23.3	24.2	20.7	12.5	6.8	11.5	20.9	6.7	23.8
Leiostomus xanthurus	4.0	2.2	8.8	5.7	1.9	1.3						
F. Scorpaenidae: *Scorpaena agassizi*	4.0	2.2	6.1	3.0	1.4	0.8						
Scorpionfish							6.3	3.4	4.1	2.8	1.4	2.7
F. Serranidae	8.0	4.4	5.9	2.9	3.5	2.4	6.3	3.4	0.9	4.4	0.8	3.3
F. Sparidae: *Stenotomus caprinus*	8.0	4.4	2.2	2.7	2.2	2.3	6.3	3.4	13.8	9.4	3.2	5.5
F. Synodontidae: *Saurida normani*	4.0	2.2	10.2	5.1	2.1	1.2						
Lizardfish	4.0	2.2	0.2	0.1	0.4	0.4	3.1	1.7	1.3	0.9	0.3	0.6
F. Triglidae: *Prionotus stearnsi*							3.1	1.7	2.9	2.0	0.4	0.8
Unidentified teleosts	16.0	17.8	3.2		14.1		46.9	35.6	6.4		57.8	
Cephalopoda	**24.0**	**24.4**	**0.6**	**26.9**	**5.4**	**12.4**	**15.6**	**11.9**	**0.9**	**6.1**	**1.3**	**1.9**
Loligo sp.	24.0	24.4	0.6	26.9	25.3	49.4	15.6	11.9	0.9	6.1	5.8	19.4
Crustacea	**16.0**	**13.3**	**3.5**	**4.1**	**2.5**	**2.8**	**25.0**	**13.6**	**1.7**	**2.3**	**2.5**	**2.7**
Shrimp	8.0	4.4	1.8	1.6	2.1	1.9	9.4	5.1	1.5	2.3	1.8	4.8
Lysosquilla sp.	16.0	8.9	1.7	2.5	7.1	7.3						
Unidentified crustaceans							15.6	8.5	0.2		4.0	
					10,988.4	**9,908.9**					**15,092.5**	**14,697.6**
Total n	25.0	45.0	777.6	1,569.3	2,378.1	2,493.8	32.0	59.0	743.9	1,059.3	3,410.5	1,450.4

Table 3. Selection values for families of fishes recovered in Atlantic angel shark stomachs. RPI is the rank preference index. In winter, Manly's α values > 0.111 indicate positive selection. In spring, Manly's α values > 0.083 indicate positive selection. Values equal to the selection values indicate neutral (no) preference, and those below suggest negative selection, or avoidance. All positive selection values are indicated in italics, and values significantly different from random selection are marked with an asterisk. The smallest (most negative) values for RPI are indicative of the most preferred prey items, with preference decreasing as the values increase.

	Winter 2005				Spring 2005			
Prey family	Manly's α	Manly's α bootstrapped	St Dev	RPI	Manly's α	Manly's α bootstrapped	St Dev	RPI
Acropomatidae					0.037	0.025	0.015	0.5
Bothidae					0.029	0.021	0.007	1.5
Carangidae					0.001	0.001	0.000	8.5
Loliginidae	*0.857**	*0.765*	0.090	−8	*0.390**	*0.501*	0.082	−8.5
Lutjanidae	0.004	0.009	0.004	4				
Mullidae	0.004	0.011	0.006	0	0.011	0.013	0.013	−1.5
Phycidae	0.039	0.055	0.028	1	*0.174**	*0.146*	0.144	−2.5
Sciaenidae	0.004	0.010	0.006	0	*0.104*	*0.098*	0.023	−4
Scorpaenidae	0.041	0.037	0.024	0	*0.191**	*0.132*	0.043	−6
Serranidae	0.030	0.052	0.033	−1	0.049	0.050	0.015	−1
Sparidae	0.001	0.003	0.002	4	0.002	0.002	0.000	3
Synodontidae	0.020	0.059	0.033	0	0.005	0.005	0.002	5.5
Triglidae					0.006	0.007	0.002	4.5

respect to %IRIBC, squid were the most important prey item in angel shark stomachs collected in winter (49%), followed by Atlantic croaker (20%), and red goatfish (6%). In spring, red goatfish were the most important prey item by %IRIBC (27%), followed by Atlantic croaker (24%), and squid (19%). Digestion codes showed that many angel shark stomachs contained several prey items in differing states of digestion. The vast majority of stomach contents assigned a digestion code of nine were fish eye lenses, degraded squid beaks, and degraded otoliths.

Niche Breadth, Overlap, and Dietary Selection.—The values of Levin's standardized index of niche breadth differed for stomach contents of angel sharks between winter and spring (0.45 and 0.58, respectively) whereas diet overlap of angel sharks between seasons was high, with a Morisita's index of similarity of 0.85. However, standard deviations from the bootstrapped diet data were low, ranging from 0.05 and 0.04 for estimates of B_A from winter and spring samples, respectively. The standard deviation from the bootstrapped diet data used to calculate Morisita's index was also low (0.04). Angel sharks collected from both seasons showed selection for squid, while those collected in spring also showed selection for hakes (Phycidae), croakers (Sciaenidae), and scorpionfishes (Scorpaenidae) (Table 3, Fig. 4) based on the values of Manly's α and the rank preference test. Analysis of one way Student's t-tests comparing α_i values to the value for random prey selection showed significant differences for squid in both samples ($P < 0.001$), as well as for hakes and scorpionfishes in the spring ($P < 0.001$). Angel sharks collected in winter showed secondary selection for seabasses (Serranidae) and showed the least selection for snappers (Lutjanidae) and porgies. In order of decreasing rank, angel sharks collected in spring preferred scorpionfishes, croakers, hakes, and goatfishes, and showed the least prey selection for jacks (Carangidae). Due to the absence of crustaceans and cusk eels (Ophidiidae) in the trawl catch, they were excluded from selection analyses. Unidentified fish

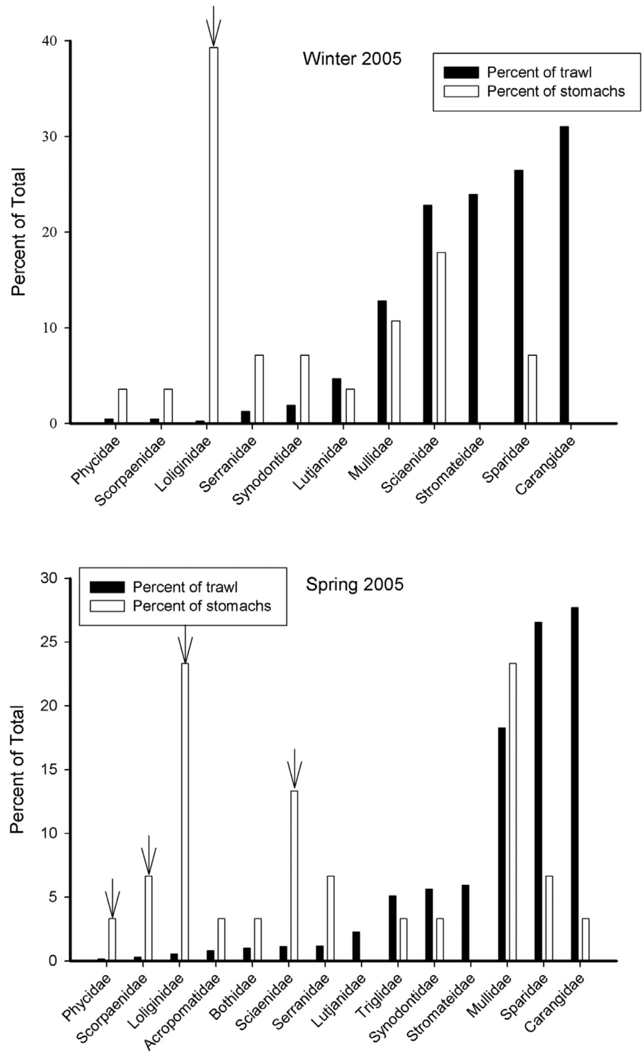

Figure 4. Percent numerical abundance of total catch by family from the trawls and in the stomach contents of Atlantic angel sharks from the northeastern Gulf of Mexico. Arrows indicate positive selection by the Atlantic angel shark, according to the standardized selection index.

remains were in high abundance (16 and 47 %O), therefore it is possible that the refinement of the unidentified remains would affect the selectivity analyses. Little difference occurred for Manly's index when estimated using a point-based analysis (i.e. no variability) and those estimated through bootstrapping of the trawl samples for prey (Table 3). In addition, standard deviations were low for most prey categories, ranging from a high of 0.09 to a low of 0.002.

Prey Size Selection.—Prey items in angel shark stomachs were within the size range of the trawl-caught prey fish (Fig. 5). Sizes of trawl-caught fish ranged from 50–750 mm TL with a median of 400 mm, while those in stomachs ranged from 70 to 200 mm TL with a median of 135 mm. When the sizes of trawl-caught fish were constrained to realistically edible sizes (< 250 mm based on the maximum sizes

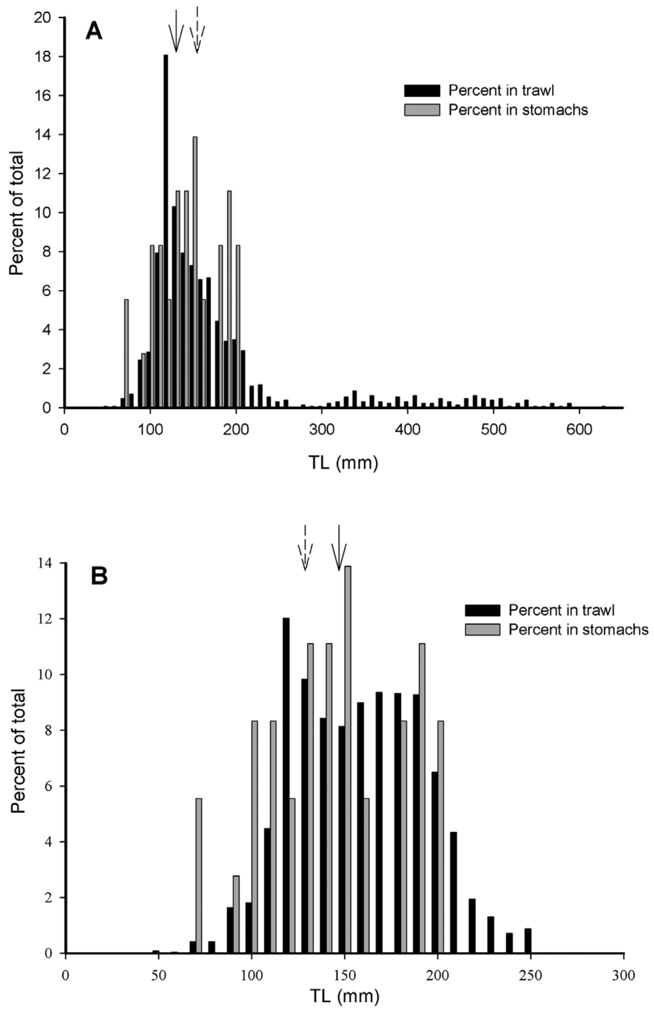

Figure 5. Length frequency of fishes caught in trawls for combined trips: (A) for all fishes recovered in the trawl, along with the sizes of those recovered in stomach contents of Atlantic angel sharks in the northeastern Gulf of Mexico; and (B) for fishes < 250 mm TL. The solid arrows indicate the median length of trawl-caught fishes (150 mm), and the dashed arrows are the median length of fish from stomach contents (135 mm).

of prey consumed by angel sharks), however, the median was 150 mm and was not significantly different from the size of prey found in angel shark stomachs (Mann-Whitney $P = 0.135$). The size frequency distribution of fishes recovered in stomachs, however, was skewed towards smaller fish than those caught in the trawl (K-S test: $D = 0.43$, $P < 0.03$).

Discussion

Evidence from this study suggests Atlantic angel sharks are not exclusively opportunistic predators, but may be selecting certain prey items. Angel sharks consumed fishes that were in high abundance in the trawl, such as croakers and goatfishes, however, they also selected for fishes and cephalopods that were in relatively low abundance in the trawl such as hakes, scorpionfishes, and squid. This resulted in a moderately broad niche breadth of 0.51 on average for the winter and spring seasons. Diet overlap between the two samples based on numerical abundance was high, indicating that there was little change in diet between the two seasons.

Squid were consumed in high quantities despite their low abundance in trawls. Although squid are packaged and sold by the fish house, butterfish trawlers do not target squid. Squid are known to be diurnal migrators, aggregating at the bottom of the ocean during the day and moving to the surface to feed at night (NMFS, 1999). Squid are thus near the bottom at the same time as the gear is deployed to catch butterfish (i.e., trawling on the bottom during daylight hours); therefore, the underrepresentation of squid in the trawl catches could have been due to gear bias. The selectivity of trawl gear is unknown, however, it is likely to be less important as the trawl fills because the animals in the trawl act as a barrier for the escapement of even the smallest organisms, as evidenced by the collection of small (< 60 mm TL) fish in the trawl catches. Larger, faster swimming animals are likely able to escape the trawl, though teleost fishes up to 600 mm TL were landed. Additionally, gear selectivity probably acted differently on teleosts than soft-bodied squid, likely excluding the smallest sizes of squid in the environment. Even if squid abundance was misrepresented by the trawl catch and therefore biased the estimates of selection, the fact remains that squid were the most prevalent single prey item in Atlantic angel shark stomachs overall. Although the number of squid could be counted in stomach contents by recovery of their beaks, %W underrepresented the actual weight of squid ingested due to their soft bodies and increased digestive state relative to fish prey in the stomachs. When the weight of squid was back-calculated to reflect the original weight when ingested (%WBC), then the importance of squid in the angel shark diet based on weight also became more evident, increasing from 25% IRI to 49% IRIBC in the winter and from 6% IRI to 19% IRI in the spring. Back-calculating size and weight of squid also allowed an estimation of the size of squid consumed by Atlantic angel sharks, which ranged widely from 0.6 to 140.1 g total weight. Squid are probably easily captured as prey by angel sharks because they require little handling time due to their lack of hard parts (Smale, 1996). This may increase their value as prey items despite their relatively low energy content (Baird, 1991; Rosen and Trites, 2000) compared to some teleosts.

Carangids were the most prevalent potential prey item sampled by the trawl, though they were very rarely encountered in the stomachs of Atlantic angel sharks. Rough scad, which comprised the majority of the carangids in the trawl, are small schooling pelagic fishes that are found on the continental shelf and are known to be bottom-associated (Katsuragawa and Ekau, 2003). Jacks are fast swimming, wide-ranging fishes and are likely more difficult for an ambush predator to capture, despite their apparent abundance (Katsuragawa and Ekau, 2003). The presence of known nocturnal species such as cusk eels in the stomachs, as well as the prevalence of prey items with digestion codes of both zero and nine implies that angel sharks may have been feeding during both day and night hours. Additionally, the high number of stomachs that were either empty or only contained food items coded zero or nine (62% and 54% of stomachs collected in winter and spring, respectively) suggests that Atlantic angel sharks may not feed every day.

Crustaceans and cusk eels were each represented by up to 9% IRIBC in the diet of Atlantic angel sharks, but were completely absent in the trawl-catch, which was likely due to the day-time fishing protocol and/or the presence of rollers on the trawl that keep the net slightly off of the bottom of the ocean. Cusk eels and other burrowing species are not easily caught by trawls, but are known to occur on the continental shelf (Darnell, 1990; Retzer, 1991). A feasibility study for the butterfish fishery conducted in 1986 reported few crustaceans, with rosy shrimp *Parapenaeus* sp. as the only reported crustacean bycatch, and with no cusk eels observed (Vecchione, 1987). Even though difficulties were encountered with quantification of crustaceans and cusk eels in the trawl, the catch was similar to other reports on benthic community structure in the Gulf of Mexico (GSMFC, 2002). Likewise, the sizes of prey items in angel shark stomachs were well within the range of sizes of fishes caught in the trawls, and therefore it is probable that fish prey abundance was accurately described and that selection indices of fish and squid were relatively unbiased. Due to confidentiality concerns, the gear specifications of the butterfish trawl could not be obtained, so future studies should attempt to address the caveats of selectivity and gear type on data of this type. In addition, the prevalence of unidentifiable teleosts in angel shark stomach contents was relatively high by both occurrence and number, but were only 3% and 6% of the total weight of all prey items. Unidentified fish remains were generally intact vertebral columns and attached flesh that had no distinguishable hard parts (e.g. otoliths), and were often found in stomachs that also contained other items in differing states of digestion. Recent advances in prey identification using DNA-based methods could be helpful in identifying specific prey species recovered in the stomach contents that are partially digested (Symondson, 2002; Parsons et al., 2005), clarifying the potential importance of unidentifiable teleosts and crustaceans.

The use of stomach contents as an indication of prey preference is somewhat biased by the capture success of the predator (Scharf et al., 1998). Capture success is influenced by numerous factors, including prey behavior and size; it is possible that Atlantic angel sharks prefer prey items, but have low capture success and therefore their true preference is not represented by stomach contents. There are no laboratory experiments testing the capture success of Atlantic angel sharks, and in situ experiments on the Pacific angel shark only reported attack frequencies on fish models and had no observations of angel sharks attacking natural prey (Fouts and Nelson, 1999). Whether Atlantic angel sharks "actively" or "passively" prefer certain prey items remains unclear, therefore further in situ or laboratory experiments are necessary to make these types of distinctions.

Sampling the prey base of marine predators is rare, and the difficulties associated with attaining these measurements may limit analyses. Prey abundance and selection estimates in this study were generated from single sampling events in two different seasons, therefore the bias and variability associated with those estimates could not be measured. By treating the two samples as the entire prey population, we were able to use bootstrap analysis to generate error and confidence limits around the selectivity indices of Atlantic angel sharks. This technique allowed us to adequately infer variation of these indices from two point estimates of prey abundance.

The Atlantic angel shark is a demersal predator that is reliant on benthic prey species, and changes in prey abundance could therefore have negative effects on the population. Vogler et al. (2003) found that angular angel sharks *Squatina argentina* (Marini, 1930) showed strong specialist traits for different prey items, with Argentine anchovy *Engraulis anchoita* (Marini, 1935) present in more than half of the stomachs of angel sharks < 440 mm TL. The moderate niche breadth values for Atlantic angel sharks indicated that while they are not highly specialized predators, they are also not entirely opportunistic. In addition, the selection of prey items that were in relatively low abundance in the trawl catches indicated a higher level of prey selection than might be assumed for a bottom-associated ambush predator. Atlantic angel sharks also consumed relatively small prey items relative to those available, indicating that they are selecting smaller prey items. The ability of predators to switch to different prey items when others become rare is vital to their survival, but some highly selective piscivores do not exhibit prey switching behavior, even at near starvation levels (Mathews et al., 1988). It is possible that Atlantic angel sharks may be vulnerable to changes in prey abundance and composition and may not be able to switch easily to other prey resources if their prey base is disrupted or becomes limiting. Although testing this hypothesis may be difficult through empirical methods, further studies on ecosystem responses of angel sharks to prey base reduction and changes could be explored through modeling efforts, such as using Ecopath/Ecosim (Christensen and Walters, 2004).

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