

FEEDING ECOLOGY OF THE ATLANTIC ANGEL SHARK IN THE NORTHEASTERN  
GULF OF MEXICO

By

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Abstract of Thesis Presented to the Graduate School  
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Atlantic angel sharks *Squatina dumeril* were collected for stomach contents (n=437) from November 2002 through February 2005 from a butterfish *Peprilus burti* bottom trawl fishery in the northeastern Gulf of Mexico. The trawl catch was sampled along with angel sharks on 11 February (n=50) and 29 April 2005 (n=59) to describe the potential prey items in the environment in relation to stomach contents of angel sharks. Teleost fishes, especially Atlantic croaker *Micropogonias undulatus*, butterfish, and goatfishes (Mullidae), dominated the diet of Atlantic angel sharks overall, and were the most important prey items of all shark size categories. Squid *Loligo* sp. were also important prey items for all shark sizes, though they became less important with increasing shark size, however squid were the most important prey item for angel sharks collected in the winter months. Crustaceans such as mantis shrimps *Lysosquilla* sp., brown rock shrimp *Sicyonia brevirostris*, and portunid crabs were also consumed by all sizes of angel sharks and during all seasons sampled. Ontogenetic and seasonal shifts in diet were detected; niche breadth narrowed with ontogeny, and the niche breadth of angel sharks was narrowest in the winter months and broadest in the fall. Atlantic angel sharks mostly consumed



prey that were less than 30% of their total length and prey with body depths less 60% of their gape width. The two samples of the catch of butterfish trawl boats showed that jacks (Carangidae, mostly *Trachurus lathami*) were the most abundantly caught group of fishes, followed by porgies (Sparidae, mostly *Stenopus caprinus*) for both dates, with goatfishes (Mullidae) and butterfishes (Stromateidae) also commonly caught. Angel sharks collected on the two sampling trips both consumed teleost fishes most often, with squid and crustaceans also important in their diets. Sharks collected on 11 February and 29 February both showed preference for squids, while those collected on 29 February also showed preference for croakers (Sciaenidae), scorpionfishes (Scorpaenidae), and hakes (Phycidae). The sizes of prey items from stomach contents were significantly smaller than those in the trawl catch, even when comparisons were restricted to sizes that were considered 'consumable' ( $p < 0.03$ ). Angel sharks showed a relatively high level of prey selection, indicating that while they are ambush predators, they are not entirely opportunistic feeders. As top level predators in the benthic community of the northern Gulf of Mexico, Atlantic angel sharks are both influenced by, and influential to, changes in species composition in their environment. This study provides an important first step towards building our knowledge of a species for which very limited biological data are available.

## CHAPTER 1 GENERAL INTRODUCTION

### **The Atlantic Angel Shark**

The Atlantic angel shark *Squatina dumeril* is a benthic, deep water species inhabiting waters of the Gulf of Mexico and U.S. Atlantic Ocean. Some life history and diet information exists for other members of the family Squatinidae (Ellis et al. 1996, Bridge et al. 1998, Fouts and Nelson 1999, Brickle et al. 2003, Vogler et al. 2003), most notably the Pacific angel shark *Squatina californica* (Bulman and Blaber 1986, Natanson and Cailliet 1986, 1990, Cailliet et al. 1992, Bridge et al. 1998), but very little published information is available for the Atlantic angel shark (Gordon 1956). Of the 11 known species of angel sharks in the world, the Atlantic angel shark is the only species known to inhabit the Gulf of Mexico (Compagno 1984).

Elasmobranchs are generally characterized by slow growth, late maturity, low fecundity, and long gestation periods (Carrier et al. 2004), making them susceptible to over-exploitation. Due to the lack of biological data and a precautionary approach to management, the Atlantic angel shark is listed as prohibited (no landings allowed) in the Gulf of Mexico and U.S. Atlantic Ocean by the Fisheries Management Plan for Sharks (NMFS 1993).

Trophic dynamics, including diet analysis, are an important aspect of the biology of fishes, particularly for those fishes thought to be vulnerable to exploitation. Fish with highly selective diets are likely to be susceptible to changes in food availability due to fishing mortality or other environmental variations (Trowbridge 1991). In addition, feeding by top predators is a significant factor that shapes fish community structures (Scharf et al. 1998); often a single or several top predators regulate the lower levels of the food web (Frank et al. 2005). Recent trends in fisheries management indicate a shift toward an ‘ecosystem-based approach’ (Brodziak and Link 2002, FAO 2003, Browman and Stergiou 2004), and as a result data on trophic interactions

are becoming critical to fisheries managers. As carnivores, Atlantic angel sharks may play an influential role in structuring communities in the Gulf of Mexico, but to date no diet information is available for this species.

Previous studies have found that squatinids are top level (Cortés 1999), ambush predators (Fouts and Nelson 1999), feed mostly on teleost fishes, cephalopods, and crustaceans (Ellis et al. 1996, Bridge et al. 1998, Vogler et al. 2003), reproduce by ovoviviparity (Compagno 1984), and may be nocturnal (Fouts and Nelson 1999). The only documented diet information for the Atlantic angel shark comes from an anecdotal account by Gordon (1956), who reported that one Atlantic angel shark captured in New England had remains of many fish in its stomach.

The overall goal of this study was to quantify the diet of Atlantic angel sharks in the northeastern Gulf of Mexico, and to assess prey selectivity and possible ontogenetic and seasonal shifts in diet. Potential prey selection by Atlantic angel sharks was evaluated using stomach content analysis of sharks caught in bottom trawls along with quantification of potential prey available in the same bottom trawls (Chapter 2). Ontogenetic and seasonal shifts in diet of angel sharks were assessed by quantifying the diet, niche breadth, and niche overlap of angel sharks of various sizes collected throughout the majority of the year (Chapter 3). In conclusion, speculation on how the diet, prey selectivity, and ontogenetic and seasonal shifts in the diet of angel sharks may affect their susceptibility to perturbations of their prey base forms the basis of Chapter 4.

## CHAPTER 2

### PREY SELECTION BY THE ATLANTIC ANGEL SHARK IN THE NORTHEASTERN GULF OF MEXICO

#### **Introduction**

Prey selection by top predators, such as marine mammals and sharks, is a key factor in shaping community structure of marine ecosystems, and the removal of top predators can have cascading effects on other species (Yodiz 1994, Juanes et al. 2001). Conversely, the removal of key prey species from an environment can have catastrophic effects on the predators that rely upon them (Hambricht 1994). Dietary preference 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. Preference, or the selection of specific food items from a variety of available food items, can be measured by comparing usage and availability. As stated by Chesson (1978), preference can be described as any change from a random sample of the prey items available. Though a relatively simple concept, preference can be difficult to measure due to the obstacles of measuring prey abundance, especially in marine environments. As a result, there are numerous studies that address prey selection in freshwater systems (Olsen et al. 2003, Carman et al. 2006), or in laboratory settings (Gill and Hart 1999, Gill 2003), but fewer examples exist for marine species in the field (Scharf et al. 2000, Bethea et al. 2004). The difficulties associated with measuring potential prey items in marine systems 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 (*Squatina* spp.) are benthic-associated ambush predators, and other than a hypothesized inshore-offshore migration on the in the US Atlantic Ocean (Compagno 1984),

little is known of their movement patterns or distribution, though evidence suggests they may have feeding site fidelity (Fouts and Nelson 1999). A bottom trawl has the unique potential to capture both the angel sharks and most of their potential prey items because they feed exclusively from the sea floor and are not highly mobile.

Estimates of prey size and number are important components of diet analysis, but partial prey remains (i.e., prey that cannot be measured whole or readily identified) are most often left out of diet analyses. Because of the importance of these measures, size regressions can be used to reconstruct whole lengths and weights of partial prey remains from such morphological characteristics as length of the vertebral column, body depth, and caudal-peduncle depth (Murie and Lavigne 1985, Scharf et al. 1998). Otoliths are species-specific in shape and size and are often distinct enough to identify prey items that are decomposed beyond recognition. In some cases the length and/or weight of the otoliths is sufficient to estimate the approximate size of the fish they belonged to (Murie and Lavigne 1985, Scharf et al. 1997, Bethea et al. 2004).

Although it has been suggested that otoliths may not be appropriate in diet studies due to changes in shape with fish size and the rapid degeneration by stomach acids, Jobling and Breiby (1986) nevertheless concluded that otoliths found in stomachs likely represent single feeding events, and that the identification and counting of otoliths provide accurate quantitative measures of consumption. The importance of these structures for fish identification and length reconstruction outweighs the disadvantages, even given possible sources of variation.

The role that an angel shark plays in its environment, or how ‘specialized’ it is, can be estimated using niche breadth, which is the quantitative measure of the amount and range of resources available to an organism (Krebs 1999a). Predators with narrow niche breadths, or specialists, may be more susceptible to changes in food availability than generalist predators.

Specialist predators also may not be able to shift to other prey resources if those resources become less abundant due to fishing or other sources of mortality.

The overall goal of this chapter was to evaluate the prey selection of the Atlantic angel shark *Squatina dumeril* feeding in the northeastern Gulf of Mexico. Specifically, the objectives were 1) to determine the diet of Atlantic angel sharks using stomach content analysis of sharks caught in bottom trawls 2) to describe the abundance and sizes of potential prey items of angel sharks based on quantification of bottom trawl landings where angel sharks were captured concomitantly and 3) to compare the types and sizes of prey items from stomach contents of angel sharks to the potential prey base in the trawl catch to assess their prey preferences.

## **Methods**

### **Angel Shark Collections**

Atlantic angel sharks were caught as bycatch in the Gulf butterfish *Peprilus burti* bottom trawl fishery in the northeastern Gulf of Mexico. Butterfish trawlers consistently fish along the 200 m contour of the continental shelf south of Port St. Joe, Florida, and travel as far as Alabama along the same depth contour seeking butterfish (E. Raffield, pers. comm.). Vessels fish for several days during daylight hours and deploy the trawl multiple times until the catch is considered to be adequate, though they rarely fish for more than five days. 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. Butterfish vessels unload the frozen catch at the fish house into a large, water-filled hold. From the hold, the fish are moved down a conveyor belt to the sorting room, where commercially important fish are removed for sale. The remainder of the catch is comprised of bycatch and packaged into 23 kg boxes. Atlantic angel sharks are frozen along with the trawl-caught fish on board, and are removed from the conveyor

belt during offloading. Because the Atlantic angel shark is a prohibited species, a special scientific exempted permit was issued to the butterfish trawl fishery to allow them to keep the angel sharks for our research purposes.

During the spring of 2005, butterfish trawl catches on 11 February and 29 April were sampled for Atlantic angel sharks, as well as their potential prey. All angel sharks collected were kept on ice and transported to the University of Florida Department of Fisheries and Aquatic Sciences (UF-FAS) where they were measured for precaudal length (length from the tip of the nose to the precaudal notch) (PCL), fork length (FL), and total length (TL) ( $\pm 1$  cm), weighed whole (kg), and then had their stomachs removed and frozen for later processing.

### **Sampling of Potential Prey**

As angel sharks were removed from the conveyor belt used in sorting the trawl catch, the bycatch portion of the 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 at UF-FAS. Subsampling continued for the duration of the offloading process (3–5 hours) because angel sharks were observed to be distributed throughout the entire catch. Packaged boxes of butterfish, ‘goggle-eye jacks’ (rough scad *Trachurus lathami*), and long-finned squid *Loligo paelei* were purchased, kept on ice during transport, and then frozen at UF-FAS until processed. A subset of any other commercially important fish were measured and weighed at the fish house.

To determine the potential prey composition in the trawl catches, boxes of bycatch were thawed at the UF-FAS facility, and all animals in each box were identified using several keys, specifically for fish Robins and Carleton (1986) and 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, species that were abundant (>20 per box) were subsampled; all subsampled fish were measured to 1 cm TL, and one fish from each cm-size group was measured in more detail for morphological features, including TL, 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. Boxes of butterfish and goggle eyes were subsampled in a similar fashion, except that complete morphological measurements were taken from ten individuals in each cm-size group. Morphological measurements were collected for all individuals for species that were less abundant. Sagittal otoliths were removed from all fish sampled for morphometrics, 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 provided by the fish house and were used to calculate the total number of boxes of each species that were packaged from each trip based on



the weight per box of fish. The average number of each species or group of species per box sampled was then multiplied by the total number of boxes to get the total number of each species in the catch. Change in the catch composition between the two sampling trips was measured with Morisita's (1959) index of similarity ( $C_\lambda$ ) (Krebs 1999a, b):

$$C_\lambda = \frac{2\sum X_{ij}X_{ik}}{(\lambda_j + \lambda_k)N_jN_k}$$

where  $X_{ij}$  and  $X_{ik}$  are the number of individuals of species  $i$  in sample  $j$  and sample  $k$ ;  $N_j = \sum X_{ij}$ , is the total number of individuals in sample  $j$ ;  $N_k = \sum X_{ik}$ , is the total number of individuals in sample  $k$ ;  $\lambda_j = [\sum X_{ij}(X_{ij}-1)]/[N_j(N_j-1)]$  and  $\lambda_k = [\sum X_{ik}(X_{ik}-1)]/[N_k(N_k-1)]$ . Morisita's index uses count data rather than proportions and ranges from zero (no overlap) to slightly greater than one (high overlap). Because the sheer number of species encountered was very high (>60 species), the catch was summarized by family.

### **Diet Analysis**

For angel shark diet analysis, stomachs were thawed, cut open, and rinsed over a collecting bowl. Contents were identified to the lowest possible taxonomic level using the reference collection described previously, 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 SL and VC 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 all fish remains to aid in identification were rinsed and dried, and then measured for otolith length, height, and weight. Whole squid were measured for ML and weighed with beaks intact,

otherwise squid beaks found separately from other squid remains were weighed, measured for UH, UL, BH, and BL, and were stored dry. All prey items were archived by shark number and prey reference number and frozen individually, or in the case of otoliths stored dry, for future reference. All partial prey and otolith measurements were used to back-calculate to the original size and wet weight of the prey item whenever possible using the morphometric regression equations developed from the sampled catch (Murie 1995).

Digestion codes were also assigned to prey items on a scale from 0 to 9, with 0 representing nearly whole items with little to no discernable degradation (0–10%), and increasing incrementally to 9 (>90%), or nearly completely digested and mostly unidentifiable (Cortés and Gruber 1990, Berens 2005). These codes were used to determine whether angel sharks fed continuously or tended to consume many prey items at once. Prey items assigned a digestion code of 9 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 0 were excluded from diet analyses to reduce bias from possible feeding events while within the trawl (Bethea et al. 2004).

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, unpub.) 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. A graph was then generated plotting the total number of stomachs versus the average number of new prey items found in each stomach. An adequate number of stomachs have been analyzed, and the diet is well described, when the curve reaches an asymptote (Ferry and Cailliet 1996).

Indices of diet composition used in this study were percent by occurrence (%O), percent by number (%N), and percent by weight (%W) (Hyslop 1980, Cortés 1997). 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. These indices were used to calculate the index of relative importance (IRI), which is the sum of %N and %W, multiplied by %O. 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), which limits the biases of the individual components of diet analysis and facilitates comparisons among other diet studies (Cortés 1997). 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 for each sampling trip was calculated with Levin's standardized index ( $B_A$ ) (Krebs 1999b). The standardized index is expressed on a scale from 0 (minimum niche breadth) to 1 (maximum niche breadth), which facilitates comparisons among species (Krebs 1999a):

$$B_A = \frac{B - 1}{n - 1}$$

where  $B$  is equal to  $1/\sum p_{ij}^2$  and  $p_{ij}^2$  is the proportion of the diet of predator  $i$  that contains prey  $j$ , and  $n$  is the number of prey categories.

Diet overlap of angel sharks collected from the two sampling trips was calculated with Morisita's index of similarity because it gives almost no bias according to sample size and number of resources (Smith and Zaret 1982).

### **Dietary Preference**

Two selection indices were employed to describe prey preference of the Atlantic angel shark. Both of these indices are essentially a comparison of prey items in stomachs with potential prey items in the environment and are based on the assumption that the sampled trawl catch is an adequate representation of the prey universe of the angel sharks.

Manly's  $\alpha$  ( $\alpha_i$ ) (Krebs 1999a, b) was used to assess preference because it offers a simple measure of preference by comparing the probabilities of encounter and capture:

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

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  $\alpha$  values are normalized so that all  $\alpha$  values sum to 1, and selective feeding occurs when  $\alpha_i$  is greater than  $1/(\text{total number of prey types})$ .

The rank preference index ( $t_i$ ) (Johnson 1980) was also calculated because it is not greatly affected by the inclusion of common but rarely consumed prey items:

$$t_i = r_i - s_i$$

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 with a Kolmogorov-Smirnov D statistic comparing size frequency histograms of 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. 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.

## **Results**

### **Angel Shark Collections and Sampling of Potential Prey**

A total of 50 and 59 angel sharks were caught on 11 Feb and 29 April 2005, respectively, in butterfly trawls and all were retained for stomach content analysis. Sharks ranged in size from 190 to 970 mm TL, with the majority between 200–500 mm TL (Fig. 2-1).

On 11 February, five out of a total of 716 boxes of bycatch were sampled (0.7% of total bycatch caught). Three boxes of bycatch (0.8% of total bycatch caught), 11 kg of butterfly (0.8% of total butterfly caught), 11 kg of goggle eye jacks (0.3% of total goggle eyes caught), and 5 kg of squid (3.4% of total squid) were collected on 29 April. Regressions relating lengths and weights of whole prey fish and squid to dimensions measurable in partial prey were all significant and predictive (Table 2-1).

### **Catch Quantification and Prey Abundance**

A total 28,204 and 14,227 kgs of fish were landed by the butterfish trawlers on 11 Feb and 29 April, 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. 2-3). The vast majority of Carangids in the catch were rough scad, which are boxed and sold for bait (E. Raffield, pers. comm.). Porgies (Sparidae) were the second most abundant family in both trawls, with longspine porgies *Stenotomus caprinus* as the dominant species. Other common families in the 11 Feb catch were Stromateidae (butterfishes), Scaenidae (croakers), and Mullidae (goatfishes), in descending order of abundance. The third most common family from 29 April was Mullidae, followed by Stromateidae, and Synodontidae (lizardfishes). Morisita's index of similarity was high between the trips, with a value of 0.87.

### **Diet Analysis**

Of the 50 angel shark stomachs collected on 11 Feb 2005, 6 (12%) were completely empty, while 17 (34%) contained prey items that were not assigned a digestion code of 0 or 9 and were therefore used in diet analyses. On 29 April 2005, 59 angel sharks were collected, of which none had empty stomachs and 27 stomachs (45%) contained prey items that were not coded 0 or 9. Cumulative prey curves showed that the diets were well described for angel sharks collected from both sampling trips (Fig. 2-2). Diets of angel sharks were similar between sampling trips, with teleosts being the most often encountered prey by occurrence (64% and 84%) and numerical abundance (62% and 75%) for the 11 Feb and 29 April trips, respectively (Table 2-2). Squid occurred most commonly of any single species, with 24% and 16% occurrence for the two trips, respectively, followed by Atlantic croaker (16% and 12% occurrence), and red goatfish *Mullus auratus* (8% and 12% occurrence) (Table 2-2). Other

major prey items included crustaceans, which were found in 16% and 25% by occurrence and 13% and 14% by numerical abundance of angel sharks with any stomach contents on 11 Feb and 29 April, respectively. With respect to %IRI, squid were the most important prey item in angel shark stomachs collected on 11 Feb (54%), followed by Atlantic croaker (23%), and red goatfish (7%). On 29 April, red goatfish were the most important prey item by %IRI (28%), followed by Atlantic croaker (25%), and squid (20%). Digestion codes showed that many angel shark stomachs contained several prey items in differing states of digestion. The vast majority of stomach contents that were assigned a digestion code of 9 were fish eye lenses, degraded squid beaks, and degraded otoliths.

### **Niche Breadth and Overlap**

Levin's standardized index of niche breadth values were similar for stomach contents of angel sharks from both sampling trips (0.42 and 0.44 for 11 Feb and 29 April, respectively). Diet overlap of angel sharks between the sampling trips was high, with a Morisita's index of similarity of 1.02.

### **Dietary Preference**

Angel sharks collected from both sampling trips showed preference for squid, while those collected on 29 April also showed preference for hakes (Phycidae), croakers (Sciaenidae), and scorpionfishes (Scorpaenidae) (Table 2-3, Fig. 2-4) based on the values of the Manly's  $\alpha$  calculation and the rank preference test. Angel sharks collected on 11 Feb showed secondary preference for seabasses (Serranidae), and showed the least preference for snappers (Lutjanidae) and porgies. In order of decreasing rank, angel sharks collected on 29 April preferred scorpionfishes, croakers, hakes, and goatfishes, and showed the least preference for jacks

(Carangidae). Due to the marked absence of crustaceans and cusk eels (Ophidiidae) in the trawl catch, they were excluded from preference analyses.

### **Prey Size Selection**

Otoliths were used often for prey identification but were rarely employed for size reconstruction because prey items coded 9 (only bones, scales, and otoliths) were excluded from diet analyses. Therefore most prey were mostly intact and other external morphological measurements, such as length of the vertebral column, were more often used. Otoliths were only useful in the size reconstruction of Atlantic croaker sizes, and the weight of the otoliths was found to be a better predictor for fish TL than the otolith length (Table 2-1).

Prey items in angel shark stomachs were well within the size range of the trawl-caught prey fish (Fig. 2-5). 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), the median was 150 mm. Kolmogorov-Smirnov analysis comparing the size distributions of trawl caught fish <250 mm TL and those from stomachs showed that fishes in stomachs were significantly smaller ( $D=0.43$ ,  $p<0.03$ ) than those caught in the trawl.

### **Discussion**

Angel sharks consumed fishes that were in high abundance, such as croakers and goatfishes, however they also selected for fishes and cephalopods that were in relatively low abundance such as hakes, scorpionfishes, and squid (Fig. 2-4). The selection of prey items that were in comparatively low abundance and the mean niche bread value 0.43 indicate that angel shark are not exclusively opportunistic predators, but may be actively selecting certain prey items. This is also reinforced by the fact that the sizes of prey items angel sharks consumed prey



items were significantly different than those caught in the trawl that were within an edible size range.

Atlantic croakers were important prey items in angel shark stomachs in both sampling trips (23 and 25% IRI, Table 2-2), although the abundance of Atlantic croaker in the trawl catch decreased from February (22.8%) to April (1.1%) (Fig. 2-4). Squid were also consumed in high quantities despite their low abundance in trawls. While squid are packaged and sold by the fish house, the butterfly trawlers are not targeting 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 therefore near the bottom at the same time as the gear is deployed to catch butterfly, and angel sharks as bycatch (i.e., trawling on the bottom during daylight hours), and if squid was under-represented in the trawl catches it was most likely due to a gear bias. Even if squid abundance was misrepresented by the trawl catch and therefore biased the estimates of preference, the fact remains that squid were the most prevalent single prey item in stomachs overall, and therefore any possible sampling bias probably would not change the implications of these results. To minimize the possibility of a 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. Squid are likely easily captured as prey by angel sharks and require little handling time due to their lack of hard parts (Smale 1996), increasing 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 diets. Rough scad, which comprised the majority of the carangids in the trawl (Fig. 2-3), are small pelagic fishes that are found in on the continental shelf and are known to school near the bottom (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 butterfly trawlers fish during the day because butterflyfish aggregate at depth during the day, and hence the squid and pelagics were caught in the trawl at the same time.

The lack of crustaceans and cusk eels in the trawl catch 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 butterfly fishery conducted in 1986 reported few numbers of crustaceans (and no cusk eels), with rosy shrimp *Parapenaeus* sp. as the only reported crustacean bycatch (Vecchione 1987). Some rock shrimp *Sicyonia* sp. were observed in the catch on 11 Feb, however, they were kept for personal use by the staff of the fish house and could therefore not be sampled. While these crustaceans were observed, they were in very low numbers despite the prevalence of crustaceans in other trawl surveys (GSMFC 2002). 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 and preference indices of fish and squid were relatively unbiased.

Vogler et al. (2003) found that angular angel sharks *S. guggenheim* showed strong specialist traits for different prey items, with Argentine anchovy *Engraulis anchoita* present in more than half of the stomachs of angel sharks <440 mm TL. The niche breadth values for Atlantic angel sharks indicated that while they are not highly specialized predators, they are not

entirely opportunistic either. In addition, the selection of prey items in relatively low abundance indicates a higher level of prey selection than might be assumed for a bottom-associated ambush predator. It is therefore possible that Atlantic angel sharks may be vulnerable to changes in prey abundance and composition and may not be able to switch to other prey resources if their prey base becomes limiting.

Table 2-1. 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), OW=otolith weight (g), OL=otolith length, and OH=otolith height (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	$W = 0.03 * SL^3.09$	0.96	64	121	210
<i>Micropogonias undulatus</i>	$W = -134.80 + 1.92 * VC$	0.93	33	86	167
	$W = 1E-06 * TL^3.41$	0.97	64	155	255
	$W = 104.7 * (LOG(OW) + 257.5)$	0.81	64	0.11	0.48
	$TL = 55.967 + 1.22 * VC$	0.91	33	86	167
	$TL = 1.14 * SL + 15.58$	0.99	64	121	210
	$TL = 59.39 * (LOG(OW) + 295.87)$	0.60	64	0.11	0.48
	$TL = 170.2 * (LOG(OL) - 169.99)$	0.56	64	7.05	11.59
	$TL = 161.5 * (LOG(OH) - 114.43)$	0.57	64	5.8	9.42
	$BD = 0.28 * TL - 7.11$	0.86	64	155	255
Butterfish	$W = 0.0002 * SL^2.67$	0.84	34	125	158
<i>Peprilus burti</i>	$W = 0.0004 * VC^2.69$	0.85	33	90	120
	$W = 0.0001 * TL^2.56$	0.79	32	168	215
	$TL = 1.30 * SL + 10.17$	0.82	32	125	158
	$TL = 1.74 * VC + 12.33$	0.84	32	90	120
	$TL = 56.47 * (LOG(OW) + 413.53)$	0.66	32	0.01	0.03
	$TL = 194.89 * (LOG(OL) - 176.21)$	0.57	32	6.01	7.43
	$TL = 117.00 * (LOG(OH) + 37.93)$	0.45	32	3.47	4.33
	$BD = 0.30 * TL + 15.33$	0.61	32	168	215
Dwarf goatfish	$W = 0.03 * SL^3.18$	0.97	55	80	160
<i>Upeneus parvus</i>	$W = 0.04 * VC^3.05$	0.91	36	58	115
	$W_t = 2E-06 * TL^3.36$	0.98	55	101	200
	$TL = 1.28 * SL - 1.62$	0.99	55	80	160
	$TL = 1.67 * VC + 3.55$	0.96	36	58	115
	$TL = 43.94 * (LOG(OW) + 376.18)$	0.92	55	0.002	0.01
	$TL = 150.52 * (LOG(OL) - 39.39)$	0.93	55	2.58	4.65
	$TL = 123.76 * (LOG(OH) + 37.05)$	0.89	55	1.70	3.49
	$BD = 0.21 * TL - 3.98$	0.89	54	101	200
Longfin squid	$W = 3.3991 * UL^1.625$	0.88	22	190	415
<i>Loligo paelei</i>					
Longspine porgy	$W = -114.32 + 1.53 * SL$	0.97	77	86	173
<i>Stenotomus caprinus</i>	$W = 0.05 * VC^2.93$	0.93	57	61	120
	$W = 7E-05 * TL^2.72$	0.97	57	104	225
	$TL = 1.29 * SL + 1.90$	0.98	77	86	173
	$TL = 1.87 * VC - 1.18$	0.91	57	61	120
	$TL = 472 * OW^0.32$	0.92	77	0.01	0.07
	$TL = 24.79 * OL - 0.34$	0.93	77	4.41	8.45
	$TL = 47.29 * OH - 27.33$	0.88	77	2.99	4.99
	$BD = 0.37 * TL + 5.09$	0.93	77	104	225

Table 2-1. Continued.

Prey Species	Regression Equation	$r^2$	n	Min (x)	Max (x)
Pinfish	$W = 7E-06 * SL^{3.28}$	0.9	56	133	200
<i>Lagodon rhomboides</i>	$W = 0.0002 * VC^{2.75}$	0.81	57	95	156
	$W = 3E-06 * TL^{3.3}$	0.92	57	175	262
	$TL = 1.30 * SL + 3.77$	0.96	56	133	200
	$TL = 1.45 * VC + 38.44$	0.86	34	95	156
	$BD = 2.31 * TL + 66.64$	0.87	57	175	262
Red goatfish	$W = 0.03 * SL^{2.97}$	0.87	60	116	170
<i>Mullus auratus</i>	$W = 0.04 * VC^{3.05}$	0.9	30	91	125
	$W = 1E-05 * TL^{2.93}$	0.87	60	154	215
	$TL = 1.21 * SL + 11.83$	0.98	60	116	170
	$TL = 1.55 * VC + 18.1$	0.87	30	91	125
	$BD = 0.21 * TL + 1.45$	0.66	51	154	215
Rough scad	$W = 1E-05 * SL^{3.09}$	0.99	76	52	194
<i>Trachurus lathami</i>	$W = 3E-05 * VC^{3.07}$	0.97	69	36	131
	$W = 8E-06 * TL^{3.01}$	0.99	76	64	237
	$TL = 1.11 * SL^{1.02}$	0.99	76	52	194
	$TL = 1.60 * VC^{1.02}$	0.98	69	36	131
	$BD = 0.20 * TL - 0.60$	0.94	76	64	237
Wenchman	$W = 0.03 * SL^{3.05}$	0.98	76	56	210
<i>Pristipomoides aquilonaris</i>	$W = 0.04 * VC^{3.11}$	0.97	64	38	145
	$W = 6E-06 * TL^{3.12}$	0.99	76	76	282
	$TL = 1.33 * SL + 0.01$	0.99	76	56	210
	$TL = 1.89 * VC + 1.46$	0.98	64	38	145
	$TL = 61.7 * (LOG(OW) + 319.52)$	0.98	76	0.01	0.57
	$TL = 22.52 * OL - 12.76$	0.98	74	3.65	12.15
	$TL = 33.02 * OH - 25.61$	0.97	74	2.95	9.15
	$BD = 0.28 * TL - 1.65$	0.97	76	76	282

Table 2-2. Occurrence (%O), numerical abundance (%N), weight (%W), and Index of Relative Importance (%IRI) for prey sampled from stomach contents of angel sharks collected in the northeastern Gulf of Mexico on 11 Feb and 29 April 2005. Occurrence for prey groups (e.g., Teleosts) is the total number of stomachs containing that prey group divided by the total number of stomachs containing food.

Prey identification	11-Feb-05				29-Apr-05			
	%O	%N	%W	%IRI	%O	%N	%W	%IRI
<b>Teleosts</b>	<b>64.00</b>	<b>62.22</b>			<b>84.38</b>	<b>74.58</b>		
Acropmatidae: <i>Synagrops bellus</i>					3.13	1.69	0.76	0.55
Bothidae					3.13	1.69	6.54	1.84
Carangidae: <i>Trachurus lathami</i>					3.13	1.69	6.31	1.78
Lutjanidae: <i>Pristomoides aquilonaris</i>	4.00	2.22	5.59	1.35				
Mullidae: <i>Mullus auratus</i>	8.00	6.67	13.24	6.87	12.50	6.78	24.85	28.19
<i>Upeneus parvus</i>					6.25	5.08	13.88	8.45
Ophidiidae: <i>Lepophidium sp.</i>	8.00	6.67	7.46	4.87				
Phycidae: <i>Urophycis sp.</i>	4.00	2.22	1.00	0.56	3.13	1.69	0.19	0.42
Sciaenidae: <i>Micropogonias undulatus</i>	16.00	8.89	24.35	22.93	12.50	6.78	21.35	25.07
<i>Leiostomus xanthurus</i>	4.00	2.22	5.98	1.42				
Scorpaenidae: <i>Scorpaena agassizi</i>	4.00	2.22	3.16	0.93				
<i>Scorpaena sp.</i>					6.25	3.39	2.87	2.79
Serranidae: <i>Centropristis sp.</i>	8.00	4.44	3.05	2.58	6.25	3.39	4.47	3.50
Sparidae: <i>Stenotomus caprinus</i>	8.00	4.44	2.80	2.50	6.25	3.39	9.61	5.79
Synodontidae: <i>Saurida normani</i>	4.00	2.22	5.28	1.29				
<i>Synodus sp.</i>	4.00	2.22	0.09	0.40	3.13	1.69	0.89	0.58
Triglidae: <i>Prionotus stearnsi</i>					3.13	1.69	2.02	0.83
Unidentified teleosts	16.00	17.78			46.88	35.59		
<b>C. Cephalopoda</b>	<b>24.00</b>	<b>24.44</b>	<b>28.02</b>	<b>54.30</b>	<b>15.63</b>	<b>11.86</b>	<b>6.27</b>	<b>20.21</b>
<i>Loligo sp.</i>	24.00	24.44	28.02	54.30	15.63	11.86	6.27	20.21
<b>C. Crustacea</b>	<b>24.00</b>	<b>13.33</b>			<b>25.00</b>	<b>13.56</b>		
Shrimp	8.00	4.44			9.38	5.08		
<i>Lysosquilla sp.</i>	16.00	8.89						
Unidentified crustaceans					15.63	8.47		
<b>Totals % (number)</b>	<b>100 (25)</b>	<b>100 (45)</b>	<b>100 (1504)</b>		<b>100 (32)</b>	<b>100 (59)</b>	<b>100 (1070)</b>	

Table 2-3. Preference values for families of fishes recovered in Atlantic angel shark stomachs. RPI is the rank preference index. For 11 Feb, Manly's  $\alpha$  values greater than 0.111 indicate positive selection. For 29 April, Manly's  $\alpha$  values greater than 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 bold. The smallest (most negative) values for RPI are indicative of the most preferred prey items, with preference decreasing as the values increase.

	11 Feb 2005		29 Apr 2005	
	Manly's $\alpha$	RPI	Manly's $\alpha$	RPI
Acropomatidae			0.037	0.5
Bothidae			0.029	1.5
Carangidae			0.001	8.5
Loliginidae	<b>0.857</b>	-8	<b>0.390</b>	-8.5
Lutjanidae	0.004	4		
Mullidae	0.004	0	0.011	-1.5
Phycidae	0.039	1	<b>0.174</b>	-2.5
Sciaenidae	0.004	0	<b>0.104</b>	-4
Scorpaenidae	0.041	0	<b>0.191</b>	-6
Serranidae	0.030	-1	0.049	-1
Sparidae	0.001	4	0.002	3
Synodontidae	0.020	0	0.005	5.5
Triglidae			0.006	4.5

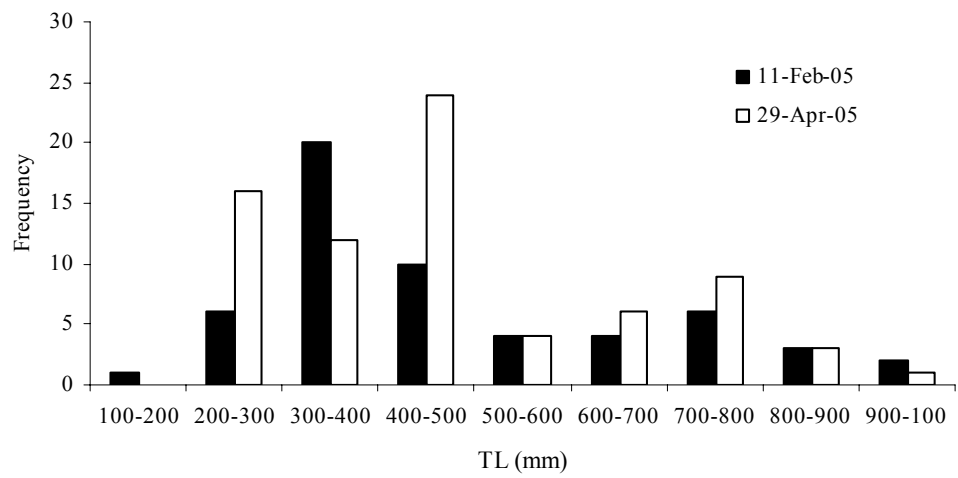


Figure 2-1. Length frequency of Atlantic angel sharks collected for stomach content analysis on 11 February and 29 April, 2005, in the northeastern Gulf of Mexico.



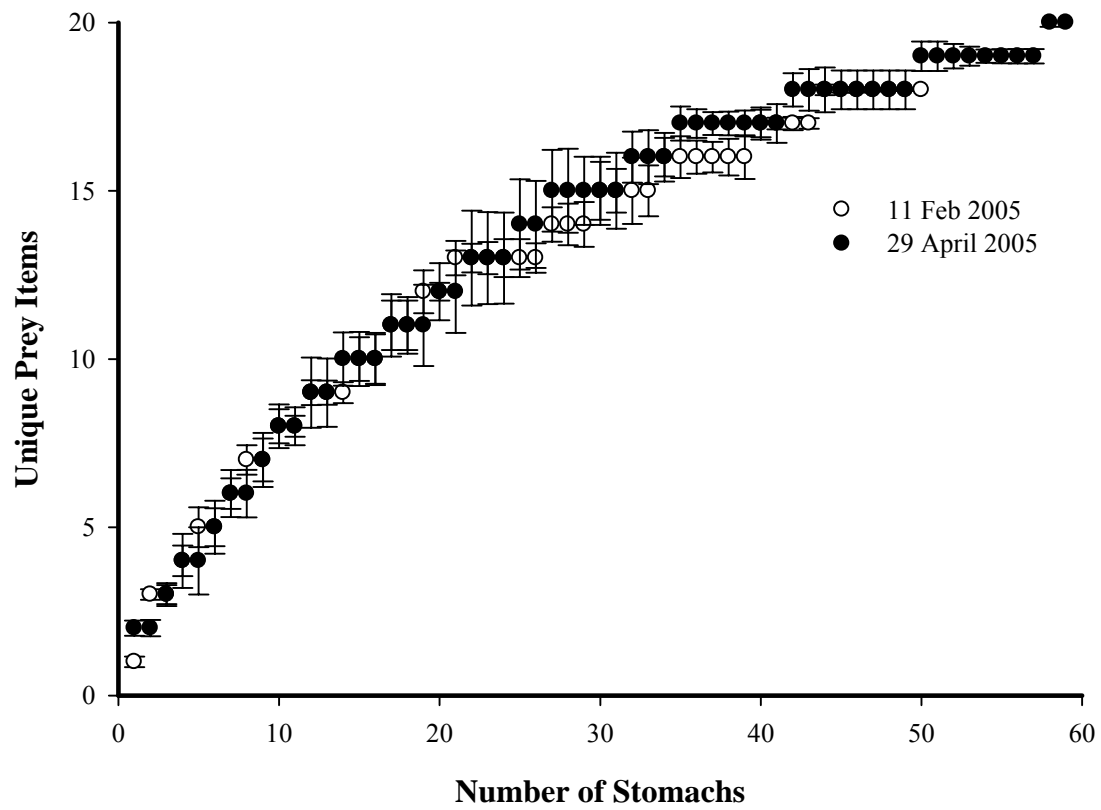


Figure 2-2. Cumulative prey curves for stomach contents of all angel sharks collected on 11 Feb (open circles) and 29 April (filled-in circles), 2005. Asymptotes in the curves indicate that the diets were well described for each sampling trip. Error bars represent standard error.

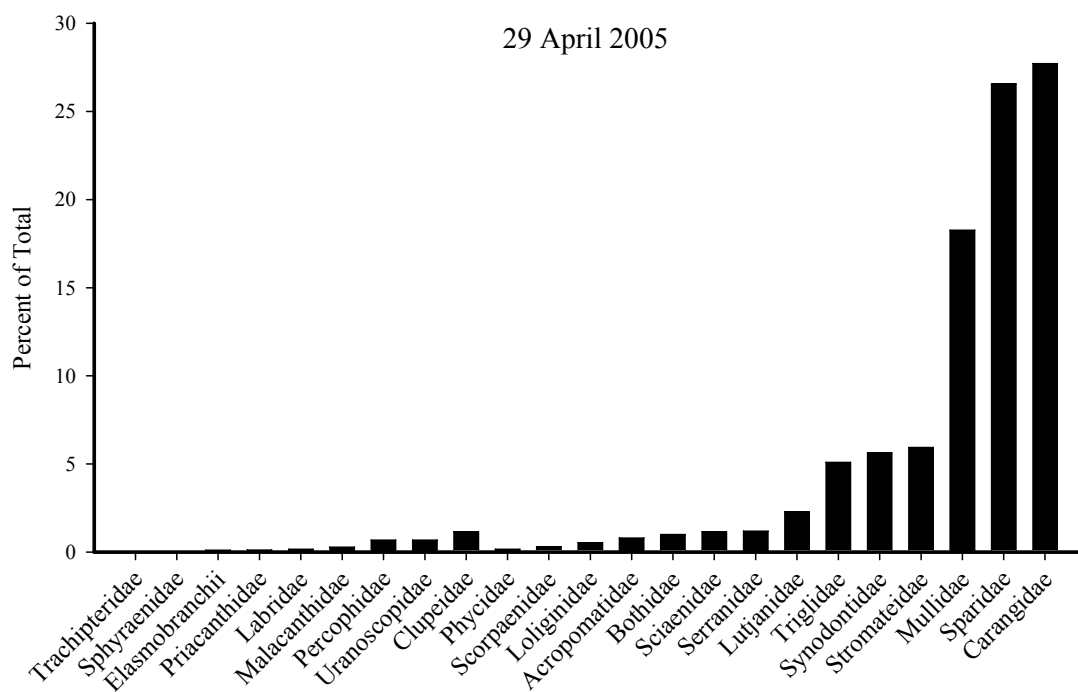
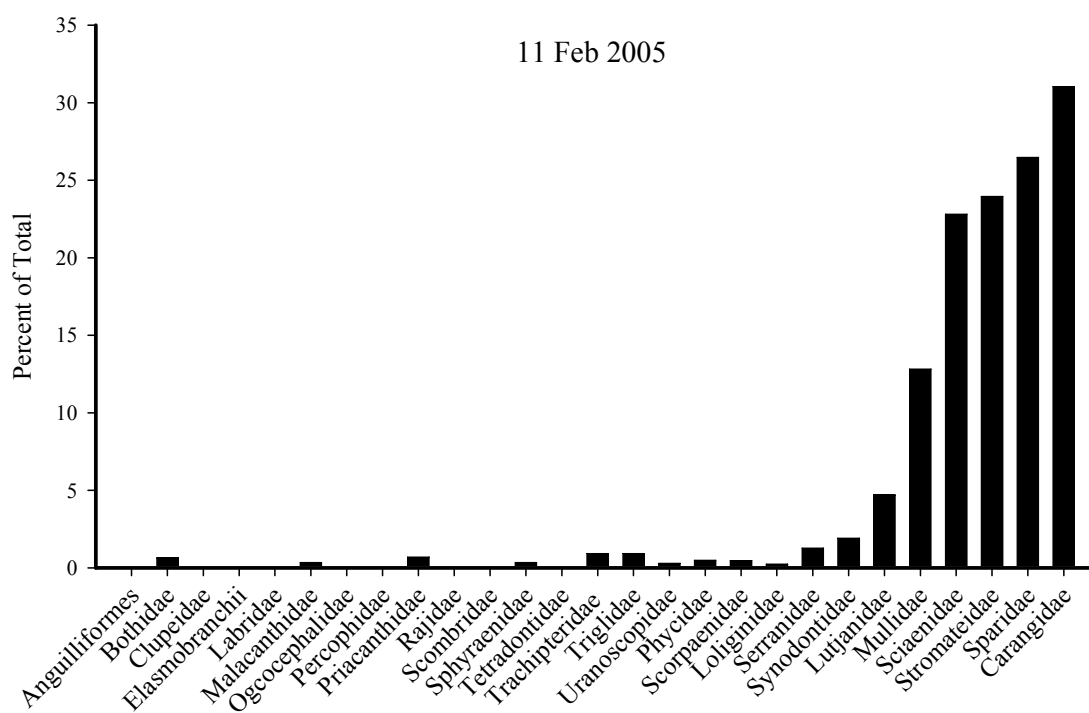


Figure 2-3. Trawl catches by number on 11 Feb and 29 April 2005, summarized by family.

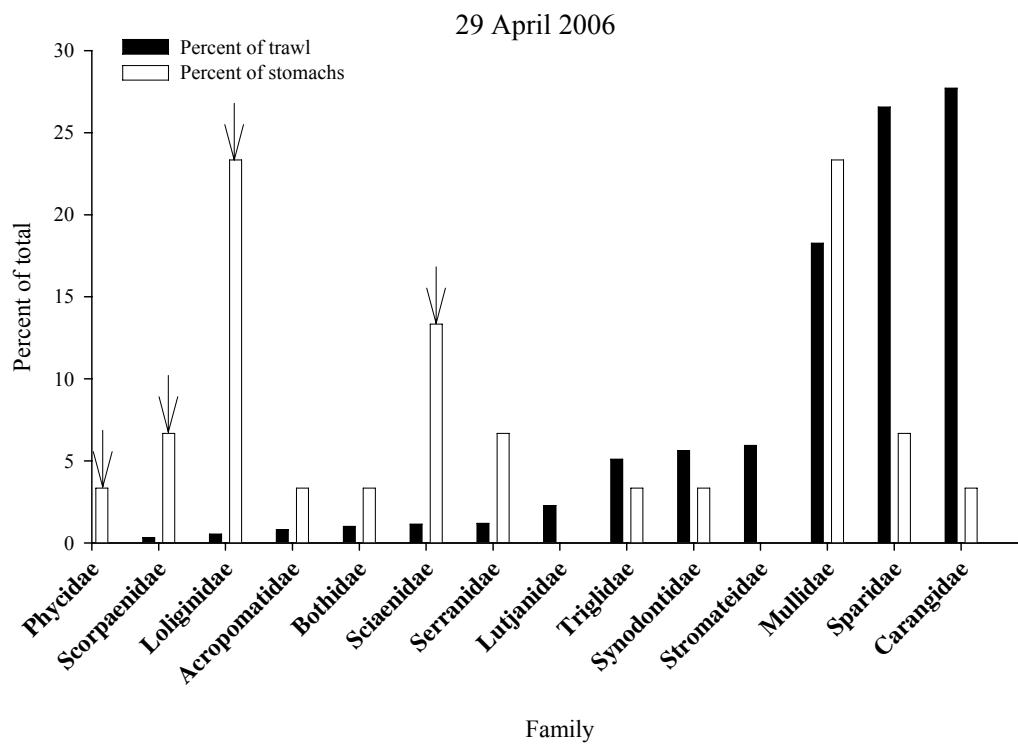
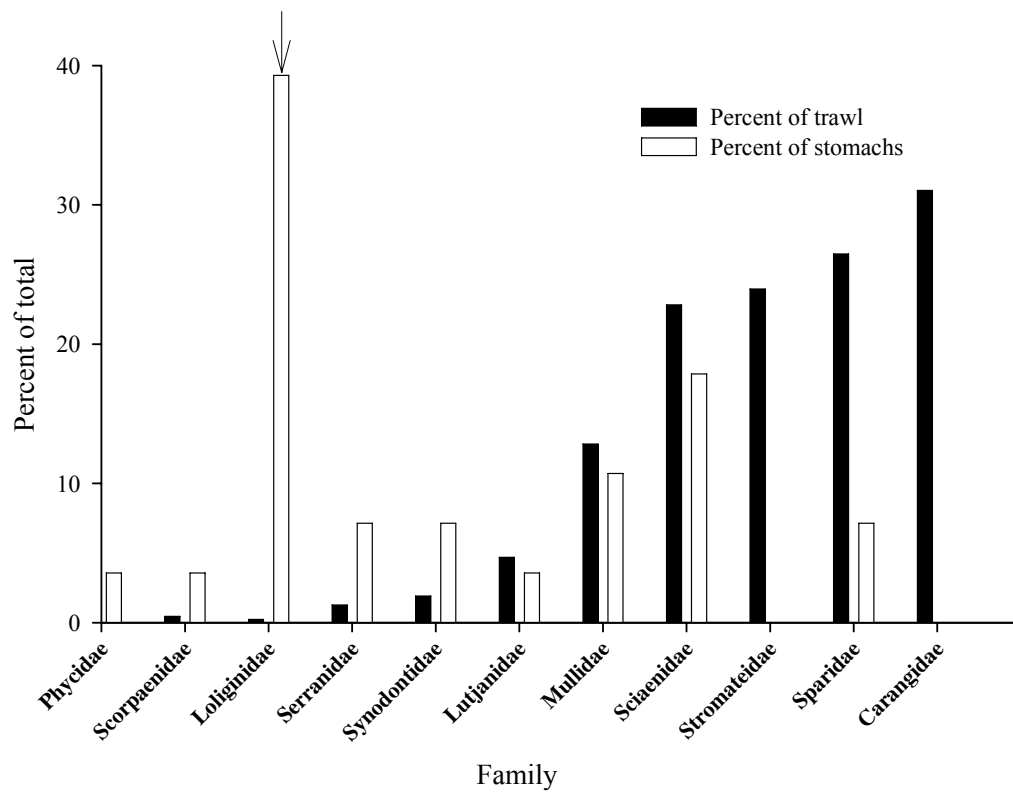
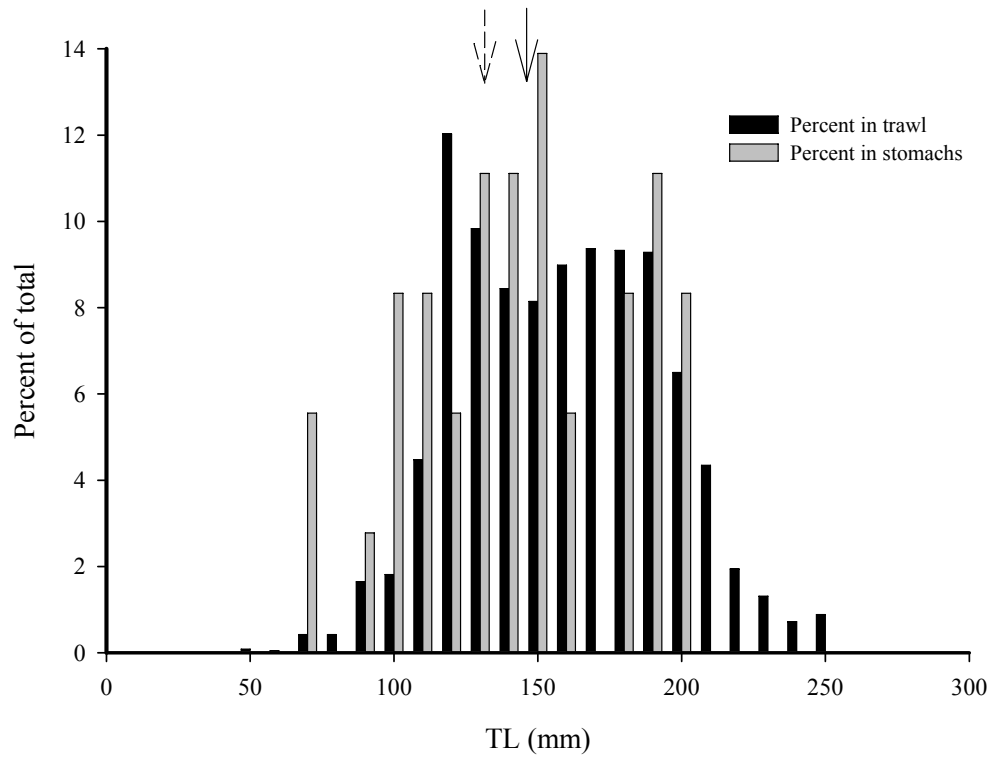


Figure 2-4. Percent of total catch based on number by family from the trawls and in the stomach contents of Atlantic angel sharks from the northeastern Gulf of Mexico. Arrows indicate positive selection according to the standardized selection index by the Atlantic angel shark.

A



B

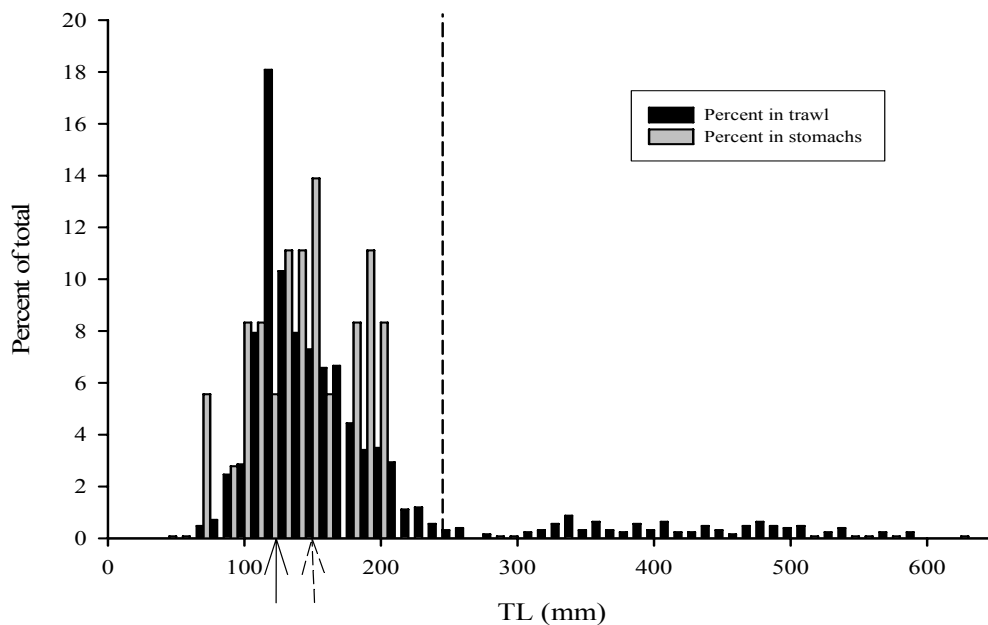


Figure 2-5. Length frequency of fishes caught in trawls for combined trips A) <250 mm TL and B) for all fishes recovered in the trawl, along with the sizes of those recovered in stomach contents of Atlantic angel sharks in the northeastern Gulf of Mexico. The solid arrows indicate the median length of trawl-caught fishes (150 mm), and the dashed arrows are the median length of fish from stomach contents (135 mm).

## CHAPTER 3

### FOOD HABITS OF THE ATLANTIC ANGEL SHARK IN THE NORTHEASTERN GULF OF MEXICO

#### **Introduction**

The quantification of diet is essential for recognizing the roles that predators play in an ecosystem. Analysis of food habits can give indications of many factors, including prey preference and the movement patterns of predators and prey, and can also reveal how an organism might respond to changes in its habitat and forage base (Hambright 1994, Juanes et al. 2001). Although diet analysis of top predators is vital to our knowledge of ecosystem dynamics, it is lacking for many species of elasmobranchs, especially squatinids (Vogler et al. 2003). This chapter provides the first quantification of diet for the Atlantic angel shark *Squatina dumeril* in the Gulf of Mexico, and describes trends in the diet with shark size and season.

Ontogenetic shifts in diet are nearly ubiquitous among marine fishes, and elasmobranchs are no exception (Stillwell and Kohler 1982, Cortés and Gruber 1990, Lowe et al. 1996, Ebert 2002). Shifts in diet with size often are indications of changes in morphology and ability to capture prey, but larger predators are also exposed to a wider range of potential prey than smaller predators (Juanes 1994). Though diet information for squatinids is limited, Vogler et al. (2003) found that cephalopods and crustaceans became more important in the diet of the angular angel shark *Squatina guggenheim* with increasing size; the diet shifted from almost exclusive piscivory to become more diverse.

Diet and prey preference of predators is also affected by factors such as prey size. Angel sharks consume their prey whole (Fouts and Nelson 1999), which functionally limits the size range of prey items available to them (Gill 2003). The maximum size of

prey items increases as predator size increases, and the range of prey sizes available also increases with increasing predator size (Juanes 1994, Gill 2003). Another significant factor in prey size selection for piscivorous fishes is the relationship between their mouth size (gape) and the body depth (BD) of the prey item (Gill 2003). Size-selectivity of predators may be related to habitat, morphological specializations, and spatial overlap with prey items (Greene 1986). In particular, angel sharks are dorso-ventrally flattened benthic predators that consume their prey whole, therefore the body depth of prey items may have more of an effect of angel shark prey size selection than the overall length of the prey.

The objectives of this chapter were 1) to quantify the diet of the Atlantic angel shark, 2) to determine if angel shark diet or prey preferences change with ontogeny, 3) to determine whether angel shark diet changes with season, and 4) to describe angel shark prey size selection.

## **Methods**

### **Data Collection**

Angel sharks were collected from the butterfly trawl fishery in Port St. Joe, Florida, from November 2002 through April 2005 by biologists at the National Oceanic and Atmospheric Administration (NOAA) Fisheries Service. Most sharks were collected as they were unloaded from the boats, though on rare occasions they were set aside on ice at the fish house until they could be collected by the biologists.

Sharks were placed on ice and transported to the NOAA Fisheries, Panama City Laboratory, for processing. At the laboratory, precaudal (length from the tip of the nose to the notch at the base of the upper lobe of the caudal fin), fork, and total lengths were

measured ( $\pm$  mm) and sharks were weighed (kg). Gape width, which is the lateral width of the mouth when opened, was also measured ( $\pm$  mm). Each shark was dissected and the stomach was removed and frozen for later processing. In addition, reproductive organs were measured and weighed, and pups from gravid females were counted, sexed, weighed (g), and measured (TL) for future studies. The liver was weighed and frozen, and several vertebrae from the middle of the vertebral column were removed and frozen for possible future bioenergetic and ageing studies. To test for changes in diet with ontogeny, angel sharks were divided into three size categories: A ( $<550$  mm TL,  $n=79$ ), B ( $550\text{--}800$  mm TL,  $n=55$ ), and C ( $>800$  mm TL,  $n=47$ ). Size categories were roughly equivalent to the life history stages of young-of-the-year, juvenile, and mature, but were established to maintain similar sample sizes among comparisons. Maturity state was assessed based on size and internal examination: mature male *S. dumeril* possess calcified claspers and have highly coiled epididymides, and mature females have large, well developed ovaries and nidamental glands (unpubl. data).

Seasonal shifts in diet were tested by comparing diets of angel sharks collected during different times of the year. Seasons were established based on calendar seasonal dates and by using differences in average surface water temperatures in the northeastern Gulf of Mexico by month (<http://www.nodc.noaa.gov/dsdt/cwtg/egof.html>), and diets for consecutive months with similar temperatures were combined. Because angel sharks were most commonly caught at 200 m, surface temperatures may not be reflective of the temperatures at that depth, so surface temperatures were only used as a tool for seasonal divisions. Seasonal comparisons were made between winter (January and February:  $n=74$ ,  $59^{\circ}\text{C}$ ), spring (March, April, and May:  $n=58$ ,  $73^{\circ}\text{C}$ ), and fall (October, November,

and December:  $n=51$ ,  $67^{\circ}\text{C}$ ). Stomachs collected in summer months were not included in seasonal overlap analyses due to low sample size (August:  $n=3$ ).

### **Stomach Content Analysis**

Stomach contents analyzed and identified in the same manner described in Chapter 2. Diet indices used in this study were percent by occurrence (%O), percent by number (%N), percent by weight (%W), and percent index of relative importance (%IRI) (Chapter 2, Cortés 1997). Weight values were back-calculated to the original wet weight of the prey item when possible from regression equations described in Chapter 2. Weight values for prey categories (e.g. teleosts, cephalopods, and crustaceans) were calculated using only identified prey items, while IRI values for those prey categories were calculated with %O and %N values for all.

Prey items were assigned a digestion code from 0 (no digestion evident) to 9 (nearly completely digested and unidentifiable). To reduce the inclusion of prey items from previous feeding events (code 9) and the possibility of post-capture feeding (code 0), prey items assigned 0 or 9 were excluded from diet analyses. Cumulative prey curves were used to assess the adequacy of the sample size overall and for angel shark size categories A ( $<550$  mm TL), B (550–800 mm TL), and C ( $>800$  mm TL). Diets were considered well described when the prey curve approached an asymptote (Ferry and Cailliet 1996), i.e. when the percent of new unique prey items in the diet increased by less than 5% over the last 10 stomachs analyzed.

### **Ontogenetic and Seasonal Diet Shifts**

Changes in the diet of angel sharks with ontogeny and season were assessed by comparing Levin's standardized niche breadth index values,  $B_A$  (Krebs 1999a, b; Chapter



2) for each shark size category and season. Additionally, diet overlap among shark size categories and seasons was assessed with Morisita's index of similarity,  $C_\lambda$  (Krebs 1999a, b; Chapter 2).

### **Prey Size**

Portions of the trawl catch were sampled in February and April, 2005 (see Chapter 2 methods) to estimate sizes of potential prey items. Regression equations developed from the sampled catch were used to back-calculate TL and body depth for prey items that were not whole for all stomach contents (Table 2-1), based on the assumption that the morphological relationships of potential prey items did not change over time. Scatter plots of the lengths of prey items in relation to shark size were used to gauge prey size use with increasing shark size. Because of the dorsoventral flattened morphology and ambush feeding of angel sharks, shark gape as a function of prey body depth was also measured. Gape was defined as the lateral width (mm) of the opened mouth of an angel shark at its widest point. Angel shark gape width was plotted as a function of shark TL to estimate gape widths when they were not available. These data were fitted to linear, log-transformed linear, logarithmic, exponential, and power regression equations to assess changes in size utilization with shark size and gape width. The 'best fit' model was selected based on the highest coefficient of determination ( $r^2$ ) or adjusted  $r^2$ , and assessment of the residual plots. Prey size ratios (prey TL/shark TL and prey BD/shark gape) were also calculated to determine if there was a relationship between prey size and shark size and gape width. These relationships were assessed by using the maximum prey size/prey body depth ratio per stomach to investigate gape limitation. Additionally, prey size was examined by shark size category, with the same

classifications described previously. In cases where gape width was not measured directly, it was estimated based on the regression of gape width in relation to TL of the shark.

## **Results**

### **Diet Analysis**

Of 437 stomachs analyzed, 24 (5%) were completely empty while 187 (43%) contained at least 1 prey item with a digestion code  $>0$  and  $<9$ , and were therefore used in this study (inclusive of sharks stomach contents analyzed in Chapter 2). The sharks included in the diet analysis ranged in size from 305 to 1160 mm TL, of which 88 were females and 99 were males (Fig. 3-1). All size categories of sharks were collected in the same locations and over all months. Roughly half of the collected stomachs in all months were assigned a code of 9, with spring months tending to have the highest proportion (59%) and fall months the lowest proportion (48%) of prey items coded 9 (Fig. 3-2a). The smallest sharks ( $<500$  mm TL) had the highest proportion of prey items coded 9 (as high as 73%), and this proportion decreased with size (Fig. 3-2b). Cumulative prey curve analysis showed that diets were well described overall and for size categories A and B (sharks  $\leq 800$  mm TL), with a 1.3 and 3.6% increase in new prey items over the last 10 stomachs analyzed (Fig. 3-3a,b). The diet of size category C (sharks  $>800$  mm TL) was possibly not adequately described, as unique prey items increased 6.4% over the last 10 stomachs analyzed (Fig. 3-3c).

Teleost fishes dominated the diets of Atlantic angel sharks in this study (Table 3-1), occurring in 81.0% O and 77.0% N, 67.6% W, and 46.7% IRI of stomachs containing food. Atlantic croaker *Micropogonias undulatus* were the most common teleost prey

items overall (10.1% O, 7.2% N, 13.3% W, 18.0% IRI), followed by longspine porgies *Stenomus caprinus* (6.7% O, 4.8% N, 4.3% W, 5.3% IRI), spot *Leiostomus xanthurus* (5.0% O, 3.1% N, 6.1% N, 4.0% IRI), butterfish (5.0% O, 4.5% N, 8.1% W, 5.5% IRI), and red goatfish *Mullus auratus* (4.2%O, 3.1% N, 5.3% N, 3.3% IRI). On a species-specific basis, squid were the most important single prey item in the diet of Atlantic angel sharks (14.0% O, 10.7% N, 31.9% W, 51.7% IRI). Crustaceans were also important prey items, and were found in 19.0% O, 12.0% N, 0.4 % W, and 1.6% IRI.

Summarized by shark size category, teleosts dominated the diets of sharks in all size categories. By prey category, teleosts made up 76.8, 77.8, and 91.5% occurrence and 72.1, 75.7, and 83.3% numerical frequency of the diets of size classes A, B, and C, respectively. In the same order, crustaceans made up 18.8, 27.0, and 8.5% O and 15.1, 14.8, and 5.6% N of stomach contents, and squid were found in 11.6, 14.3, and 14.5% O and 12.8, 9.6, and 10.0% N of stomachs. Within the smallest size category, however, squid (11.6% O, 12.8% N, 36.9% W, 63.0% IRI) were the most important single prey item in the diet (Table 3-2), followed by hake *Urophycis* spp. (4.3% O, 3.5% N, 15.7% W, 9.1%IRI), cusk eels *Lepophidium* spp. (4.3% O, 4.7% N, 10.5% W, 7.2% IRI), and seabasses (Serranidae) (4.3% O, 3.5% N, 5.5% W, 4.3% IRI). Atlantic croaker (15.7% O, 9.6% N, 17.0% W, 25.7% IRI) and squid (14.3% O, 9.6% N, 22.5% W, 27.9% IRI) were the most common prey items overall for sharks in size class B, followed by red goatfish (11.1% O, 7.0%N, 12.1%W, 12.9% IRI), longspine porgies (11.1% O, 7.0%N, 7.4% W, 9.7% IRI), and mantis shrimp *Lysosquilla* sp. (11.1% O, 6.1% N, 0.4% W, 4.4% IRI). Overall, croakers (Sciaenidae) and goatfishes (Mullidae) were the most common families represented in the diets of the intermediate size class of angel sharks. The diet of

the largest size class of sharks was dominated by butterfish (19.1% O, 14.4% N, 17.0% W, 28.9% IRI) and squid (17.0% O, 10.0% N, 39.4% W, 40.4% IRI), followed by Atlantic croaker (12.8% O, 8.9% N, 11.2% W, 12.3% IRI).

Squid were the most important prey item for angel sharks collected during winter months (13.5% O, 11.5% N, 31.9% W, 40.9% IRI), followed by Atlantic croaker (13.5% O, 10.7% N, 16.5% W, 25.7% IRI), and longspine porgies (9.5% O, 7.4% N, 5.1% W, 8.2% IRI) (Table 3-3). Angel sharks collected in spring months most frequently consumed butterfish (17.2% O, 12.4% N, 28.0% W, 47.3% IRI), followed by squid (10.3% O, 8.2% N, 16.3% W, 17.3% IRI), Atlantic croaker (8.6% O, 5.2% N, 10.6% W, 9.3% IRI), and red goatfish (8.6% O, 5.2% N, 9.9% W, 8.9% IRI). Butterfish were also the most common prey item in stomachs collected in the fall months (27.5% O, 10.7% N, 25.3% W, 43.6% IRI). Squid were also commonly consumed (17.6% O, 12.0% N, 30.5% W, 33.2% IRI), as were shortjaw lizardfish *Saurida normani* (9.8% O, 5.3% N, 11.6% W, 7.3% IRI).

### **Ontogenetic and Seasonal Diet Shifts**

Although teleosts were the most important component of the diets of all size categories of angel sharks (Table 3-2), ontogenetic shifts in diet were indicated by niche overlap estimates. Morisita's index of similarity indicated that shark size classes B (550–800 mm) and C (>800 mm TL) were the most similar ( $C=0.67$ ), while A (<550 mm) and C were the least similar ( $C=0.40$ ). Size classes A and B also had a high niche overlap value, with a Morisita's index of similarity of 0.60. Niche breadth narrowed with ontogeny, with Levin's standardized niche breadth values of 0.54, 0.57, and 0.44 for size classes A, B, and C, respectively.

Seasonal shifts in diet were also detected, with winter and fall diets overlapping the least according to Morisita's index (0.66), followed by spring and fall (0.83), and with winter and spring being the most similar (0.99). Levin's simplified niche breadth showed the narrowest niche for winter months (0.45), followed by spring, (0.57), and fall (0.61).

### **Prey Size**

Gape width of angel sharks was linearly related to their TL (Fig. 3-4). The maximum size of prey items consumed increased with increasing shark size, and the relationship was best described by a linear equation (Fig. 3-5a), though the relationship was weak ( $r^2=0.15$ ). Most prey items consumed (75.6%) were less than 30% of shark TL, and 95% of prey items were <40% of shark TL (Fig. 3-5b). The relationship between prey body depth and shark gape width was best described by a log-log regression and showed a stronger trend for utilization of larger prey items with increasing size than shark TL (Fig. 3-6a). Sharks consumed prey with a body depth < 60% of their gape width most frequently (70.37%, Fig. 3-6b), and 95% of prey items were <90% of shark gape. Compared by size category, the smallest sharks consumed the largest prey items (by prey body depth) in relation to their gape width, while angel sharks in the largest size category consumed the smallest (Fig. 3-7). Though the maximum sizes of prey items consumed generally increased with increasing shark size, sharks of all sizes consumed small prey items.

### **Discussion**

Teleost fishes were the most often encountered prey items in the stomachs of Atlantic angel sharks in this study, while squid and crustaceans were also frequently found. Squid (most likely *Loligo pealeii*) were the most frequently consumed individual

species, and Atlantic croaker were the most common teleosts in the diet overall, followed by longspine porgies and butterfish. The %IRI value for squid was very high (51.7%), however this number is likely inflated due to the absence of back calculated weight values for unidentified teleost and crustacean prey items. The importance of squid in the diet of Atlantic angel sharks should not be understated, however, as they were present in high numbers in the stomach contents of all size classes and seasons studied. The calculations of IRI and %IRI for prey categories were conducted with total %O and %N values, but only with %W values from identified prey items. This makes the %IRI a conservative estimate for teleost fishes, but is included because of its value in describing the importance of all prey categories in relation to one another and overall.

Levin's standardized niche breadth values between 0.44 and 0.54 indicate that Atlantic angel sharks of all sizes are neither specialists nor generalists, though their niche breadth narrows with ontogeny (0.54, 0.57, and 0.44, for size classes A to C, respectively). The low niche overlap values also indicate little potential for competition for resources among size classes. The largest sharks are the most specialized, which is not unexpected because larger animals are able to swim faster, have larger mouths, and have experience handling prey items (Juanes 1994). Scharf et al. (2000) found decreasing trophic-niche breadths with ontogeny in large predators (>500 mm), which was postulated to be due to greater behavioral and morphological capacities along with high prey encounter rates. The realm of available prey increases with predator size, therefore the largest animals are able to be more selective when choosing prey (Juanes 1994). Ontogenetic shifts seen among the shark size categories likely reflect these morphological and behavioral adaptations (Scharf et al. 2000, Gill 2003). In addition,

any ontogenetic shifts were not likely due to changes in habitat or season because sharks of all sizes were collected in the same locations and over the same months.

Atlantic angel sharks were only collected from October through May in the butterfish trawl fishery, even though fishermen continue to trawl for butterfish throughout the summer. It is therefore likely that angel sharks exhibit some sort of seasonal inshore-offshore migration as well. Seasonal shifts in diet were detected, with the diets of angel sharks collected in winter months being the most different from those collected in fall months. Angel sharks collected during the fall consumed crustaceans more frequently than during other seasons, while squid were consumed least frequently in the spring. Butterfish were consumed during all times of the year, but were much more common in spring and fall diets than winter. Conversely, Atlantic croakers were most important in the winter months, and less so in spring and fall months. Goatfishes were important prey items during winter and spring months, but were completely absent in the fall diets. It is unclear whether the seasonal shifts in diet reflect a change in benthic fish community or are the result of natural variation in the diet of angel sharks, though the broadening of niche breadth with season (winter through fall) could indicate a shift in prey base over the year. Year-round sampling of potential prey (see Chapter 2 methods) will be necessary to determine whether a shift in the prey-base occurs.

Angel sharks are dorso-ventrally flattened, and consume their prey whole by lunging up from the sea floor (Fouts and Nelson 1999). Their internal morphology is more similar to the rays than other sharks (e.g., requiem sharks), and they have a j-shaped stomach (Fig. 3-8) rather than the straight stomach that runs the length of the body cavity of the requiem sharks (pers. obs.). The result is an increase in stomach surface area in

relation to its compressed body cavity, but the bend in the stomach probably acts as a limitation to the lengths of prey that can be consumed. This constraint, along with the terminal mouth, likely makes body depth of prey items more important than TL in the size selection of prey. Indeed, some evidence suggests that for many piscivores the body depth of prey items is more important to the selection of prey than species (Einfalt and Wahl 1997, Gill 2003).

Angel sharks most frequently consumed fishes that had body depths less than 30% of TL and body depths less than 60% of their gape width (Figs. 3-5b, 3-6b), based on maximum prey sizes consumed. While the maximum length and body depth of fishes consumed increased with increasing angel shark length and gape (Figs. 3-5a, 3-6a), angel sharks of all sizes consumed relatively small prey items. This is not uncommon as Juanes (1994) described that most of the piscivores he studied selected smaller size ranges of prey items than predicted by optimal diet models. Scharf et al. (2000) showed significant increases in the maximum sizes of prey items as predator size increased for 18 species of marine fishes, although the majority (12 of 18) of the predators studied also increased the minimum sizes of prey items consumed as their size increased. Bethea et al. (2004) likewise reported that finetooth sharks *Carcharhinus isodon* and Atlantic sharpnose sharks *Rhizoprionodon terraenovae* fed mostly on relatively small prey in relation to the body size of the shark (<20% of body length), though larger prey were readily available in the study area.

The fact that angel sharks in the smallest size category selected the largest prey items by body depth in relation to their gape width likely has biological implications. Small fishes can direct much of their energy intake into somatic growth to grow out of



predation vulnerability and to reach reproductive size quickly (Helfman et al. 1997), and selection for larger prey items presumably maximizes their energy intake per feeding event (Gill 2003). Because of physical limitations, such as gape size and swimming speed, smaller predators are also exposed to fewer potential prey items than their larger counterparts (Juanes 1994, Sharf et al. 2000), and therefore it may be beneficial for them to attack larger prey items when they are encountered (Gill 2003). Though the larger sharks were exposed to the same prey, they continued to consume smaller prey items in relation to their body size. Smaller organisms are often more abundant than larger ones (Scharf et al. 2000), therefore the encounter rate with predators such as angel sharks is expectedly higher for smaller prey items.

Benthic community species composition is stochastic in nature, changing with season and diurnally with the daily migrations of many species of fishes, crustaceans, squids, and other invertebrates (Darnell 1990). Butterfish are known to be diurnal vertical migrators (Vecchione 1987), aggregating over the bottom during daylight hours and dispersing at night in surface waters. The high proportion of butterfish in the stomachs of the largest animals indicates that Atlantic angel sharks are not exclusively nocturnal feeders, which is similar to the behavior observed for Pacific angel sharks (Fouts and Nelson 1999). Other common teleosts in the diet of angel sharks were Atlantic croakers, red goatfish, and longspine porgies, all of which are common demersal fishes in the northern Gulf of Mexico (McEachran and Fechhelm 2005, Darnell 1990, McCormick 1995). There are some seasonal shifts in abundance of resident demersal fishes, but these changes reflect inshore-offshore migrations (Darnell 1990). Squid are also known diurnal vertical migrators, moving into the upper water column at night and

descending to the bottom during the day (NMFS 1999). The prevalence of squid in the diet of angel sharks therefore also suggests that angel sharks feed during the day. In contrast, the presence of cusk eels in the diet suggests that some night time feeding occurred as well because cusk eels are nocturnal, burrowing during the daylight hours (Darnell 1990, Retzer 1991).

Squid are easily digestible due to a lack of hard parts except the beak, though they do not provide the high energy content of some teleost fishes (Rosen and Trites 2000). The high rate of digestion of squid was apparent from stomach content analysis, as very few whole squid were encountered. Most of the squid beaks were found in the folds of the rugae or near the pyloric sphincter, so they were considered to be remnants of a previous feeding event. Crustaceans are likely readily available prey items to a demersal predator, but become less important in the diet of angel sharks with size. Crustaceans such as crabs and shrimps have relatively low lipid content, and the exoskeleton resists digestion (Jackson et al. 1987, Berens 2005), therefore they may become less desirable to larger sharks.

Net feeding by other shark species has been documented in sharks captured using gillnets (Bethea 2003). Gillnets are passive gear, but the presence of fish caught in the net likely attract sharks, which may become entangled as a result. The presence of a large number of completely undigested butterfish in the stomachs of angel sharks in the largest size class prompted the disuse of prey items with a digestion code of 0. On the whole, 16 butterfish in seven stomachs were excluded, while only two other undigested prey items in two stomachs were also excluded (one rough scad and one shortwing searobin *Prionotus stearnsi*). The inclusion of these data would cause butterfish to far

outweigh all other prey items in terms of dietary importance, and would narrow the niche breadth of size class C from 0.44 to 0.26. Most stomachs that contained butterfish that were coded 0 contained more than one butterfish in the same digestion state, a phenomenon that was rare in other stomachs. This occurrence, along with the observation of some angel sharks with several fish in their mouths, suggests that either net feeding was occurring or that fish were forced into the mouths of angel sharks in the trawl. Given the morphology of the mouth, the wide esophagus, and the fact that angel sharks are lie-and-wait predators, the latter explanation seems more feasible than the sharks feeding while in the trawl. While it is possible that these angel sharks fed upon the butterfish minutes before they were caught, it seems prudent to exclude them from the analysis of food habits.

Atlantic angel sharks consumed mostly benthic teleost fishes and squid, and crustaceans were important in the diet as well. Angel sharks showed an ontogenetic shift in diet, with teleost fishes becoming more prevalent in the diet with size. Additionally, niche breadth narrowed with ontogeny, meaning that the largest angel sharks were the most specialized. Seasonal shifts in diet were also detected, though it could not be determined if this was due to shifts in prey abundance/composition or was because of other variables. Angel sharks of all sizes consumed fairly small fish prey items, though sharks in the smallest size category (A) consumed the largest prey items in relation to their TL. Prey body depth in relation to shark gape width appeared to be a more important factor for prey size selection than the TL of the prey fish. Angel sharks are top predators in the benthic species communities of the Gulf of Mexico and although they are ambush predators they show a relatively high level of prey selectivity, both by prey group

and by size. Therefore changes in not only species composition, but the overall size characteristics of the community structure could have significant impacts on Atlantic angel sharks.

Table 3-1. Diet of the Atlantic angel shark by occurrence (O), percent occurrence (%O), number (N), percent number (%N), back-calculated weight (W), percent weight (%W), index of relative importance (IRI), and percent index of relative importance (%IRI). Weight was not back-calculated for crustaceans and unidentified fishes. N=191 non-empty stomachs, all sizes.

Prey identification	O	%O	N	%N	W	%W	IRI	%IRI
<b>Teleosts</b>	<b>145</b>	<b>81.0</b>	<b>224</b>	<b>77.0</b>	<b>7644.9</b>	<b>67.6</b>	<b>536.3</b>	<b>46.7<sup>a</sup></b>
Anguilliformes	7	3.9	7	2.4	98.0	0.9	12.8	1.1
Acropomatidae								
<i>Synagrops bellus</i>	1	0.6	1	0.3	8.1	0.1	0.2	<0.1
Bothidae								
<i>Syacium papillosum</i>	1	0.6	1	0.3	58.0	0.5	0.5	<0.1
Unid. flounder	3	1.7	3	1.0	114.5	1.0	3.4	0.3
Brotulidae								
<i>Brotula</i> sp.	1	0.6	1	0.3	85.0	0.8	0.6	0.1
Carangidae								
<i>Trachurus lathami</i>	3	1.7	3	1.0	137.5	1.2	3.8	0.3
Clupeidae								
<i>Etrumeus teres</i>	4	2.2	4	1.4	97.9	0.9	5.0	0.4
Lutjanidae								
<i>Rhomboplites aurorubens</i>	1	0.6	1	0.3	190.0	1.7	1.1	0.1
<i>Pristomoides aquilonaris</i>	6	3.4	6	2.1	312.6	2.8	16.2	1.4
Mullidae								
<i>Upeneus parvus</i>	2	1.1	4	1.4	278.6	2.5	4.3	0.4
<i>Mullus auratus</i>	8	4.5	9	3.1	596.5	5.3	37.4	3.3
Unid. Goatfish	2	1.1	2	0.7	98.9	0.9	1.7	0.2
Ophidiidae								
<i>Lepophidium</i> sp.	4	2.2	5	1.7	157.2	1.4	6.9	0.6
Percophidae								
<i>Bembrops anatrostris</i>	1	0.6	1	0.3	4.9	<0.1	0.2	<0.1
Phycidae								
<i>Urophycis</i> sp.	7	3.9	7	2.4	291.1	2.6	19.5	1.7
Polymixiidae								
<i>Polymixia</i> sp.	1	0.6	2	0.7	26.2	0.2	0.5	<0.1
Sciaenidae								
<i>Micropogonias undulatus</i>	18	10.1	21	7.2	1505.6	13.3	206.5	18.0
<i>Leiostomus xanthurus</i>	9	5.0	9	3.1	693.5	6.1	46.4	4.0
<i>Cynoscion</i> sp.	1	0.6	1	0.3	150.0	1.3	0.9	0.1
Scorpaenidae	3	1.7	3	1.0	54.4	0.5	2.5	0.2
Serranidae								
<i>Serranus atrobranchus</i>	1	0.6	1	0.3	25.0	0.2	0.3	<0.1
<i>Centropristis</i> sp.	6	3.4	6	2.1	216.8	1.9	13.3	1.2
Sparidae								
<i>Stenotomus caprinus</i>	12	6.7	14	4.8	481.0	4.3	60.8	5.3
<i>Lagodon rhomboides</i>	1	0.6	1	0.3	65.0	0.6	0.5	<0.1

Table 3-1. Continued

<b>Prey identification</b>	<b>O</b>	<b>%O</b>	<b>N</b>	<b>%N</b>	<b>W</b>	<b>%W</b>	<b>IRI</b>	<b>%IRI</b>
Stromateidae								
<i>Peprilus burti</i>	9	5.0	13	4.5	919.9	8.1	63.4	5.5
Synodontidae								
<i>Saurida normani</i>	5	2.8	6	2.1	573.3	5.1	19.9	1.7
Unid. lizardish	3	1.7	3	1.0	311.3	2.8	6.3	0.6
<i>Synodus</i> sp.	1	0.6	1	0.3	9.5	0.1	0.2	<0.1
Triglidae								
<i>Prionotus longispinosus</i>	1	0.6	1	0.3	62.8	0.6	0.5	<0.1
<i>Prionotus stearnsi</i>	1	0.6	1	0.3	21.6	0.2	0.3	<0.1
Unidentified teleosts	67	37.4	86	29.6				
<b>Cephalopods</b>	<b>25</b>	<b>14.0</b>	<b>31</b>	<b>10.7</b>	<b>3606.1</b>	<b>31.9</b>	<b>594.4</b>	<b>51.7</b>
<i>Loligo</i> sp.	25	14.0	31	10.7	3606.1	31.9	594.4	51.7
<b>Crustaceans</b>	<b>34</b>	<b>19.0</b>	<b>35</b>	<b>12.0</b>	<b>50.1</b>	<b>0.4</b>	<b>18.1</b>	<b>1.6<sup>a</sup></b>
<i>Portunus spinicarpus</i>	1	0.6	2	0.7	14.7	0.1	0.5	<0.1
<i>Sicyonia brevirostris</i>	1	0.6	1	0.3	5.8	0.1	0.2	<0.1
<i>Sicyonia</i> sp.	2	1.1	2	0.7	4.8	<0.1	0.8	0.1
Stomapoda	9	5.0	9	3.1	24.8	0.2	16.7	1.4
Unidentified crustaceans	21	11.7	21	7.2				
<b>Elasmobranchs</b>	<b>1</b>	<b>0.6</b>	<b>1</b>	<b>0.3</b>				
Elasmobranch remains	1	0.6	1	0.3				
Totals	179	100	291.0	100.0	11301.1	100.0	1142.2	100.0

<sup>a</sup>Does not include unidentified prey items

Table 3-2. Diet for Atlantic angle sharks in size classes A (TL<550 mm, N=69), B (550<TL<800 mm, N=67), and C (TL>800 mm, N=55), by %O, %N, %W, and %IRI.

Prey identification	Size Class A				Size Class B				Size Class C			
	%O	%N	%W	%IRI	%O	%N	%W	%IRI	%O	%N	%W	%IRI
<b>Teleosts</b>	<b>76.8</b>	<b>72.1</b>	<b>62.7</b>	<b>36.1<sup>a</sup></b>	<b>77.8</b>	<b>75.7</b>	<b>76.9</b>	<b>67.6<sup>a</sup></b>	<b>89.4</b>	<b>83.3</b>	<b>60.2</b>	<b>59.2<sup>a</sup></b>
Anguilliformes	4.3	3.5	0.5	1.9	1.6	0.9	0.2	0.1	6.4	3.3	1.5	1.5
Acropomatidae												
<i>Synagrops bellus</i>									2.1	1.1	0.1	0.1
Bothidae												
<i>Syacium papillosum</i>									2.1	1.1	1.1	0.2
Unid. flounder					4.8	2.6	2.4	1.5				
Brotulidae												
<i>Brotula sp.</i>					1.6	0.9	1.8	0.3				
Carangidae												
<i>Trachurus lathami</i>					3.2	1.7	2.4	0.8	2.1	1.1	0.4	0.2
Clupeidae												
<i>Etrumeus teres</i>	1.4	1.2	1.2	0.4					6.4	3.3	1.6	1.5
Lutjanidae												
<i>Rhomboplites aurorubens</i>									2.1	1.1	3.5	0.5
<i>Pristomoides aquilonaris</i>	2.9	2.3	9.8	3.8	3.2	1.7	0.9	0.5	4.3	2.2	3.0	1.1
Mullidae												
<i>Upeneus parvus</i>					3.2	3.5	6.0	1.8				
<i>Mullus auratus</i>					11.1	7.0	12.1	12.9	2.1	1.1	0.6	0.2
Unid. Goatfish					1.6	0.9	1.0	0.2	2.1	1.1	0.9	0.2
Ophidiidae												
<i>Lepophidium sp.</i>	4.3	4.7	10.5	7.2					2.1	1.1	0.7	0.2
Percophidae												
<i>Bembrops anatirostris</i>									2.1	1.1	0.1	0.1
Phycidae												
<i>Urophycis sp.</i>	4.3	3.5	15.7	9.1	4.8	2.6	2.1	1.4	2.1	1.1	0.3	0.1

Table 3-2. Continued

Prey identification	Size Class A				Size Class B				Size Class C			
	%O	%N	%W	%IRI	%O	%N	%W	%IRI	%O	%N	%W	%IRI
Polymixiidae												
<i>Polymixia sp.</i>	1.4	2.3	2.3	0.7								
Sciaenidae												
<i>Micropogonias undulatus</i>	2.9	2.3	9.1	3.6	15.9	9.6	17.0	25.7	12.8	8.9	11.2	12.3
<i>Leiostomus xanthurus</i>					9.5	5.2	10.4	9.1	6.4	3.3	3.8	2.2
<i>Cynoscion sp.</i>					1.6	0.9	3.2	0.4				
Scorpaenidae	4.3	3.5	4.9	4.0								
Serranidae												
<i>Serranus atrobranchus</i>	1.4	1.2	2.2	0.5								
Unid. seabass	4.3	3.5	5.5	4.3	4.8	2.6	3.3	1.7				
Sparidae												
<i>Stenotomus caprinus</i>					11.1	7.0	7.4	9.7	10.6	6.7	2.4	4.7
<i>Lagodon rhomboides</i>					1.6	0.9	1.4	0.2				
Stromateidae												
<i>Peprilus burti</i>									19.1	14.4	17.0	28.9
Synodontidae												
<i>Saurida normani</i>					3.2	1.7	3.3	1.0	6.4	4.4	7.8	3.7
Unid. lizardish	1.4	1.2	0.1	0.2					4.3	2.2	5.7	1.6
<i>Synodus sp.</i>	1.4	1.2	0.8	0.3								
Triglidae												
<i>Prionotus longispinosus</i>					1.6	0.9	1.3	0.2				
<i>Prionotus stearnsi</i>					1.6	0.9	0.5	0.1				
Unidentified teleosts	44.9	41.9			28.6	24.3			38.3	24.4		



Table 3-2. Continued.

Prey identification	Size Class A				Size Class B				Size Class C			
	%O	%N	%W	%IRI	%O	%N	%W	%IRI	%O	%N	%W	%IRI
<b>Cephalopods</b>	<b>11.6</b>	<b>12.8</b>	<b>36.9</b>	<b>63.0</b>	<b>14.3</b>	<b>9.6</b>	<b>22.5</b>	<b>27.9</b>	<b>17.0</b>	<b>10.0</b>	<b>39.4</b>	<b>40.4</b>
<i>Loligo sp.</i>	11.6	12.8	36.9	63.0	14.3	9.6	22.5	27.9	17.0	10.0	39.4	40.4
<b>Crustaceans</b>	<b>18.8</b>	<b>15.1</b>	<b>0.4</b>	<b>0.8<sup>a</sup></b>	<b>27.0</b>	<b>14.8</b>	<b>0.5</b>	<b>4.5<sup>a</sup></b>	<b>8.5</b>	<b>5.6</b>	<b>0.4</b>	<b>0.4<sup>a</sup></b>
<i>Portunus spinicarpus</i>									2.1	2.2	0.3	0.3
<i>Sicyonia brevirostris</i>									2.1	1.1	0.1	0.1
<i>Sicyonia sp.</i>					1.6	0.9	0.1	0.1	2.1	1.1		
<i>Lysosquilla sp.</i>	2.9	2.3	0.4	0.8	11.1	6.1	0.4	4.4				
Shrimp remains									2.1	1.1		
Unidentified crustaceans	15.9	12.8			14.3	7.8						
<b>Elasmobranchs</b>									2.1	1.1		
Elasmobranch remains									2.1	1.1		
Total Number (Percent)	69 (100)	86 (100)	1121 (100)	914 (100)	63 (100)	115 (100)	4681 (100)	1643 (100)	47 (100)	90 (100)	5417 (100)	2083 (100)

<sup>a</sup>Does not include unidentified prey items

Table 3-3. Diet of the Atlantic angel shark, divided by season. Winter=January and February (n= 74), Spring =March, April, and May (n= 58), and Fall= October, November, and December (n=51).

	Winter				Spring				Fall			
	%O	%N	%W	%IRI	%O	%N	%W	%IRI	%O	%N	%W	%IRI
<b>Teleosts</b>	<b>78.4</b>	<b>76.2</b>	<b>67.2</b>	<b>55.5<sup>a</sup></b>	<b>87.9</b>	<b>84.5</b>	<b>83.7</b>	<b>82.6<sup>a</sup></b>	<b>80.4</b>	<b>72.0</b>	<b>69.2</b>	<b>66.2<sup>a</sup></b>
Anguilliformes					5.2	3.1	0.4	1.2	7.8	5.3	2.0	2.5
Acromopidae												
<i>Synagrops bellus</i>					1.7	1.0	0.3	0.2				
Bothidae												
<i>Paralichthys</i> sp.	1.4	0.8	1.6	0.2	3.4	2.1	0.8	0.7				
Brotulidae												
<i>Brotula</i> sp.	1.4	0.8	1.5	0.2								
Carangidae												
<i>Trachurus lathami</i>	1.4	0.8	1.0	0.2	3.4	2.1	3.7	1.4	2.0	1.3	0.5	0.2
Clupeidae												
<i>Etrumeus teres</i>	2.7	1.6	1.3	0.6					3.9	2.7	0.6	0.6
Lutjanidae												
<i>Pristomoides aquilonaris</i>	1.4	0.8	1.5	0.2	1.7	1.0	4.2	0.6	5.9	4.0	6.1	2.6
<i>Rhomboplites aurorubens</i>									2.0	1.3	4.5	0.5
Mullidae												
<i>Upeneus parvus</i>	2.7	2.5	3.3	1.1	5.2	4.1	7.3	4.0				
<i>Mullus auratus</i>	5.4	4.1	5.1	3.5	8.6	5.2	9.9	8.9				
Goatfish	2.7	1.6	1.7	0.6								
Ophidiidae												
<i>Lepophidium</i> sp.	4.1	3.3	2.4	1.6					2.0	1.3	0.5	0.2
Percophidae												
<i>Bembrops anatirostris</i>									2.0	1.3	0.1	0.1
Phycidae												
<i>Urophycis</i> sp.	4.1	2.5	2.9	1.5	1.7	1.0	0.2	0.1	5.9	4.0	2.6	1.7

Table 3-3. Continued.

	Winter				Spring				Fall			
	%O	%N	%W	%IRI	%O	%N	%W	%IRI	%O	%N	%W	%IRI
Sciaenidae												
<i>Micropogonias undulatus</i>	13.5	10.7	16.5	25.7	8.6	5.2	10.6	9.3	7.8	5.3	7.5	4.5
<i>Leiostomus xanthurus</i>	8.1	4.9	8.6	7.7	3.4	2.1	4.4	1.5	2.0	1.3	1.6	0.3
<i>Cynoscion</i> sp.	1.4	0.8	1.9	0.3								
Scorpaenidae												
<i>Scorpaena agassizii</i>	1.4	0.8	0.8	0.2								
<i>Scorpaena</i> sp.	1.4	0.8	0.4	0.1								
Serranidae												
<i>Serranus atrobranchus</i>	1.4	0.8	0.4	0.1								
<i>Centropristus</i> sp.	4.1	2.5	2.4	1.4	3.4	2.1	2.1	1.0	2.0	1.3	0.4	0.1
Scorpaenidae												
<i>Scorpaena</i> sp.					1.7	1.0	1.1	0.3				
Sparidae												
<i>Stenomus caprinus</i>	9.5	7.4	5.1	8.2	6.9	4.1	7.7	5.6	5.9	2.7	3.1	1.5
<i>Lagodon rhomboides</i>					1.7	1.0	2.1	0.4				
Stromateidae												
<i>Peprilus burti</i>	2.7	1.6	2.8	0.8	17.2	12.4	28.0	47.3	27.5	10.7	25.3	43.6
Synodontidae												
<i>Saurida normani</i>	1.4	0.8	1.4	0.2	1.7	1.0	0.3	0.2	9.8	5.3	11.6	7.3
<i>Synodus</i> sp.	2.7	1.6	4.4	1.1					2.0	1.3	1.4	0.2
Triglidae												
<i>Prionotus stearnsi</i>					1.7	1.0	0.7	0.2				
<i>Prionotus longispinosus</i>									2.0	1.3	1.5	0.2
Unidentified teleosts	29.7	24.6			44.8	35.1			33.3	21.3		

Table 3-3. Continued.

	Winter				Spring				Fall			
	%O	%N	%W	%IRI	%O	%N	%W	%IRI	%O	%N	%W	%IRI
<b>Cephalopods</b>	<b>13.5</b>	<b>11.5</b>	<b>31.9</b>	<b>40.9</b>	<b>10.3</b>	<b>8.2</b>	<b>16.3</b>	<b>17.3</b>	<b>17.6</b>	<b>12.0</b>	<b>30.5</b>	<b>33.2</b>
Loliginidae												
<i>Loligo</i> sp.	13.5	11.5	31.9	40.9	10.3	8.2	16.3	17.3	17.6	12.0	30.5	33.2
<b>Crustaceans</b>	<b>17.6</b>	<b>11.5</b>	<b>0.9</b>	<b>3.5<sup>a</sup></b>	<b>12.1</b>	<b>7.2</b>	<b>&lt;0.1</b>	<b>0.1<sup>a</sup></b>	<b>23.5</b>	<b>16.0</b>	<b>0.3</b>	<b>0.6<sup>a</sup></b>
<i>Portunus spinicarpus</i>	1.4	1.6	0.3	0.2								
<i>Sicyonia brevirostris</i>									2.0	1.3	0.1	0.1
<i>Sicyonia</i> sp.	2.7	1.6	0.4	0.4								
<i>Lysosquilla</i> sp.	8.1	4.9	0.3	3.0	1.7	1.0	<0.1	0.1	3.9	2.7	0.1	0.5
Shrimp remains	4.1	2.5			6.9	4.1			5.9	4.0		
Crab remains					1.7	1.0						
Unidentified crustaceans	1.4	0.8			1.7	1.0			11.8	8.0		
<b>Elasmobranchs</b>	1.4	0.8										
	<b>1.4</b>	<b>0.8</b>										
Total number (Percent)	74 (100)	123 (100)	5743 (100)	1416 (100)	58 (100)	97 (100)	3080 (100)	1469 (100)	51 (100)	75 (100)	4270 (100)	2261 (100)

<sup>a</sup> Does not include unidentified prey items

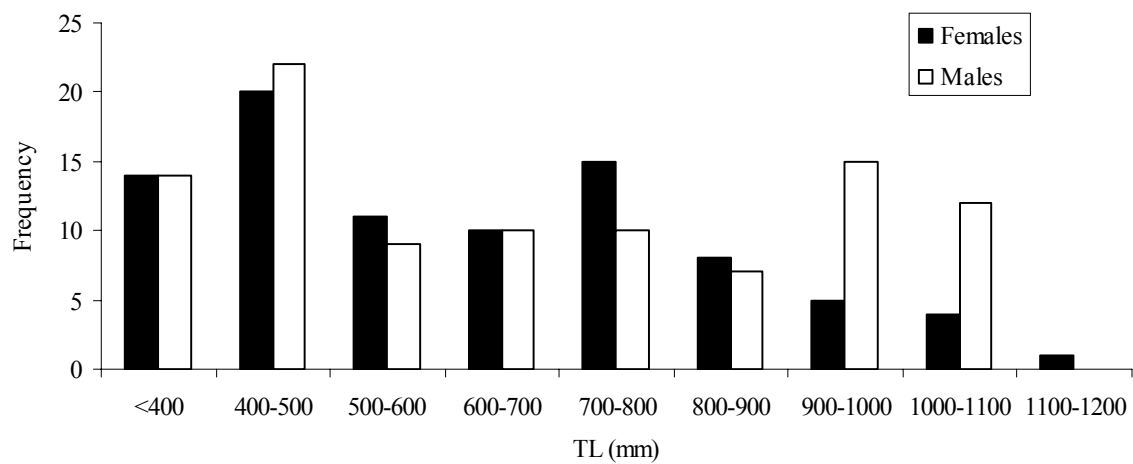
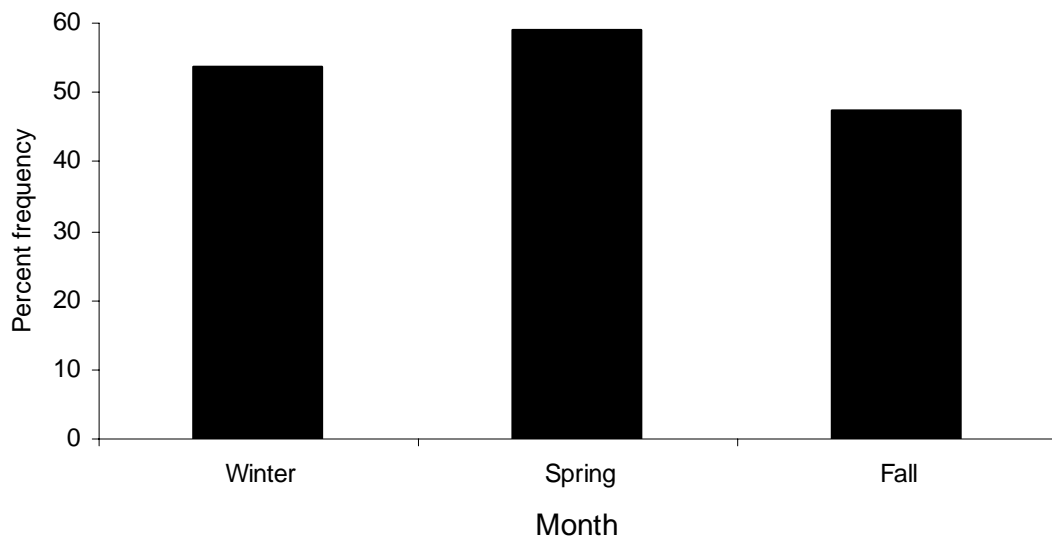


Figure 3-1. Size frequencies of Atlantic angel sharks with non-empty stomachs containing prey items coded >0 and <9.

A



B

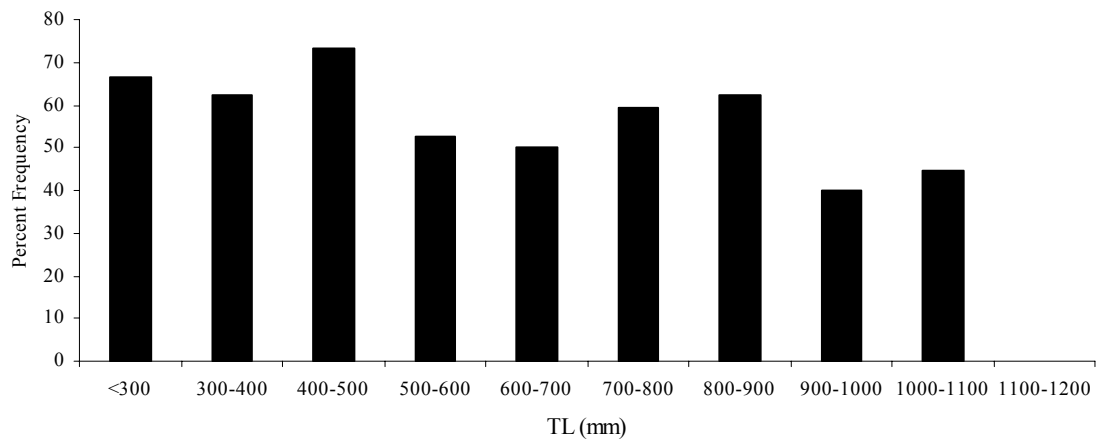
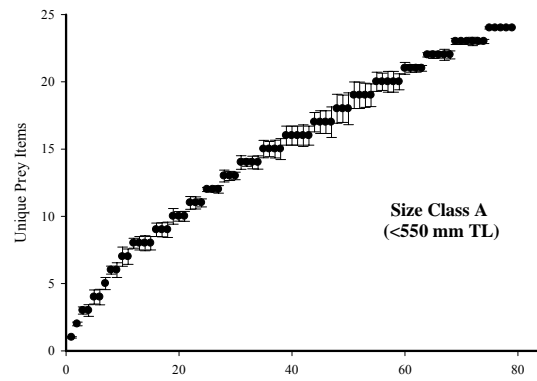
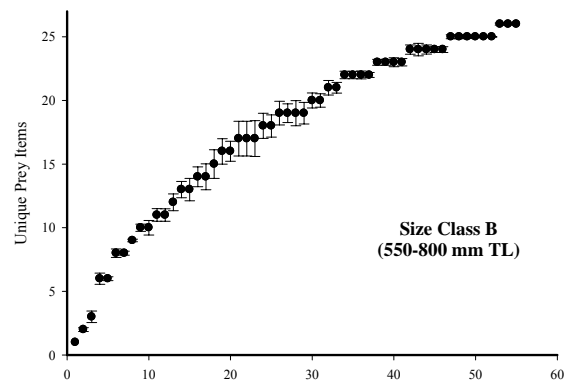


Figure 3-2. Percent frequency of Atlantic angel sharks with prey items coded 9 by A) season and B) size (TL, mm).

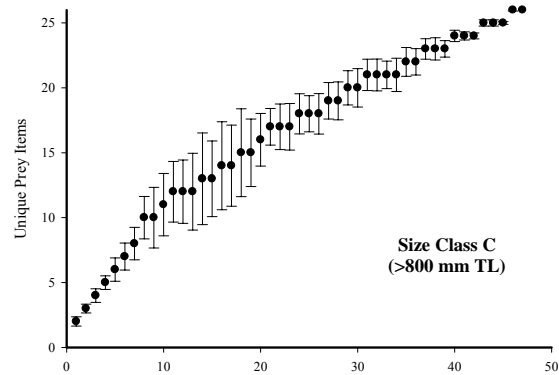
A



B



C



Number of Stomachs

Figure 3-3. Cumulative prey curves for Atlantic angel sharks in size classes A) A (<550 mm TL), B) B (550–800 mm TL), and C) C (>800 mm TL), showing that diet was well described for sharks  $\leq 800$  mm TL; with the diet of sharks >800 mm TL possibly not adequately sampled.

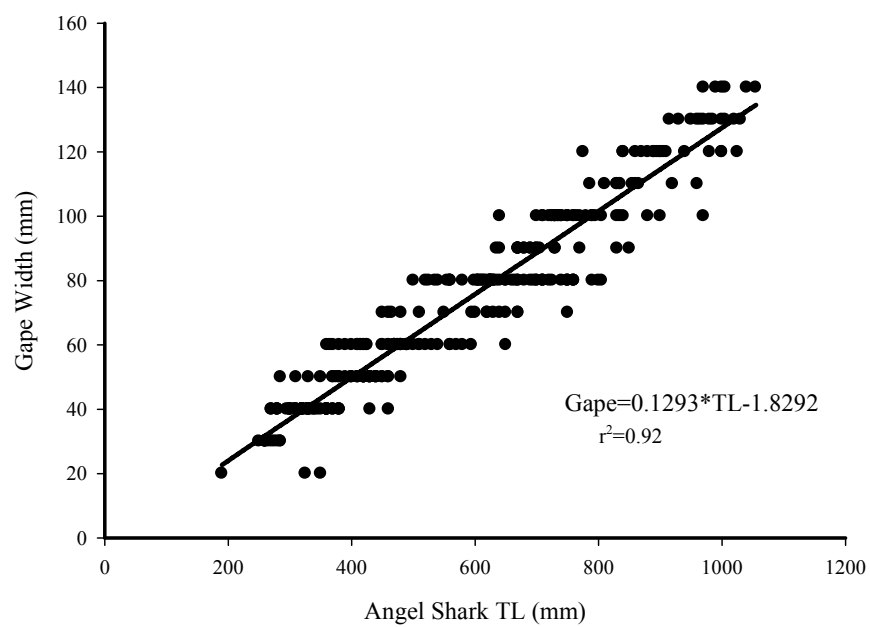
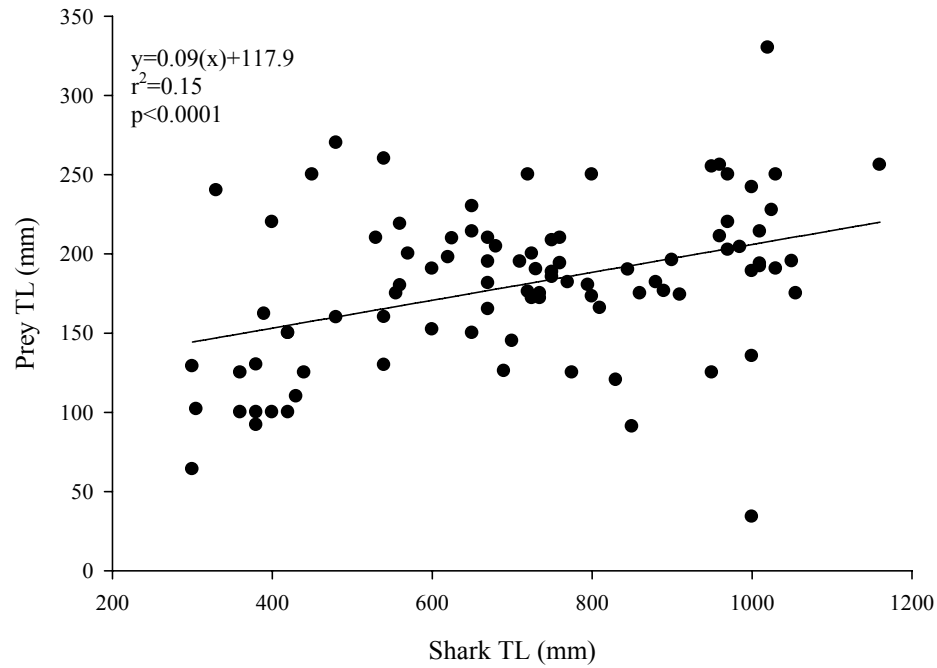


Figure 3-4. Gape width in relation to TL in Atlantic angel sharks.



A



B

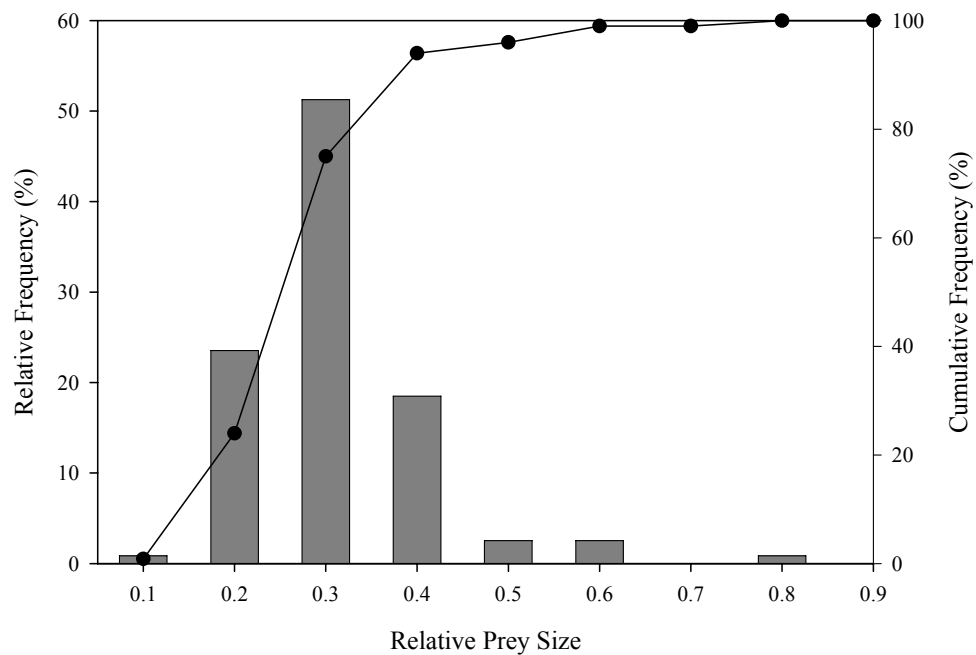
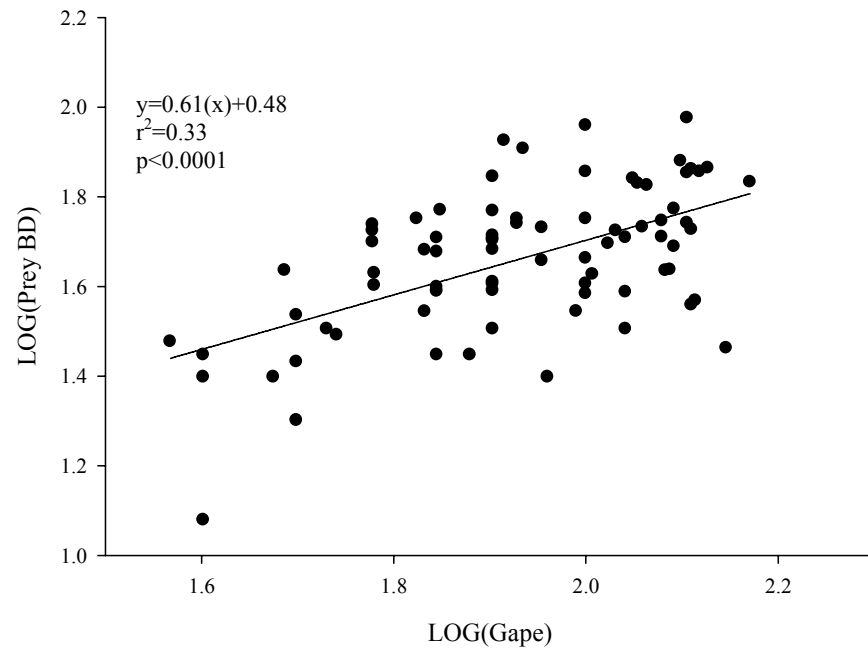


Figure 3-5. A) Largest prey item in each angel shark stomach, showing a general increase in maximum prey size with angel shark size; and B) relative and cumulative frequencies of relative prey size (prey TL/shark TL) in angel shark stomachs. Most prey items consumed were 0.3 the TL of the angel shark.

A



B

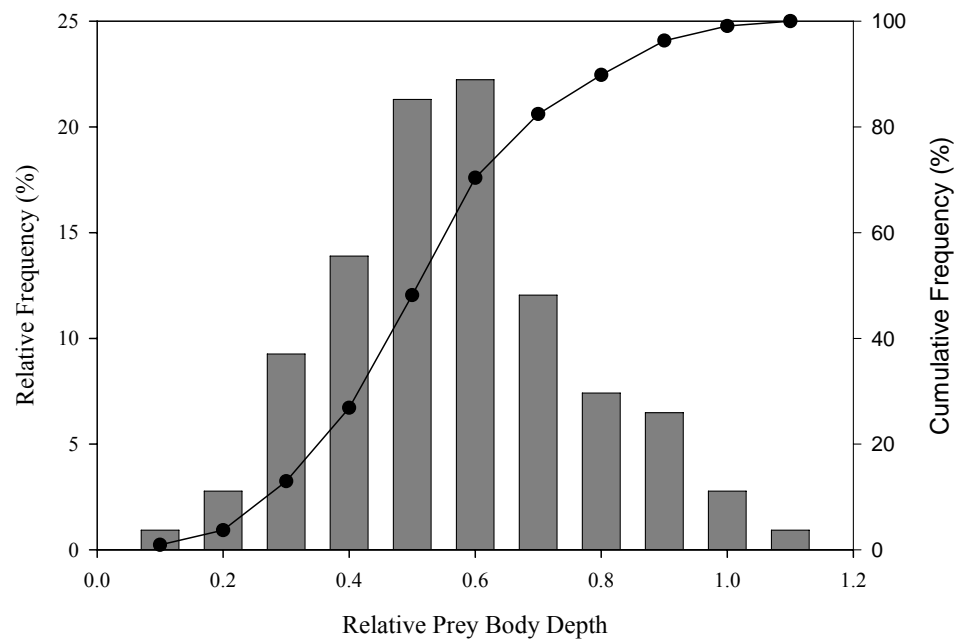


Figure 3-6. A) Prey body depth versus gape in the Atlantic angel shark; and B) relative and cumulative frequencies of relative body depth of prey items (prey body depth/angel shark gape). Prey that are 0.5–0.6 of the gape of angel sharks are the most commonly consumed.

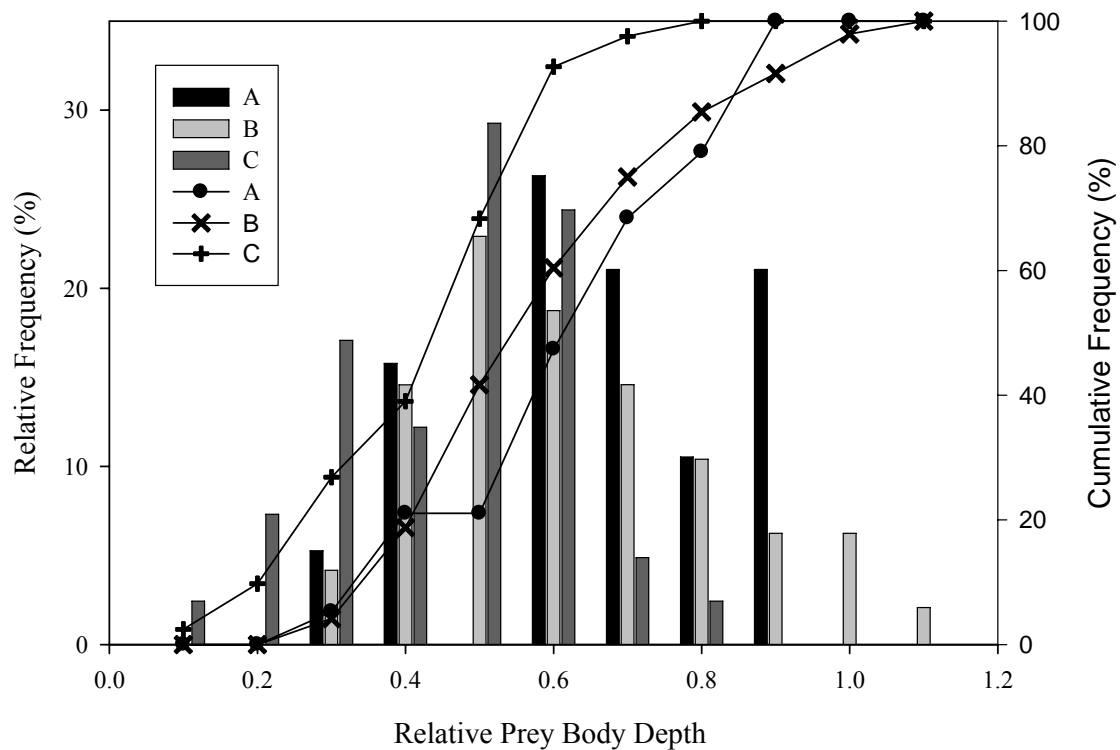


Figure 3-7. Relative and cumulative frequencies of relative body depth of prey items (prey body depth/angel shark gape) by shark size class (A <500, B 500–800, C >800 mm TL).

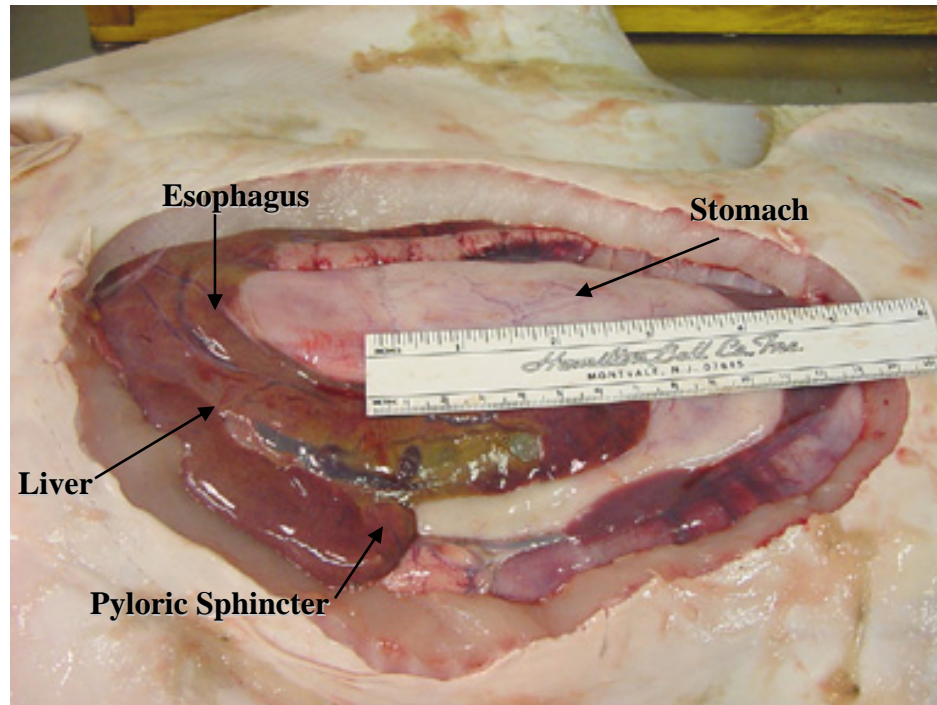


Figure 3-8. Ventral view of a dissection of an Atlantic angel shark, showing the shape of the stomach.

## CHAPTER 4 CONCLUSION

The diet of the Atlantic angel shark *Squatina dumeril* was comparable to that of the angular angel shark *S. guggenheim* from the coast of Uruguay and Argentina (Vogler et al. 2003). Angular angel shark diet included sciaenids, gadids, and triglids, though the angular angel shark appeared to consume a higher frequency of pelagic fishes, such as anchovies *Engraulis anchoita* and rough scad *Trachurus lathami*. While teleosts were the principal prey, squid and crustaceans were also consumed by the angular angel shark. Unlike the Atlantic angel shark, however, niche breadth broadened with ontogeny, with squid and crustaceans becoming more frequent in the diets of the largest sharks. Bridge et al. (1998) found that the ornate angel shark *S. turgocellata* fed primarily on arrow squid *Notodarus gouldi*, followed by fish, mostly leatherjackets. The prevalence of squid as an important prey item is common among benthic elasmobranchs, including the beaked skate *Dipturus chilensis* (Alonso et al. 2000, Lucifora et al. 2000), and deepwater fishes such as the Greenland halibut *Reinhardtius hippoglossoides* (Dawe et al. 1998). In fact, Bowering and Lily (1992) and Rodriguez-Marin et al. (1995) found that cephalopods became more prevalent in the diets of Greenland halibut with increasing depth. The beaked skate showed decreasing preference for squid with size, with the shift to teleosts occurring around the size of maturity (Alonso et al. 2000).

Gill (2003) reported that prey items that are 60% of the width of a piscivore's mouth provide the highest return for the lowest cost, and that they are the most preferred prey size. This held true in this study, with the average prey item's body depth at 60% of angel shark gape width. Gill (2003) also suggests that the relationship between prey size and gape might be a more important factor in prey selection than prey species. This proposal may be applicable in the case of Atlantic angel sharks, and could account for ontogenetic shifts in diet seen in this

study. For instance, the most important prey item for the largest size class of angel sharks was butterfish, but butterfish were markedly absent in the diet of either of the other size classes. All butterfish sampled by the fishery were very similar in size, with an average body depth of 74 mm, which corresponds to exactly 60% of the average gape width of Atlantic angel sharks in size class C. Butterfish were within the size range of available prey for size class B, though were generally above the 60% body depth to gape threshold.

Atlantic angel sharks are currently not a targeted species due to their protected status in the Gulf of Mexico and Atlantic Ocean (NMFS 1993), but they are commonly caught by trawlers on the continental slope of the Gulf of Mexico at depths greater than 100 m (GMFC 2002). Despite their relative prevalence, very little biological data exist for this species. A commercial fishery for the Pacific angel shark was established in California in the late 1970's, and the Pacific angel shark was the most common shark species caught for food in California for the years 1985–1986 (CDFG 2001). Concerns about declining numbers caused a nearshore area closure in 1991, inadvertently moving the fishery to Mexico, where it is unregulated (GDFG 2001). Due to heavy trawling activities, angel sharks (specifically *S. squatina*) are globally assessed as 'Critically Endangered', are considered extinct in the North Sea, and are considered extirpated from areas of the Mediterranean (IUCN 2006). The smoothback *S. oculata* and sawback *S. aculeata* angel sharks are also listed as 'Critically Endangered' in the Mediterranean and 'Endangered' globally (IUCN 2006). Given the decline of the red snapper *Lutjanus campechanus* fishery (GSFMC 2001) and the consistently over-fished commercial grouper stocks in the Gulf of Mexico (NMFS 2002), it is not unreasonable to think that Atlantic angel sharks may one day be a targeted species in the Gulf of Mexico. Shrimp trawls generally fish too shallow to have a major impact on the relatively deep water Atlantic angel shark, but large

boats with onboard freezer storage that are able to stay at sea for longer periods of time can travel to and fish the deeper waters with angel shark habitat (Vecchione 1987). In fact, the butterfish fishery was established in the 1980's as an alternative to shrimp trawling, as butterfish trawling requires very little equipment change from the standard shrimp trawl setup (Vecchione 1987).

Changes in prey abundance may have a less direct effect on Atlantic angel sharks than a targeted fishery, but could nonetheless impact the population. Because the Atlantic angel shark is a demersal predator, and therefore reliant on benthic prey species, changes in prey abundance could have negative effects on the population. The relatively narrow diet niche breadth ( $\sim 0.4$ ) indicated that angel sharks are not exclusively opportunistic predators and therefore could be susceptible to changes in their prey base. While the Gulf butterfish trawl fishery is currently small and unlikely to have a large impact on prey abundance, those potential prey species are susceptible to fishing mortality from other sources. Diamond et al. (2000) found that Atlantic croaker populations were in rapid decline in the Gulf of Mexico, largely due to mortality from shrimp trawl discards. While squid fisheries in the Gulf of Mexico are small and undeveloped, the *Loligo pealeii* fishery in the Northeastern United States has been fully utilized (NEFSC 1999) because of a diversification of fisheries in the region due to the decline of many finfish species (Hatfield et al. 2001). Likewise, many species of fishes recruit to the deeper waters of the continental shelf after spending part of their life histories inshore, also making them vulnerable to fishing mortality. Squid are generally short lived (less than one year) (Brodziak and Macy 1996), and recruitment is highly dependent on environmental variations (Hatfield et al. 2001), therefore any squid fisheries that might develop in the Gulf of Mexico would have the potential to impact a major prey item of Atlantic angel sharks. Many species of fishes that inhabit the

continental shelf make seasonal migrations inshore, making them vulnerable to mortality from the shallower shrimp trawls (Darnell 1990).

Current biological data are vital for the management of fish stocks. Whilst little is known about the life history and movement patterns of the Atlantic angel shark, their role as a top predator likely makes them a principal manipulator of the benthic environment of the Gulf of Mexico (Hambright 1994, Yodiz 1994, Juanes et al. 2001). Basic trophic data provide the foundation for ecosystem-based management, which takes a multi-species approach to fisheries management (Brodziak and Link 2002, FAO 2003, Browman and Stergiou 2004). This paper provides the first description of the trophic dynamics of the Atlantic angel shark, which is an important first step toward responsible management of this species.



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## BIOGRAPHICAL SKETCH

Ivy Elizabeth Baremore was born in the back seat of a Mercury Cougar on May 16, 1979 just outside of Dubach, Louisiana. From Louisiana she moved to Arkansas, then Oklahoma, and she graduated from high school in Hawaii in 1997. Ivy came back to the mainland to attend Florida State University in 1997, and she received her bachelor's degree in biological sciences in 2001. Upon graduating, she began working as a technician for the NOAA Fisheries Laboratory in Panama City, where she honed her scientific interests while gaining invaluable experience in field and laboratory biology and scientific writing and collaboration. She began her graduate career in 2004 in the Fisheries and Aquatic Sciences Department at the University of Florida, where she worked to complete her master's degree. Ivy is currently back at the NOAA Fisheries Panama City Laboratory, working as an observer coordinator for the shark gillnet fishery observer program. She hopes one day to work abroad in her field.