FEEDING HABITS OF THE TIGER SHARK, *GALEOCERDO CUVIER*, IN THE
NORTHWEST ATLANTIC OCEAN AND GULF OF MEXICO

by

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EXECUTIVE SUMMARY

Sharks are apex predators that structure marine communities through predation. Studies of diet and feeding patterns contribute to developing ecosystem models and it is critical that whenever possible, diet information specific to the area of concern is applied when developing an ecosystem model. Despite a number of studies conducted on tiger shark feeding, most comprehensive studies have been from the Pacific Ocean. There is little knowledge of the diet of tiger sharks in the Atlantic Ocean and Gulf of Mexico, with most studies in that area being localized and anecdotal. This study examines diet by life stage and tests for the presence of ontogenetic shifts, as well as how the diet of these sharks might be changing under certain environmental conditions and geographic variations.

This study reviews the information collected on tiger shark feeding to date. It summarizes the results from previous studies on tiger shark diet: what prey items were found in studies of Pacific tiger sharks, and results from the anecdotal studies in the Atlantic, most of which took place in the early to mid 1900s, included small sample sizes, and were conducted in localized regions.

For this study 169 sharks were caught as part of the U.S. shark bottom longline fishery and by the National Marine Fisheries Service Apex Predators scientific survey. Sharks were caught from North Carolina to Southern Florida and throughout the Gulf of Mexico and were divided, based on fork length, amongst three life-stage groups: young-of-the-year (YOY), juvenile, and adult. To quantify diet, index of relative importance was computed. Prey items were classified to the lowest taxon possible and sorted into 15 categories: aves, cephalopods, cnidarians, arthropods, elasmobranchs, bryozoan, mammals, molluscs, plants, reptiles, teleosts, porifera, other (rocks, trash), unknown, and free-living nematodes that were not tiger shark parasites. Overall, teleosts were the most significant prey category, followed by molluscs and birds. For YOY sharks, molluscs were the dominant category, followed by teleosts and birds. Juveniles primarily fed on teleosts, followed by molluscs and birds. Adults primarily consumed teleosts followed by reptiles and cephalopods. Cumulative prey curves were created for overall tiger sharks and each life stage to examine if sample size was large enough to describe the diet. Cumulative prey curves showed that the number of overall stomachs examined was enough to define the diet in the northwest Atlantic and Gulf of Mexico. However, although individual life stage curves approached asymptote, they did not fully reach one, indicating sample size was not necessarily sufficient for each individual life stage.

Diet by life stage and region was also looked at using the Simplified Morisita-Horn Coefficient, as well as prey diversity using Simpson's Index. Dietary overlap was significant between all life stages except for YOY and adult. Prey diversity increased as sharks transitioned from one life stage to another. Effects of environmental factors (sea surface temperature, primary productivity, depth, and salinity) on diet were evaluated using the Marine Geospatial Ecology Tool and unequal variance t-tests. Dietary overlap between the Gulf of Mexico and the Atlantic was biologically relevant with similar prey diversity. Environmental results indicated that depth was an important factor in prey type for the categories of molluscs, reptiles, and teleosts.

This study is the first comprehensive study of tiger shark diet in the northwest Atlantic and Gulf of Mexico. The tiger sharks analyzed consumed prey from a diverse number of prey categories, which was also found in the studies from the Pacific and Atlantic anecdotal studies. An ontogenetic shift in diet was discovered with YOY sharks primarily feeding on mostly gastropods and some teleosts, juveniles feeding mostly on teleosts and some gastropods, and adults feeding on teleosts and

reptiles. Tiger sharks from the Pacific also showed ontogenetic shifts. This could be attributed to a limitation on the ability of smaller sharks to catch or ingest certain prey items. Past studies in the Pacific also found prey diversity increasing with size. This was true for this study as well. An increase in prey diversity could suggest that although larger sharks might be eating larger prey, they might also be eating a wider variety of smaller prey items, increasing the overall diversity of their diet, not just the diversity in prey size.

The overwhelming presence of gastropod foot (and not the shell) was something that was not found in previous studies from the Pacific Ocean. Benthic foraging has been observed before in tiger sharks but this is the first time sharks appear to be selective for a certain part of the body. This could be an interesting example of diet specialization to increase foraging success. A comparison of other northwest Atlantic coastal species of sharks is included to show that tiger sharks appear to have the most varied diet for larger wide-ranging sharks in the northwest Atlantic. Possible restrictions to the study are discussed as well. Sharks play a part in shaping marine communities through what they eat. Understanding trophic interactions, species interactions with the environment, and the ecological effects of fishing is necessary to inform decision support tools for ecosystem-based management approaches. Ecosystem models have become essential tools for evaluating species interactions. Our study will provide valuable information for any future study examining food-web responses to the removal of potential keystone predators in the northwest Atlantic Ocean and Gulf of Mexico.

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INTRODUCTION

Tiger sharks, *Galeocerdo cuvier*, inhabit temperate and tropical oceans throughout the world, where they live in both shallow coastal waters and the open ocean (Ebert et al. 2013). In the northwest Atlantic, tiger sharks are typically found from New England to the Florida Keys, and throughout the Gulf of Mexico (Lea et al. 2015). Both sexes are thought to mature at about 250 cm fork length (Branstetter et al. 1987) and to reach sizes larger than 450 cm (Castro 2010). The International Union for the Conservation of Nature (IUCN) Red List of Threatened Species currently classifies tiger sharks as “Near Threatened” throughout their range (Simpfendorfer 2009).

Tiger sharks are considered opportunistic foragers, feeding on an extensive range of taxa including teleosts, sea turtles, cephalopods, gastropods, crabs, and marine birds, as well as trash. Tiger sharks also exhibit ontogenetic shifts in their diet. Rancurel & Intes (1982) observed small tiger sharks in New Caledonia feeding more on reef fish, while larger tiger sharks consumed turtles, birds, and squid. Simpfendorfer (1992) determined that smaller tiger sharks in Australia fed predominantly on teleosts and sea snakes while bigger sharks fed on birds, elasmobranchs, and turtles. Lowe et al. (1996) found that teleost and cephalopod prey items decreased in their frequency as sharks got larger and were replaced by elasmobranchs, crustaceans, turtles, and marine mammals.

Despite a number of studies conducted on tiger shark feeding, most comprehensive studies have been from the Pacific Ocean. There is little knowledge of the diet of tiger sharks in the Atlantic and Gulf of Mexico, with most information coming from descriptive studies conducted in localized regions. Nichols and Murphy (1916) noted that stomachs included whelks, conch, squid, and fish in tiger sharks caught off of Long Island, New York. Coles (1919) and Bell & Nichols (1921) found that tiger sharks caught off of North Carolina ate crabs, birds, other sharks, turtles and porpoises and Gudger (1949) found marine birds, turtles, trash, livestock, fish, conch opercula, horseshoe crabs, and worm tubes in 6 tiger sharks collected in the Florida Keys. Clark and von Schmidt (1965) noted prey items of sharks, birds, turtles, tunicates,

octopuses, crabs, molluscs, jellyfish, and trash in tiger shark stomachs from the Central Gulf Coast of Florida.

Studying the foraging patterns of top level predators is important for informing our understanding of their role in the environment. Apex predators, such as tiger sharks, influence ecosystem organization and function through feeding and trophic cascades (Estes et al. 1998). As findings about diet and feeding patterns contribute to developing ecosystem models used in management, it is critical that whenever possible, diet information specific to the area of concern is applied when developing the ecosystem model. Accordingly, I quantitatively define the diet of tiger sharks in the northwest Atlantic Ocean and the Gulf of Mexico. I examine diet by life stage and test for the presence of ontogenetic shifts, as well as how the diet of these sharks might be changing under certain environmental conditions and geographic variations.

METHODS

Tiger shark stomachs were collected by on-board scientific observers in the shark bottom longline fishery (Enzenauer et al. 2016) and the National Marine Fisheries Service (NMFS) Apex Predators Program's scientific survey. Observers collect fishery and environmental information for each haul of the gear. The shark bottom longline fishery operates in the northwest Atlantic Ocean from North Carolina to Florida and throughout the Gulf of Mexico. Bottom longlines in this fishery consist of 1-20 kilometers of mainline with weights placed throughout and up to 500 hooks. Bait can vary from elasmobranchs to mixed teleost species. Sex and fork length (cm) were noted for each landed shark. Stomachs were taken out of the body and frozen before transport to the laboratory.

Sharks collected by the Apex Predators Program were captured on research surveys from North Carolina to Florida. Standard sampling gear was a 300 hooks/set longline with spiny dogfish used as bait. Sharks captured were sexed and measured (precaudal length, fork length and total length). Sharks in good condition were tagged and released. Sharks that died on the longline had their stomachs removed and frozen prior to returning to the laboratory. Some sharks

(n=71) had their stomachs everted prior to being tagged and released. Contents were immediately frozen prior to transport to the laboratory.

Stomachs were thawed, cut open, and washed with water over a 595 μm sieve. Stomach contents were classified to the lowest identifiable taxon, counted, length was measured (closest cm), and the weight was taken (wet weight, closest 0.001 g). Level of digestion was ranked for each prey item with 1 designated as fresh prey and 5 as almost completely digested. To avoid bias associated with sharks caught on baited longlines, we excluded any item found that potentially was used as bait on the longline. For sharks captured within the bottom longline fishery, the bait used on the specific set recorded by the observer was compared to items found in the stomach. If any item matched and appeared to be fresh, it was excluded from the analysis. Similarly, any spiny dogfish part that appeared to be fresh was removed if the shark was captured as part of the Apex Predators Program survey. Diets were assessed by life stage following Kneebone et al. (2008): young-of-the-year (YOY), age 0, (≤ 100 cm fork length (FL)), juvenile (101-250 cm FL) and adult (≥ 251 cm FL). If only total length (TL) information was available, TL was transformed to FL using the equation $FL = (0.8761)TL - 13.3535$ (Kneebone et al. 2008).

Diet was analyzed using percent by number (%N), percent by weight (%W), and percent frequency occurrence (%O). Completely digested items were not included in the analysis. Plants, trash, and rocks were all included in the analysis. Nematodes that were free-living and not tiger shark parasites were included and placed in their own category when the prey item they originated from could not be identified. Fish lenses were counted in pairs and if there was an odd number, the additional lens was counted as an additional fish. The index of relative importance (IRI) was calculated as $IRI = \%O(\%N + \%W)$ (Pinkas 1971, Hyslop 1980). The IRI for individual items was then divided by the overall IRI for total items found in stomachs to find the IRI as a percent (Mearns et al. 1981, Cortés 1997).

Items identified were sorted into major taxonomic categories: aves, cephalopods, cnidarians, arthropods, elasmobranchs, bryozoan, mammals, molluscs, plants, reptiles, teleosts, porifera, other (rocks and trash), and unknown. Free-living nematodes that couldn't be connected

with a prey item were placed in their own category. It is imperative to note that this category is not meant to be a major diet category as the nematodes were most likely consumed as part of other prey items, not intentionally. Percent IRI was calculated for all fifteen diet categories.

Randomized cumulative prey curves were created by graphing cumulative number of prey types versus the number of stomachs analyzed. Curves were created with Primer v6+ PERMANOVA (PRIMER-E, Auckland, New Zealand) to conclude if the sample size of stomachs was adequate to accurately define the diet (Ferry & Cailliet 1996, Cortés 1997). If a cumulative prey curve asymptotes, the number of stomachs in the sample size is considered to be adequate in drawing conclusions about dietary habits. To figure out if the cumulative prey curve made it to an asymptote, the slope of the line produced from the endpoints of the curve is compared to a zero slope line. Endpoints were the mean cumulative number of prey types produced for the last five stomachs. A linear regression was then performed using the endpoints to see if the best-fit line slope was significantly dissimilar from zero slope line. Slopes were not significantly unlike if $p > 0.05$, meaning the curve made it to an asymptote (Bizzarro et al. 2007).

Dietary overlap by life stage and area was determined using the Simplified Morisita-Horn Coefficient (C_{MH}) (Morisita 1959) using the Ecological Methodology software v7.2 (Exeter Software, Setauket, New York). The amount of overlap is measured from 0 to 1, with zero indicating no overlap, values above 0.6 designating a biologically relevant overlap, and a value of one signifying complete overlap in communities. Prey diversities were compared using Simpson's Index (1-D) (Ecological Methodology software v7.2). Typical values are between 0 and 1 with 1 indicating maximum diversity for Simpson's Index (Krebs 1989).

The effects of environmental factors on diet were also evaluated. Environmental factors included sea surface temperature, primary productivity, depth, and salinity. Information on environmental factors was extracted using the Marine Geospatial Ecology Tool (MGET) for ArcGIS 10.3 (Esri, Redlands, California) to fill in missing shark environmental data (Roberts et al. 2010). Sea surface temperature information was gathered from NASA JPL PO.DAAC, primary productivity was collected from NASA GSFC OceanColor Group, depth was collected from the University of Maine ROMS-CoSiNE, and salinity was collected from HYCOM+ NCODA Global 1/12 ° Analysis. Only recently consumed prey (i.e. 1 or 2 on the digestion scale)

was utilized in the analysis in order to ensure the prey was consumed in similar environmental conditions to where the shark was caught. Nematodes, trash, and rocks were omitted from the analysis. Sixteen unequal variance t-tests were performed using PAST software v3.14 (Hammer&Harper, Oslo, Norway) to assess the relationship amongst the four environmental factors and the four most commonly consumed prey items overall (birds, molluscs, reptiles, and teleosts). Average means for the four environmental factors for sharks with freshly digested prey from one of each of the four main prey categories (e.g. birds) were independently compared with sharks that had recently eaten, but had not consumed any items from the same prey category (e.g. birds). This was then done for the other three remaining prey categories. A difference in average means would indicate a possible difference in depth, salinity, primary productivity, or sea surface temperature between where, for example, fresh bird prey was consumed and where it was not consumed.

RESULTS

A total of 169 tiger sharks were collected from October 2000-July 2016. Sharks were captured from southeast Louisiana to southeast of the Albemarle Sound, North Carolina (Fig. 1). Of those, 53 were YOY sharks, 111 juveniles, and 5 adults. The range of shark sizes for this study is showed in Figure 2. Average size of all sharks analyzed was 135 cm FL. Of the stomachs analyzed, 71 stomach samples were collected through eversion, while the remaining samples were the whole stomach.

The cumulative prey curve for combined age classes did make it to an asymptote, indicating the amount of stomachs examined was enough to define the overall diet ($p=0.182$). By life stage, YOY and juvenile curves approached an asymptote, but were significant from zero ($p=0.00006$ and $p=0.0006$, respectively). The cumulative prey curve for adults also did not asymptote ($p=0.002$) (Fig. 3).

Overall, teleosts were the most important out of the fifteen diet categories (73.81 %IRI), with the orders Perciformes (4.27 %IRI) and Tetraodontiformes (2.95 %IRI) being the most consumed identifiable types of teleosts. The next most dominant diet category was molluscs

(13.33 %IRI), with gastropoda being the most consumed (10.99 %IRI). Birds were the third most consumed category (4.81 %IRI), followed by reptiles (1.85 %IRI), elasmobranchs (1.68 %IRI), and arthropods (1.59 %IRI), and remaining categories (<1.0 %IRI) (Fig. 4d). Seven stomachs were empty. Figure 5 shows while teleosts were the dominant category, birds had a high percent occurrence, molluscs had both high percent number and percent occurrence, and arthropods had high occurrence even though they did not have a high %IRI overall.

For YOY sharks, molluscs were the dominant diet category (45.79 %IRI), particularly gastropoda foot and operculum being the most consumed type of mollusc (43.85 %IRI). Teleosts were the second most consumed category (44.38 %IRI), with the orders of Tetraodontiformes (2.99 %IRI) and Scorpaeniformes (2.72 %IRI) being the most consumed identifiable types of teleosts. The third most dominant prey category was birds (6.27 %IRI), followed by arthropods (3.01%IRI) (Fig. 4a). Remaining major diet categories were less than 1.0 %IRI (Table 1).

Juveniles primarily fed on teleosts (76.56 %IRI) with the orders Tetraodontiformes (3.38 %IRI) and Perciformes (3.24 %IRI) being the most consumed identifiable teleosts. The second most important diet category was molluscs (7.14 %IRI), particularly gastropoda (4.99 %IRI), and the next most dominant category was birds (6.04 %IRI), followed by elasmobranchs (2.2 %IRI), reptiles (2.08 %IRI), and arthropods (1.19 %IRI) (Fig. 4b). Remaining major diet categories were less than 1.0 %IRI (Table 2).

Adults consumed primarily teleosts (66.96 %IRI), with the order Perciformes being the only order of teleosts that could be identified (26.12 %IRI). The second most consumed diet category was reptiles (10.41 %IRI), with green sea turtles (*Chelonia mydas*) being the most consumed type of reptile (5.91 %IRI). Reptiles were followed by cephalopods (9.82 %IRI), mainly the order Teuthida (3.27 %IRI), molluscs (4.12 %IRI) (all gastropoda), elasmobranchs (1.96 %IRI), and birds (1.66 %IRI) (Fig 4c). The remaining major diet categories were less than 1.0 %IRI (Table 3).

Dietary overlap using the Morisita-Horn Coefficient (C_{MH}) revealed significant overlap between YOY and juvenile life stages ($C_{MH}=0.717$). The overlap between adult and YOY was

0.458, which was not biologically relevant, and the overlap between adult and juvenile was 0.768, the highest overlap amongst life stages. Prey diversity using Simpson's Index (1-D) also varied among the three life stages of sharks. YOY diversity was 0.629, juvenile sharks were 0.782, and adults had a value of 0.812, indicating that prey diversity increased as sharks transitioned from one life stage to another. The overall Simpson's Index value was 0.775

Dietary overlap between the Gulf of Mexico and Atlantic was 0.756, a biologically relevant overlap. Prey diversity was similar for both regions, with a Simpson's Index (1-D) value of 0.764 for the Atlantic and a value of 0.714 for the Gulf of Mexico. There were a total of 24 sharks captured in the Gulf of Mexico and 145 in the Atlantic. A total of 417 prey items (9 prey items for YOY sharks, 401 prey items for juvenile sharks, and 7 prey items for adult sharks) were found in the stomachs of Gulf of Mexico sharks, and a total of 1,185 prey items (474 prey items for YOY sharks, 675 prey items for juvenile sharks, and 36 prey items for adult sharks) were discovered in the stomachs of Atlantic sharks.

A regression using SPSS software (IBM, Armonk, New York) indicated a significant positive correlation ($n=436$, $p=.004$) between prey size (intact items that were measured during stomach dissection) and shark size (FL) in this study.

Unequal variance t-tests on sharks that had recently consumed prey ($n=60$) showed that depth was a significant factor in prey type. Of the 16 t-tests performed, three were significant: molluscs and depth ($p=0.001$, $t=3.40$, average depth of sharks who had recently consumed molluscs=25 m, avg. depth of sharks who had recently eaten but had not consumed any molluscs=48 m), reptiles and depth ($p=0.039$, $t=2.12$, avg. depth of sharks who had recently consumed reptiles=31 m, avg. depth of sharks who had recently eaten but had not consumed any reptiles=46 m), and teleosts and depth ($p=0.05$, $t=-2.01$, avg. depth of shark who had recently consumed teleosts=53 m, avg. depth of sharks who had recently eaten but had not consumed any teleosts=34 m). All other relationships between the four environmental factors (sea surface temperature, primary productivity, depth, and salinity) and the four major prey items (birds, molluscs, reptiles, and teleosts) were not significant.

DISCUSSION

This study is the first comprehensive study of tiger shark diet in the northwest Atlantic and the first to examine ontogenetic shifts, geographic variation on a large scale, and the possible effects of environmental conditions on diet. Tiger sharks from North Carolina to the Gulf of Mexico consumed prey from a diverse number of prey groups. This is similar to previous research in the Pacific (Rancurel & Intes 1982, Simpfendorfer 1992, Lowe et al. 1996, Simpfendorfer et al. 2001), and anecdotal studies from the Atlantic (Nichols and Murphy 1916, Coles 1919, Bell and Nichols 1921, Gudger 1949, Clark and von Schmidt 1965). In general, prey diversity and ontogenetic shifts in the northwest Atlantic and Gulf of Mexico were similar with those of studies in the Pacific Ocean, but predominant prey categories were different, especially the presence of certain species groups. Implications using diet data that differs spatially for developing ecosystem models may overvalue the predation effects on prey if diet is assumed to be similar across ocean basins. In this situation, overfishing tiger sharks could result in incorrect assumptions on predation release of certain species.

One important restriction to all diet studies is that prey items that are easily and quickly digested might have been under-represented and items that are digested slowly would be overrepresented. Each item was classified to the lowest taxon possible, but there were some items that were too digested to put into a specific category and were placed in the “unknown” category. There were instances where sharks had not eaten in several days, and there were some remnants of prey items e.g. fish eye lenses, but anything that is quickly digested would not have been detected at all. Another source of potential error is that some of the tiger sharks could have been attracted to baited longlines and captured only because they did not have full stomachs. There are also documented regurgitation events in tiger sharks (Heithaus 2001, Simpfendorfer et al. 2001, Gallagher et al. 2011), and the possibility exists that a shark could have regurgitated some or all of its food while on the longline.

Tiger sharks in this study showed an ontogenetic shift in prey size and diet from young-of-the-year, juvenile, to adult stages. Rancurel & Intes (1982), Simpfendorfer (1992), Lowe et al. (1996), and Simpfendorfer et al. (2001) also found an analogous ontogenetic shift in tiger

sharks from the Pacific, with prey size increasing with shark size. Ontogenetic shifts could be attributed to a limitation in the ability of smaller sharks to catch or ingest certain prey items (Lowe et al. 1996). As maximum swim speed increases with body size for sharks (Carlson et al. 2004), smaller sharks may be limited in the types of prey they can capture. This may be reflected in the high number of slower moving prey such as gastropods in the diet of YOY tiger sharks. In older age classes, more mobile taxa (teleosts, cephalopods and reptiles) became more important prey items. Likewise, smaller sharks may be limited by the ability to ingest certain prey items as gape size decreases with body size (e.g. Bethea et al. 2004).

Dietary overlap was biologically significant for all life stages except for YOY and adult. This is not surprising given the differences in size and ecological role between these two age classes. Whereas, intermediate sized sharks likely have more overlap in ecology with both size classes. This suggests that the transition in feeding preference with size in tiger sharks occurs gradually and does not occur through a rapid ontogenetic shift. Geographic overlap was also biologically significant between the northwest Atlantic and Gulf of Mexico, suggesting tiger sharks play a similar ecological role in both these regions. Tiger sharks are also highly migratory and move between the Atlantic Ocean and Gulf of Mexico (Kohler et al 1998; Hammerschlag et al. 2012).

Prey diversity increased as tiger shark size increased. An increase in prey diversity could suggest that although larger sharks might be eating larger prey, they might also be eating a wider variety of smaller prey items, increasing the overall diversity of their diet, not just the diversity in prey size (Lowe et al. 1996). This could again potentially be due to increased swim speed and/or hunting ability in larger sharks allowing for the capture of fast moving or elusive prey items. Although it is challenging to draw strong conclusions about the diet diversity of adult tiger sharks due to small sample size, this size class did have the highest diversity in diet, reflecting a lower limitation in either ability to capture and/or ingest a larger diversity of prey items.

We found a significant relationship between depth and three major prey categories: molluscs, reptiles, and teleosts. Results showed that at shallower depths, tiger sharks were doing more benthic feeding on molluscs, and more pelagic feeding on teleosts and reptiles at deeper

depths. Since YOY sharks consumed more molluscs and adult sharks consumed more teleosts and reptiles, this suggests that adult sharks spent more time away from shore feeding, and YOY sharks fed in shallower waters closer to shore.

Gastropods have previously been found in the stomachs of tiger sharks in the northwest Atlantic, including whelks (Nichols and Murphy 1916), and conch (Nichols and Murphy 1916, Gudger 1949). However, in this study, gastropods made up a large portion of the tiger sharks' diet with gastropods found in all life stages versus a few found in the previous studies (Fig. 6). Gastropods were most important for YOY tiger sharks, comprising 49% by occurrence and 36% by weight. This high number of a specific prey item across multiple YOY sharks suggests gastropods are particularly important for small tiger sharks, and could be an interesting example of diet specialization to increase foraging success. Most interesting was the presence of gastropod foot, not accompanied by any shell fragments which suggests a selective feeding mode to bite off only gastropod foot and not consume the shells. Benthic foraging has been observed before in tiger sharks (Heithaus 2001, Lowe et al. 1996) but this is the first time sharks appear to be selective for a certain part of the body.

Tiger sharks appear to have the most diverse diet for larger wide-ranging sharks in the northwest Atlantic. For example, Gelsleichter et al. (1999) found that dusky sharks, *Carcharhinus obscurus*, mostly consumed teleosts (85 %IRI), elasmobranchs (11 %IRI), and crustaceans (3 %IRI) and sand tiger sharks, *Carcharias taurus*, primarily ate teleosts (65 %IRI) and elasmobranchs (35 %IRI). Stillwell and Kohler (1982), stated that shortfin mako sharks, *Isurus oxyrinchus*, predominantly consumed teleosts and cephalopods. Porbeagle sharks, *Lamna nasus*, preyed mostly on teleosts (91% of diet by weight) and cephalopods (5.4% weight) (Joyce et al. 2002). Blue sharks (*Prionace glauca*) were similar to tiger sharks with approximately 6 equivalent prey categories above 1% frequency occurrence, predominantly consuming teleosts, elasmobranchs, and cephalopods (McCord and Campana 2003). Like many of these species of sharks, tiger sharks, regardless of life stage, had teleosts and molluscs as major prey categories. However, unlike some of these other species, tiger sharks had 7 of 15 prey categories above 1 %IRI whereas most other sharks fed on 2 or 3 prey categories above 1 %IRI (Fig. 4d). Tiger

sharks in this study also had 7 of 15 prey categories above 1% of diet by weight and every category above 1% for frequency occurrence, for comparison to other shark diet studies.

There were very few empty stomachs in this study compared to other studies. For example, in a study using baited longlines 61% of dusky shark stomachs and 22% of sand tiger stomachs were empty (Gelsleichter et al. 1999). Similarly, Stillwell and Kohler (1982) and Joyce et al. (2002) found 31.6% of shortfin mako and 52% of porbeagle stomachs were empty when using longlines for sampling. Tiger sharks in this study had a total of seven stomachs out of 169 empty, only 4%. This could be due to the frequency that tiger sharks eat and compared with most other sharks, the tiger shark is disposed to eat a variety of prey, possibly making opportunities to eat more frequent.

It is generally presumed that sharks are at the top of the food-chain and therefore play a part in shaping marine communities through what they eat (Cortés 1999, Stevens et al. 2000). Understanding trophic interactions, species interactions with the environment, and the ecological effects of fishing and other anthropogenic pressures (e.g., climate change) is necessary to inform decision support tools for ecosystem-based approaches to management (Murawski et al. 2009). Ecosystem models have become essential tools for evaluating species interactions, and forecasting the impacts of potential management actions on ecosystem dynamics (e.g. Kitchell et al. 1999). Our study will provide valuable information for any future study examining food-web responses to the removal of potential keystone predators in the northwest Atlantic Ocean and Gulf of Mexico.

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FIGURES

Fig. 1 Capture locations of tiger sharks in the shark bottom longline fishery and NMFS Apex Predators Program scientific survey, 2000-2016 (n=169)

Fig. 3 Randomized cumulative prey curves for all sharks, and three life stages (YOY, juvenile, adult) showing cumulative number of prey types versus the number of stomachs analyzed. The prey curve for all sharks did asymptote, indicating sample size was enough to define the diet of tiger sharks in this area. The prey curves for YOY and juvenile sharks approached an asymptote but were significant from zero. The cumulative prey curve for adults did not asymptote. Lines signify mean standard deviation values

Young-of-the-year

Prey Item	%N	%W	%O	%IRI
Birds	5.18	11.14	39.62	6.27
Order: Passeriformes				
<i>Mniotilta varia</i>	0.21	0.35	1.89	0.01
Unid. Aves	4.97	10.79	39.62	6.06
Cephalopods	0.62	0.01	5.66	0.03
Unid. Cephalopoda	0.41	<.01	3.77	0.02
Cnidarians	0.41	0.35	1.89	0.01
Class: Anthozoa	0.41	0.35	1.89	0.01
Arthropods	5.80	2.87	35.85	3.01
Subphylum: Crustacea	0.83	0.38	7.55	0.09
Class: Malacostraca	4.76	2.49	30.19	2.12
Order: Decapoda	2.90	2.47	26.42	1.38
Family: Portunidae	0.83	1.40	7.55	0.16
<i>Ovalipes ocellatus</i>	0.21	0.61	1.89	0.01
Family: Sicyoniidae				
<i>Sicyonia brevirostris</i>	0.41	0.03	3.77	0.02
Order: Mysida	1.86	0.02	1.89	0.03
Elasmobranchs	1.24	0.60	7.55	0.13
Family: Rajidae	1.04	0.58	5.66	0.09
Bryozoan	0.41	0.10	1.89	0.01
Mammals	0.41	3.53	3.77	0.14
Order: Cetacea	0.21	1.97	1.89	0.04
Unid. Mammals	0.21	1.56	1.89	0.03
Molluscs	56.11	36.56	50.94	45.79
Class: Gastropoda	55.69	36.46	49.06	43.85
Family: Naticidae	6.21	2.81	5.66	0.50
<i>Sinum perspectivum</i>	6.00	2.77	3.77	0.32
Family: Buccinidae	0.83	0.35	1.89	0.02
Unid. Gastropoda	48.65	33.30	47.17	37.50
Unid. Molluscs	0.21	0.09	1.89	0.01
Plants	0.62	0.09	3.77	0.03
Unid. Plants	0.41	0.09	1.89	0.01
Teleosts	19.88	43.93	71.70	44.38
Order: Perciformes				
Family: Scombridae	0.21	1.62	1.89	0.03
Order: Clupeiformes				
Family: Clupeidae	0.41	0.48	3.77	0.03
Order: Lophiiformes				
Genus: <i>Ogcocephalus</i>	0.41	4.11	3.77	0.17
Order: Pleuronectiformes				
Genus: <i>Paralichthys</i>	0.83	0.74	3.77	0.06
<i>Paralichthys oblongus</i>	0.21	0.08	1.89	0.01
Order: Tetraodontiformes	2.48	13.89	18.87	3.00
Family: Ostraciidae	1.24	8.67	11.32	1.09
Genus: <i>Lactophrys</i>	0.83	1.68	7.55	0.18
Family: Tetraodontidae	0.62	1.61	3.77	0.08
Family: Diodontidae				
Genus: <i>Chilomycterus</i>	0.62	3.61	5.66	0.23
<i>Chilomycterus schoepfi</i>	0.41	2.92	3.77	0.12
Order: Scorpaeniformes				
Family: Triglidae	5.80	5.66	24.53	2.73
Genus: <i>Prionotus</i>	3.31	2.78	11.32	0.67
Order: Anguilliformes				
Family: Ophichthidae	0.21	0.08	1.89	0.01
Order: Siluriformes	0.83	0.98	1.89	0.03

Order: Aulopiformes				
Family: Synodontidae	1.66	4.80	7.55	0.47
<i>Trachinocephalus myops</i>	1.04	1.56	3.77	0.10
<i>Synodus foetens</i>	0.21	2.95	1.89	0.06
Unid. Teleosts	7.04	11.58	37.74	6.82
Porifera	0.21	0.18	1.89	0.01
Empty	-----	-----	-----	-----
Unknown	8.28	0.09	1.89	0.15
Other (trash, rocks)	0.41	0.48	1.89	0.02

Table 1 Diet composition for young-of-the-year (≤ 100 cm fork length, n=53, 0 stomachs empty) tiger sharks by percent number (%N), percent weight (%W), percent frequency of occurrence (%O), and index of relative importance on a percent basis (%IRI). Omission of any categories indicate that prey was not present in the diet. In addition, categories with a %IRI less than 0.01 were omitted from the table

Juvenile				
Prey Item	%N	%W	%O	%IRI
Birds	5.20	7.88	50.96	6.04
Order: Charadriiformes	0.28	2.57	2.88	0.07
Family: Sternidae	0.19	2.28	1.92	0.04
<i>Hydroprogne caspia</i>	0.09	2.07	0.96	0.02
Order: Passeriformes	0.19	0.11	1.92	0.01
Order: Suliformes				
Genus: <i>Phalacrocorax</i>	0.09	0.67	0.96	0.01
Unid. Aves	4.46	3.99	43.27	3.31
Cephalopods	3.90	0.04	14.42	0.52
Order: Teuthida	1.12	0.01	6.73	0.07
Order: Octopoda	0.37	<.01	1.92	0.01
Unid. Cephalopoda	2.42	0.03	6.73	0.15
Cnidarians	0.65	0.25	1.92	0.02
Class: Anthozoa	0.65	0.25	1.92	0.02
Arthropods	3.72	1.16	26.92	1.19
Subphylum: Crustacea	0.37	0.01	3.85	0.01
Class: Malacostraca	3.44	1.15	23.08	0.96
Order: Decapoda	2.97	0.98	21.15	0.76
Family: Portunidae	1.30	0.45	11.54	0.18
Genus: <i>Ovalipes</i>	0.74	0.37	5.77	0.06
<i>Ovalipes stephensoni</i>	0.46	0.13	2.88	0.02
Order: Stomatopoda	0.28	0.16	2.88	0.01
Elasmobranchs	2.97	8.50	21.15	2.20
Order: Rajiformes				
Family: Rajidae	0.93	0.20	5.77	0.06
Order: Selachimorpha	0.84	3.55	7.69	0.31
Order: Myliobatiformes	0.46	1.15	3.85	0.06
<i>Rhinoptera bonasus</i>	0.09	0.77	0.96	0.01
Order: Carcharhiniformes	0.28	2.05	2.88	0.06
<i>R. terraenovae</i>	0.19	2.02	1.92	0.04
Unid. Elasmobranchs	0.37	1.38	3.85	0.06
Mammals	0.93	4.42	9.62	0.47
Unid. Mammals	0.84	4.08	8.65	0.39
Molluscs	23.33	3.99	28.85	7.14
Class: Bivalvia	0.46	0.11	3.85	0.02
Class: Gastropoda	20.07	3.80	23.08	5.00
Family: Cancellariidae				
<i>Cancellaria reticulata</i>	1.39	0.02	1.92	0.02
Family: Olividae	1.39	0.10	2.88	0.04
Family: Conidae				
<i>Conus dalli</i>	0.84	0.01	0.96	0.01
Family: Naticidae				
<i>Sinum perspectivum</i>	7.53	1.15	1.92	0.15

Family: Buccinidae	0.28	0.07	2.88	0.01
Unid. Gastropoda	8.64	2.46	20.19	2.03
Unid. Molluscs	2.79	0.07	1.92	0.05
Plants	3.81	0.19	23.08	0.84
Class: Phaeophyceae	1.21	0.08	7.69	0.09
Order: Fucales				
Genus: <i>Sargassum</i>	1.12	0.08	6.73	0.07
Unid. Plants	2.51	0.11	16.35	0.39
Reptiles	1.86	12.17	16.35	2.08
Family: Cheloniidae				
<i>Caretta caretta</i>	0.74	10.61	6.73	0.69
Unid. Cheloniidae	0.84	1.21	7.69	0.14
Teleosts	36.62	59.87	87.50	76.56
Order: Perciformes	2.14	21.08	15.38	3.24
Family: Pomatomidae				
<i>Pomatomus saltatrix</i>	0.09	1.13	0.96	0.01
Family: Lutjanidae				
<i>Lutjanus campechanus</i>	0.09	1.83	0.96	0.02
Family: Scombridae	0.93	6.45	6.73	0.45
<i>Acanthocybium solandri</i>	0.19	5.16	1.92	0.09
Family: Serranidae	0.19	9.23	1.92	0.16
Genus: <i>Epinephelus</i>	0.09	9.17	0.96	0.08
Family: Echeiidae	0.28	3.73	1.92	0.07
Family: Sciaenidae	0.56	0.69	2.88	0.03
Genus: <i>Pogonias</i>				
<i>Pogonias cromis</i>	0.28	0.33	0.96	0.01
Genus: <i>Menticirrhus</i>	0.19	0.36	1.92	0.01
Order: Clupeiformes				
Family: Clupeidae	0.09	0.66	0.96	0.01
Order: Lophiiformes				
Genus: <i>Ogcocephalus</i>	0.37	2.09	2.88	0.06
Order: Tetraodontiformes	5.30	11.57	22.12	3.38
Family: Ostraciidae	1.58	2.03	12.50	0.41
Genus: <i>Lactophrys</i>	0.74	1.28	3.85	0.07
Family: Tetraodontidae	1.21	2.39	3.85	0.13
Family: Monacanthidae	0.19	1.95	1.92	0.04
<i>Aluterus monoceros</i>	0.09	0.76	0.96	0.01
Family: Balistidae	0.19	0.85	1.92	0.02
Family: Diodontidae				
Genus: <i>Chilomycterus</i>	2.14	4.35	10.58	0.62
<i>Chilomycterus schoepfi</i>	1.49	3.83	6.73	0.32
Order: Acipenseriformes				
Family: Acipenseridae	0.19	4.58	1.92	0.08
Order: Scorpaeniformes				
Family: Triglidae	0.74	0.20	6.73	0.06
Genus: <i>Prionotus</i>	0.46	0.15	4.81	0.03
Order: Anguilliformes	0.28	1.43	2.88	0.04
Order: Siluriformes	0.84	<.01	0.96	0.01
Order: Elopiformes				
<i>Elops saurus</i>	0.19	0.44	1.92	0.01
Order: Aulopiformes				
Family: Synodontidae	0.28	0.46	1.92	0.01
Unid. Teleosts	26.02	17.27	74.04	29.06
Empty	-----	-----	-----	-----
Unknown	0.93	1.09	9.62	0.18
Other (trash, rocks)	1.67	0.37	8.65	0.16
Worms				
Phylum: Nematoda	14.22	0.03	20.19	2.61

Table 2 Diet composition for juvenile (101-250 cm fork length, n=111, 7 stomachs empty) tiger sharks by percent number (%N), percent weight (%W), percent frequency of occurrence (%O), and index of relative importance on a percent basis (%IRI).

Omission of any categories indicate that prey was not present in the diet. In addition, categories with a %IRI less than 0.01 were omitted from the table

Adult				
Prey Item	%N	%W	%O	%IRI
Birds	4.65	0.07	40.00	1.66
Unid. Aves				
Cephalopods	27.91	0.03	40.00	9.82
Order: Teuthida	18.60	0.01	20.00	3.27
Order: Octopoda	9.30	0.01	20.00	1.64
Arthropods	4.65	0.93	20.00	0.98
Family: Portunidae				
<i>Callinectes sapidus</i>	4.65	0.93	20.00	0.98
Elasmobranchs	2.33	8.85	20.00	1.96
Order: Myliobatiformes	2.33	8.85	20.00	1.96
Molluscs	11.63	0.09	40.00	4.12
Unid. Gastropoda	11.63	0.09	40.00	4.12
Plants	2.33	<.01	20.00	0.41
Unid. Phaeophyceae	2.33	<.01	20.00	0.41
Reptiles	9.30	20.33	40.00	10.41
Family: Cheloniidae				
<i>Caretta caretta</i>	2.33	2.73	20.00	0.89
<i>Chelonia mydas</i>	4.65	12.16	40.00	5.91
<i>E. imbricata</i>	2.33	5.43	20.00	1.36
Teleosts	25.58	69.70	80.00	66.96
Order: Perciformes	4.65	69.68	40.00	26.12
Family: Istiophoridae				
<i>I. platypterus</i>	2.33	60.22	20.00	10.99
Family: Serranidae				
<i>E. flavolimbatus</i>	2.33	9.47	20.00	2.07
Unid. Teleosts	20.93	0.02	60.00	11.04
Empty	-----	-----	-----	-----
Unknown	2.33	<.01	20.00	0.41
Worms				
Phylum: Nematoda	9.30	<.01	40.00	3.27

Table 3 Diet composition for adult (≥ 251 cm fork length, n=5, 0 stomachs empty) tiger sharks by percent number (%N), percent weight (%W), percent frequency of occurrence (%O), and index of relative importance on a percent basis (%IRI). Omission of any categories indicate that prey was not present in the diet. In addition, categories with a %IRI less than 0.01 were omitted from the table

Fig. 2 Length frequency distribution of all tiger sharks caught (n=169) from the northwest Atlantic and Gulf of Mexico. YOY sharks were ≤ 100 cm fork length (FL), juveniles 101-250 cm FL, and adults ≥ 251 cm FL

All Sharks (a)

YOY (b)

Juvenile (c)

Adult (d)

Fig. 4 %IRI for all sharks (a), YOY (b), juvenile (c), and adult (d)

Fig. 5 Stomach contents of 169 tiger sharks in the northwest Atlantic and Gulf of Mexico. Teleosts (T), birds (B), molluscs (M), arthropods (A), elasmobranchs (E), reptiles (R), and 8 other major prey categories (bryozoan, cephalopods, cnidarians, mammals, other, plants, porifera, and unknown) plus nematodes, clustered together and not labeled

Fig. 6 Picture showing gastropod foot found in stomachs of tiger sharks. A total of 490 gastropods were found in 169 stomachs of all life stages, making up a large portion of the diet of tiger sharks, especially for the YOY category. No shells were found, just gastropod foot