Abstract

Spiny dogfish (*Squalus acanthias*) are small, highly migratory sharks that occur in large numbers in North Carolina nearshore waters between November and March. This species has long been considered a pest by commercial fishermen, and is suspected of being a major source of predation mortality for economically-valuable species. The goals of this thesis research were 1.) to assess the efficiency of a non-lethal method for collecting stomach contents from dogfish, 2.) to determine if ontogeny, sex, and habitat selection influence the dogfish diet, 3.) to identify important prey species for dogfish overwintering off of North Carolina, and 4.) to describe the predatory and competitive interactions between spiny dogfish and another piscivore (striped bass, *Moronoe saxatilis*) during the overwintering period. To accomplish this, 399 spiny dogfish were captured in North Carolina waters during research bottom trawl surveys in February and March, 2010. Size and sex data were recorded for each dogfish, as well as depth, salinity, and temperature data at each station. Stomach contents were sampled by either dissection or stomach tube gastric lavage, in which an acrylic tube was inserted through the esophagus and flushed with water. Prey items were identified to the lowest possible taxa and quantified in terms of number, weight, and frequency of occurrence, then importance was determined by calculating the Index of Relative Importance for each taxa. Consumption during the sampling period was estimated using estimates of daily ration from previous studies. Stomach tube lavage proved to be efficient, and tube diameters within 10-20 mm of the shark's mouth width were nearly 100% efficient. Spiny dogfish showed significant differences in habitat selection by sex and size: females occupied significantly shallower, less saline, and cooler water than males, and dogfish began utilizing shallower depths between 600-650 mm total length (TL). The dogfish diet also shifted from an invertebrate-based to a teleost fish-based diet between 650-700 mm TL. Atlantic menhaden, (*Brevoortia tyrannus*) and bay anchovy (*Anchoa mitchili*) were the most important prey for dogfish sampled in this survey, though menhaden only dominated the diet in February. Dogfish predation may account for 14.08-3.56% of menhaden landings. Spiny dogfish and striped bass showed high spatial and potential dietary overlap, and dogfish consumed the equivalent of less than 0.91% of the striped bass stock biomass. Dogfish and striped bass are potential intraguild predators, but this relationship does not appear to affect the abundance and distribution of either species

Food and feeding habits of the spiny dogfish *Squalus acanthias* overwintering off the coast of North Carolina and the effects on the marine community

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Food and feeding habits of the spiny dogfish *Squalus acanthias* overwintering off the coast of North Carolina and the effects on the marine community

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Introduction

The spiny dogfish *Squalus acanthias* is considered one of the most abundant shark species on the planet, as well as one of the most wide-ranging, occurring in temperate marine waters worldwide. In North American waters the species is prevalent along the Atlantic coast between Newfoundland and Cape Hatteras (McMillan and Morse 1999). *S. acanthias* has long been considered a pest by fishermen, known for stealing bait and causing damage to gear. In the Northeastern United States, a marked increase in dogfish abundance has been observed, coinciding with significant decreases in the commercially valuable groundfish species of that area (Fogarty and Murawski 1998). For this reason there has been much interest in the ecological interactions between spiny dogfish and commercially important fishes.

Spiny dogfish are a highly social species, congregating into large schools based on size and sex. Segregation by size and sex can be a determinant of the habitat of an individual dogfish. Generally smaller sharks tend to inhabit deeper, cooler water, with the largest dogfish occurring inshore. Females show a preference for warm, inshore waters with lower salinity, while males are found in deep high-salinity water along the bottom. This behavior may be a result of female dogfish seeking warm water where more of their metabolic activity can be put toward growth and reproduction (Shepherd et al. 2002).

Dogfish are highly migratory. Seasonal abundance surveys have shown evidence of a North-South migration among spiny dogfish, with the population inhabiting nearshore New England waters during the summer and overwintering offshore from the Eastern edge of George's Bank to North Carolina. During the winter juvenile spiny dogfish are virtually absent from New England waters and adults are rare (McMillan and Morse 1999).

Despite their abundance, spiny dogfish are a slow-growing, late-maturing species that produces few young when compared with most teleost fishes. Nammack et al. (1985) found that male spiny dogfish were not sexually mature until approximately 6 years of age, while females took an average of 12 years to reach reproductive age. The gestation period of spiny dogfish is 2 years, after which they give birth to litters of 1-15 pups.

Dogfish compensate for their low reproductive rate by being highly successful survivors. As small sharks they occupy a relatively high trophic level in the continental shelf ecosystem, with large migratory sharks representing the only significant predatory threat (Link et al. 2002, Bowman et al. 2000). In addition, spiny dogfish have a high survival rate in encounters with fishing gear. Rulifson (2007) found a 100% survival rate among spiny dogfish caught in trawls pulled for 90 minutes and only a 17.5% mortality rate in gillnets. Many of the dogfish caught in the study showed scars, abrasions, and other evidence of frequent encounters with fishing gear, suggesting that the species interacts with fishing gear on a routine basis. This can lead to saturation of gear by dogfish, consumption of valuable catch, and a high probability of gear damage due to their sharp teeth and spines.

Aside from causing gear damage, spiny dogfish have been suspected of preying extensively upon commercially-important fishes. As with most sharks, spiny dogfish diet can be influenced by several ecological and behavioral factors. These can include the size, age, sex, and dietary overlap with other species in the same habitat. Most sharks show ontogenetic shifts in feeding habits, usually shifting from invertebrates and small teleosts to larger prey as they age (Wetherbee and Cortés 2004). Wide-ranging species such as spiny dogfish tend to vary their diet with location, and the prevalent sexual segregation among dogfish can cause males and females to be feeding out of significantly different marine communities (Wetherbee and Cortés 2004).

Feeding habits studies were among the first to be conducted on spiny dogfish, but there are still large gaps in knowledge on this subject. The wide distribution and highly adaptable diet of this shark make a definitive survey of its diet across the entire population difficult. Bowman et al. (2000) found that geographic area influenced which Osteichthyan species were present in spiny dogfish stomachs and the percentage of each species in the diet. Holden (1966) noted that stomach content analysis of spiny dogfish tended to show whichever prey species was most common in the sample area. This suggests a generalist diet for spiny dogfish where the main prey species tends to be the most locally abundant.

However, more recent evidence points to a sort of limited prey selectivity. Link et al. (2002) performed a comprehensive study on the dietary habits of spiny dogfish and other common elasmobranchs that spanned the entire Northeastern U.S. continental shelf from Nova Scotia to New Brunswick and utilized data collected from 1977 to 2001. The purpose of the Link et al. (2002) study was to determine whether direct predation upon commercially-important groundfish species by elasmobranchs could account for the rapid increase in abundance among dogfish and skates, which coincided with the crash in groundfish populations. These data showed that though spiny dogfish are the most piscivorous of the common continental shelf elasmobranchs, they show a definite preference for pelagic prey over groundfish species. Of the principal groundfish species in the study, only silver hake (*Merluccius bilinearis*) appeared as a significant prey item, and this species occurred in less than 1% of dogfish stomachs. The bulk of teleost fishes found in dogfish stomachs were pelagic species such as herring and mackerel (Link et al. 2002). Further evidence that dogfish may select for pelagic prey was found by Lapikohvsky et al. (2001) in a study analyzing dietary overlap between spiny dogfish and narrowtooth catsharks (*Schroderichthys bivius*) in the continental shelf ecosystem of the Falkland Islands. Despite being similar-sized and occupying the same habitat, both species showed little dietary overlap due to the preference for pelagic prey shown by spiny dogfish. The only time significant dietary overlap was observed was during the spring spawning run of Falklands herring, during which enough herring were present to adequately feed both species (Lapikohvsky et al. 2001).

This general preference for pelagic species could potentially have serious implications for commercial fisheries. Though Link et al. (2002) were unable to show significant predation impact on groundfish species, they did determine that the biomass of Atlantic herring and Atlantic mackerel removed by spiny dogfish predation equaled or exceeded the biomass removed by commercial fishermen. Pelagic forage species such as these fishes are highly productive, but the combination of predation and fishing pressure may produce profound population affects.

In terms of metabolic activity, spiny dogfish occupy the low end of the spectrum for cartilaginous fishes (Brett and Blackburn 1978, Wetherbee and Cortés 2004). Jones and Green (1977) calculated an extremely slow gastric evacuation rate for the species, determining that 111 hours would be needed to pass 90% of a meal from the stomach. However, more recent information suggests a much faster gastric evacuation rate with only 51.5 hours needed to eliminate 90% of stomach contents and all stomach contents removed by 103 hours (Hannan 2009). This is still a slow rate of digestion when compared to most teleosts and larger sharks, and a 2 kg adult dogfish may only need to consume 1.5-2.5 times its body weight per year (Jones and Geen 1977, Brett and Blackburn 1978). Therefore the large amounts of biomass lost to dogfish predation may be more a function of sheer abundance than high feeding rate. However, spiny dogfish are known to congregate in large numbers near sources of food.

One important limitation of the Link et al. (2002) study was the large spatial scale of the data collected. The authors themselves admitted that a data set that encompassed the entire Northeastern U.S. continental shelf over the course of decades most likely missed small-scale feeding events such as seasonal spawning runs. These small-scale events can last a matter of days but involve large groups of actively feeding dogfish. Beamish et al. (1992) noted a significant interaction between spiny dogfish and hatchery-raised salmon in a single estuary on the Pacific coast of Canada. The salmon hatchery on the Big Qualicum River in British Columbia performed an annual release of coho (*Oncorhynchus kisutch*) and chinook salmon (*Onchorhynchus tshawytshca*) smolts on May 19th. By June 15th all smolts had entered the marine waters of the Strait of Georgia. During this time the local abundance of spiny dogfish rose from an average of 173,000 to 1.4 million sharks in 1988 and from 126,000 to 1 million sharks in 1989. During these four weeks chinook and coho salmon smolts would make up a significant portion of the diet of the local dogfish, and it was estimated that 7.7 million smolts were consumed by spiny dogfish in 1988 and 1.1 million in 1989. The number of salmon eaten in 1988 nearly equaled the total number of smolts released by the Big Qualicum River hatchery. According to this data, one four-week spiny dogfish feeding event may be a major source of early marine mortality in hatchery-raised chinook and coho salmon (Beamish et al. 1992). Thus short-term feeding events can have potentially significant ecological and economic impacts.

Direct predation is not the only way large aggregations of spiny dogfish can affect the marine community. Link et al. (2002) found a low frequency of co-occurrence between dogfish and large predatory groundfish. However, large dogfish and several commercially-important piscivores occupy the same feeding guild and utilize many of the same prey species (Garrison and Link 2000). According to Garrison and Link (2000) the amount of prey available in the shelf ecosystem combined with the large variety of species taken by most piscivores should prevent heavy competition for food. This is an ecosystem-wide assessment and may not be true in observations on a smaller geographic scale where the presence of large numbers of dogfish may exert a greater influence on species composition and abundance for both prey species and other predators. Fogarty and Murawski (1998) noted a significant increase in the populations of small elasmobranchs, particularly spiny dogfish, that coincided with a crash in many of the commercial groundfish stocks on Georges Bank. This suggests that the increase in dogfish abundance resulted from competitive release due to overfishing of principle groundfish species, and competition with dogfish has been cited as a possible reason for the slow recovery of the Georges Bank fishery.

Though it is known that spiny dogfish overwinter in the waters off of North Carolina, their feeding habits in North Carolina waters are currently poorly understood. However, they occur in high enough abundance to potentially create a significant loss of commercially-important and recovering species through predation. In addition, the possibility exists for these large seasonal aggregations to affect species diversity in areas where they occur.

Goals and Objectives

The goals of this research were to provide data on spiny dogfish food and feeding habits specific to North Carolina waters and determine their potential effects on species important to commercial and recreational fisheries. This was accomplished by fulfilling five major objectives. 1.) The effectiveness of stomach tube gastric lavage on spiny dogfish was assessed. 2.) A representative sample of stomach contents were collected from spiny dogfish across a wide range of sizes and environmental factors. 3.) All stomach contents were identified to the lowest possible taxon and prey selectivity determined. If evidence for dietary preference was found, the species most heavily preyed upon were identified and the consumption of these species by spiny dogfish were quantified. 4.) Abundance data for dogfish and potential competitors were compared to determine if a relationship exists. Finally, 5.) the implications for commercial and recreational fisheries were analyzed and discussed.

Materials and Methods

The sample sites for this study were the NOAA/NMFS sampling strata between Cape

Hatteras and the Virginia state line as defined by Clark (1979). Spiny dogfish were captured opportunistically on research trawling vessels as they passed through the sample area. All sampling occurred during the months of February, and March, 2010. For each haul the GPS location, depth, water temperature (°C), and salinity (ppm) were recorded. The number and estimated biomass of spiny dogfish per area-swept were calculated, as well as the estimated number and biomass of all other species found in the trawl. These data were also taken for trawls containing no dogfish. If possible, individual length and weight data were recorded from a representative subsample of other species present in the trawl. Since net feeding can bias results, species caught with spiny dogfish were examined for signs of obvious net feeding such as fresh bite marks and dismemberment.

A subsample (10-15 sharks) of the spiny dogfish catch was set aside. Total length, fork length, weight, and sex were recorded for each individual shark. All sampled sharks were grouped into 50 mm size ranges for analysis.

Gastric lavage was performed on each subsampled shark using the tube method described by Kamler and Pope (2001) and employed by Overton et al. (2009). Several sizes of acrylic tubes with beveled leading edges were on hand so that a size-appropriate tube would be available for any given shark. Tonic immobility was induced in the dogfish by holding the shark with its ventral side up, and the tube was inserted down the esophagus into the stomach. The tube was flushed with seawater from the available ship's hose and the shark was lifted by the tail. Stomach contents were removed by gravity and landed in a screened stomach bag to filter out any excess water. After filtering, stomach contents were quickly preserved in 10% buffered formalin.

The minimum target sample size was 30 stomach content samples from four demographic groups; males, females, sharks > 70 cm total length, and those ≤ 70 cm total length. This would require a total of 120 sharks, though nearly 50% of the stomachs should be expected to be empty (Bowman et al. 2000, Link et al. 2002). Therefore, a minimum sampling target of 240 sharks was set. Every fifth shark was sacrificed and dissected to detect any leftover stomach contents in order to validate the efficiency of the method.

Lavage methods have been proven effective, showing a 95-100% efficiency rate and 100% survival rate across a wide variety of teleost fish species (Light et al. 1983, Fowler and Morris 2008), and have been used successfully on spiny dogfish and other shark species (Bush and Holland 2002, Hannan 2009). In addition, non-lethal stomach sampling methods allow more efficient on-deck processing of specimens than techniques requiring the sacrifice of the animal (Fowler and Morris 2008). This portion of the study was designed to determine the practicality of stomach tube lavage as a method for sampling the stomachs of sharks.

Stomach contents were analyzed in the lab and identified to the lowest possible taxa. Individual length and weight data were recorded for intact prey items. Specimens that could obviously be traced back to evidence of net feeding were discarded. If possible, hard parts such as scales and bones were used to identify prey species and estimate size.

The number, biomass, and frequency of occurrence for each species present in a given stomach content sample were recorded. These measurements were used to calculate the Index of Relative Importance, presented as a percentage as suggested by Cortés (1997). Population-wide percentage by weight was used to estimate total prey consumed within the study period.

Diet composition was compared between males and females, and among the 50 mm total length ranges. The length ranges were used to gauge ontogenetic shifts in diet, and since male and female dogfish utilize different environments the effect of sex on feeding habits was also analyzed. Finally, diet composition was compared across major depth, temperature, and salinity strata sampled by the trawls to determine the role of habitat in prey selectivity.

Relative abundance for all species was compared between trawls containing spiny dogfish and those lacking the sharks, and the rate of co-occurrence with spiny dogfish was calculated for all species that appeared in a majority of the trawls. An index of spatial overlap was developed between spiny dogfish and all other species caught in significant numbers. This was used to determine whether the presence or absence of spiny dogfish causes a significant difference in species composition.

Mean annual consumption by spiny dogfish was calculated for prey species using published gastric evacuation rates. Jones and Green (1977) determined a slightly higher annual ration than Brett and Blackburn (1978), so both were used to calculate the annual consumption rate with the latter being used as the conservative estimate. Particular attention was paid to prey species that 1.) make up a large proportion of the stomach contents, 2.) are significantly more abundant within stomach contents than trawls, or 3.) are of interest to commercial and recreational fisheries. Consumption estimates were compared with reported landings and stock assessment data from NMFS reports to determine if predation by spiny dogfish was a significant source of mortality.

Relevance

Though food and feeding studies have been performed on spiny dogfish before, these have been on such a large scale that the researchers themselves admit may have missed smaller-scale phenomena. However, seasonal predatory events involving large numbers of spiny dogfish can have profound effects on species in the marine community, some of which are highly-valued by commercial fishing interests. It is known that spiny dogfish occur in significant numbers in North Carolina waters during the winter months. What is not known is whether the overwintering presence of spiny dogfish is detrimental to commercial and recreational fisheries. This issue has become controversial in the North Carolina fishing community. The goals of this research were to provide information on this subject that is directly related to the North Carolina marine ecosystem and the fisheries that depend on it, and aid in crafting sound management policies concerning both the spiny dogfish and its prey.

References

Beamish, R.J., B.L. Thomson, and G.A. McFarlane. 1992. Spiny dogfish predation on Chinook and Coho salmon and the potential effects on hatchery-produced salmon. Transactions of the American Fisheries Society 121:444-455.

Bowman, R.E., C.E. Stillwell, W.L. Micheals, and M.D. Grosslein. 2000. Food of northwest Atlantic fishes and two common species of squid. NOAA Technical Memo. NMFS-NE 155, 138 p.

Brett, J.R. and J.M. Blackburn. 1978. Metabolic rate and energy expenditure of the spiny dogfish *Squalus acanthias*. Journal of the Fisheries Research Board of Canada 35:816-821

Bush, A. and K. Holland. 2002. Food limitation in a nursery area: estimates of daily ration in juvenile scalloped hammerheads *Sphyrna lewini* in Kaneohe Bay, Oahu, Hawaii. Journal of Experimental Marine Biology and Ecology 278:157-178.

Clark, S.H. 1979. Application of bottom-trawl data to fish stock assessment. Fisheries 4(3):9-15.

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

Fogarty, M.J. and S.A. Murawski. 1998. Large-scale disturbance and the structure of marine systems: fishery impacts on Georges Bank. Ecological Applications. 8:6-22.

Fowler, A.L. and J.E. Morris. 2008. A new stomach sample collection device for fish gastric lavage samples. North American Journal of Fisheries Management 28:1775-1778.

Garrison, L.P. and J.S. Link. 2000. Dietary guild structure of the fish community in the Northeast United States continental shelf ecosystem. Marine Ecology Progress Series

202:231-240.

Hannan, K. 2009. Determination of gastric evacuation rate for immature spiny dogfish. Pages 253-258 *in* V.F. Gallucci, G.A. McFarlane, and G.G. Bargman, editors. Biology and management of dogfish sharks. American Fisheries Society, Bethesda, Maryland.

Holden, M.J. 1966. The food of the spurdog *Squalus acanthias*. ICES Journal of Marine Science 30: 255-266

Jones, B.C. and G.H. Green. 1977. Food and feeding of spiny dogfish (*Squalus acanthias*) in British Columbia waters. Journal of the Fisheries Research Board of Canada 34:2067-2078.

Kamler, J.F. and K.L. Pope. 2001. Nonlethal methods of examining fish stomach contents. Reviews in Fisheries Science 9:1-11

Lapikhovsky, V.V., A.I. Arkhipkin, and A.C. Henderson. 2001. Feeding habits and dietary overlap in spiny dogfish *Squalus acanthias* (Squalidae) and narrowmouth catshark *Schroederichthys bivius* (Scyliorhinidae). Journal of the Marine Biological Association of the United Kingdom 81:1015-1018.

Light, R.W., P.H. Adler, and D.E. Arnold. 1983. Evaluation of gastric lavage for stomach analyses. North American Journal of Fisheries Management 3:81-85.

Link, J.S., L.P. Garrison, and F.P. Almeida. 2002. Ecological interactions between elasmobranchs and groundfish on the Northeastern U.S. Continental shelf. 1. Evaluating predation. North American Journal of Fisheries Management 22:550-562.

McMillan, D.G and W.W. Morse. 1999. Essential Fish Habitat Source Document: Spiny dogfish, *Squalus acanthias*, life history and habitat characteristics. NOAA Technical Memorandum NMFS-NE-150, 1-3, Woods Hole, Massachusetts.

Nammack, M.F., J.A. Musick, and J.A. Colvocoresses. 1985. Life History of the Spiny Dogfish off the Northeastern United States. Transactions of the American Fisheries Society 114:367-376.

Overton, A.S., F.J. Margraf, and E.B. May. 2009. Spatial and temporal patterns in the diet of striped bass in Chesapeake Bay. Transactions of the American Fisheries Society 138:915-926.

Rulifson, R.A. Spiny dogfish mortality induced by gill-net and trawl capture and tag and release. North American Journal of Fisheries Management 27:279-285.

Shepherd, T., F. Page, and B. MacDonald. 2002. Length and sex-specific associations between the spiny dogfish (*Squalus acanthias*) and hydrologic variables in the Bay of Fundy and Scotian Shelf. Fisheries Oceanography 11:78-89.

Wetherbee, B.M. and E. Cortes. 2004. Food consumption and feeding habits. Biology of Sharks and their Relatives. Pages 223-235 *in* J.C. Carrier, J.A. Musick, and M.R. Heithaus, editors. Biology of sharks and their relatives. CRC Press, Boca Raton, FL.

1. Evaluation of flushed stomach tube lavage as a nonlethal method for collecting stomach contents from sharks

Abstract

Concern over the use of lethal techniques to collect basic biological data from sharks has necessitated the development of nonlethal methods of data collection. The nonlethal method of removing stomach contents with acrylic tubes was evaluated. Stomach contents were collected using a flushed acrylic tube from spiny dogfish sharks (*Squalus acanthias*) during bottom trawl and commercial longline surveys. The largest tube used during the trawl survey was 30 mm in diameter, while a larger tube 37 mm in diameter was used during longline sampling. The average efficiency of stomach content removal was approximately 79.5% overall; 70% in trawl-caught sharks and 93% in longline-caught sharks. Recovery of 100% of the stomach contents can be reasonably expected if the tube width is within 10-20 mm of the mouth width. Stomach tube lavage is a useful and efficient method for nonlethal sampling of stomach contents from small sharks.

Introduction

Concerns over the conservation status of some shark species has resulted in researchers exploring alternative non-lethal methods of collecting biological data. As public awareness of threatened shark populations increases, societal and political pressures will necessitate the development and refinement of nonlethal sampling methods (Heupel and Simpfendorfer 2010).

A variety of nonlethal methods exist for sampling stomach contents of fishes (Kamler and Pope 2001). One such method was developed by White (1930), who collected stomach contents from eastern brook trout (*Salvelinus fontinalis*) by inserting a glass tube through the mouth into the stomach and exerting pressure on the stomach. In order to collect the entire stomach contents it was occasionally necessary to flush the tube with water (White 1930). This method was refined by Van Den Avyle and Roussel (1980), who used a set of acrylic tubes of varying diameters and matched the diameter of the tube as closely as possible to the esophageal diameter of the fish. After insertion, it was possible to visually inspect the stomach for the presence of food by shining a light down the tube. If food was detected the fish was lifted so that the mouth was facing downward, allowing gravity to remove the stomach contents. This method was tested on three species of Centrarchids, and post-lavage dissections showed that out of 266 fish only one still contained stomach contents (Van Den Avyle and Roussel 1980).

However, this method is not without limitations, and its effectiveness can vary by species. Van Den Avyle and Roussel (1980) recognized this, noting that acrylic tubes may be ineffective on fishes with small mouths and large stomachs. Using glass tubes, Gilliland et al. (1981) recovered over 90% of stomach contents by weight from percichthyid basses but only 75% of stomach contents from white crappie (*Pomoxis annularis*), most likely due to the stomach morphology of white crappie. Cailteux et al. (1990) found that the efficiency of stomach tubes when sampling largemouth bass (*Micropterus salmoides*) was size-dependent, with the method giving the best results for fish 120-590 mm total length. Quist et al. (2002) only recovered slightly above 50% of stomach contents by weight from walleye (*Stizostedion vitreum*), and attributed the poor results to features of the species' stomach morphology. Waters et al. (2004) compared the use of gastric lavage methods between blue catfish (*Ictalurus furcatus*) and flathead catfish (*Pylodictus olivaris*) and found that both diet and morphology played a role in creating a significant difference in the efficiency of stomach tubes (14.6% for blue catfish, 86.9% for flathead).

Flushing the stomach with water is a common method for dislodging stomach contents. Foster (1977) described a method known as pulsed gastric lavage, in which a tube connected to a water pump was inserted through the esophagus of the fish and pulsed flushes essentially forced the fish to regurgitate its stomach contents. This method removed 100% and 98% of stomach contents from grass pickerel (*Esox americanus*) and largemouth bass (Foster 1977) and 96% from catfishes (Waters et al. 2004). Hartleb and Moring (1995) modified this method by building a trough to contain the fish during flushing, which allowed the stomach contents to flow into a mesh screen at the end of the trough for collection. This method was used by Hannan (2009) to remove stomach contents from juvenile spiny dogfish (*Squalus acanthias*), though the efficiency of stomach content removal was not reported. Barnett et al. (2010) used stomach flushing to remove the stomach contents of broadnose sevengill sharks (*Notorynchus cepedianus*), and successfully removed all contents from seven of eight stomachs that were dissected to verify effectiveness.

Nonlethal stomach sampling of sharks is often accomplished by stomach eversion. As described by Cortés and Gruber (1990), stomach eversion involves anesthetizing the shark, grasping the stomach with a pair of forceps and everting it out the mouth. Sharks are capable of everting the entire stomach without permanent damage, and may do so in the wild on a regular basis as a means of regurgitation (Brunnschweiler et al. 2005). Bush (2003) found that five of 25 juvenile scalloped hammerheads (*Sphyrna lewini*) dissected after stomach eversion still contained stomach contents, though these were small teleost bones and crustacean shell fragments that comprised less than 0.05% of the shark body weight.

The most desirable field sampling method is one that is quick, efficient, and requires a minimum of equipment. Though effective, stomach eversion can be time-consuming, and the flushing techniques described by Foster (1977) and Hartleb and Moring (1995) require the use of equipment that may be cumbersome in certain field situations. The stomach tube method requires only the tubes themselves, but can be confounded by stomach morphology (Gilliland et al. 1981, Quist et al. 2002), which poses a particular challenge in sharks. Shark stomachs are divided into two regions: the cardiac stomach, which leads straight from the esophagus, and the pyloric stomach, which curves upwards from the end of the cardiac stomach and leads into the intestine (Gilbert 1973).

Because the stomach tube method is easily performed and requires a minimum of equipment, it remains popular as a nonlethal method of collecting stomach contents despite its limitations (Cailteux et al. 1990, Quist et al. 2002). When originally developing the method, White (1930) used flushing with water to dislodge stomach contents, and this may be a way of overcoming the confounding influence of stomach morphology. The goal of this study was to estimate the efficiency of acrylic tubes flushed with water in collecting stomach contents from live spiny dogfish.

Methods

In March 2010, 31 spiny dogfish were collected by bottom trawl aboard the NOAA/NMFS R/V *Henry B. Bigelow* in Atlantic nearshore and continental shelf waters between Cape May, New Jersey and Cape Hatteras, North Carolina. An additional 14 dogfish were sampled by longline aboard a commercial fishing vessel in Massachusetts waters in May and June 2011. After capture, total length (TL), fork length (FL), and mouth width (MW) were recorded in millimeters for each shark. Mouth width was measured horizontally between the hinges of the jaw using calipers.

Gastric lavage was performed using four acrylic tubes of 360 mm in length and 3 mm thick, with beveled edges at one end (Figure 1). The outer diameter of each tube measured 30, 25, 20, and 18 mm, respectively. Another tube 37 mm in diameter was added during sampling in 2011. The sharks were held ventral side up to induce tonic immobility. At this point the shark's mouth would usually open readily, but occasionally needed to be pried open using a flat metal ruler as an improvised lever. The tube with the largest diameter that would fit through the esophagus was inserted through the mouth and into the stomach. Once the tube felt as though it could not travel any further it was pulled out enough that it was not pressed against the posterior section of the cardiac stomach. The tube was flushed with water using a marine hose already available aboard both vessels. The shark was lifted so that the mouth faced downward, and stomach contents were captured in a mesh sample bag at the outer end of the tube. This procedure was repeated until no stomach contents were observed exiting the tube in three consecutive flushes. In the final flush the shark was held in a vertical position as the tube was removed, and the mouth was checked for the presence of additional food items.

Each shark was immediately sacrificed post-lavage to validate the efficiency of the method. For each of these sharks the weight (g) was recorded for the stomach contents removed by the tube. Remaining stomach contents were recovered by dissection and the weight was recorded. Both weights were added together to determine the total weight of stomach contents. The efficiency (% efficiency ratio) by weight was estimated as the ratio between the weight of stomach contents recovered using the tube and the total weight of stomach contents. Stomach contents were identified to determine if the morphology of the prey species affected the efficiency of the method. Sharks with empty stomachs were excluded from the calculations.

An analysis of variance (ANOVA) was used to determine the effect of size on the efficiency of stomach content removal. Correlations between efficiency and total length, mouth width, and total weight of stomach contents were calculated using SAS 9.2. Student's t-tests were performed to determine if the % efficiency ratio was significantly different between the trawl and longline-sampled sharks. Interactions between tube size and size variables were also analyzed by calculating correlations between efficiency, tube width:total length ratio, tube width:mouth width, and the difference between mouth and tube width. T-tests were used to determine significant differences between the means of these variables within efficiency ranges of 100%, 99-51%, and 50-0% in order to establish an effective range for high lavage efficiency.

Results

In total 33 spiny dogfish were sampled from North Carolina waters, and 14 were sampled in Massachusetts, of which four from North Carolina and one from Massachusetts had empty stomachs. Generally, sharks with food in their stomachs had a larger mean total length (841.31 ± 46.1 mm) and stomach weight (21.23 ± 23.19 g) in the longline samples, while mean mouth width was slightly greater (49.60 ± 5.83 mm) in trawl-caught dogfish (Table 1). Efficiency of stomach content removal was 79.49% of stomach content weight overall, with efficiencies of 69.65% in the trawl-caught dogfish and 93.01% in the longline samples (Table 1). Lavages performed on longline-captured sharks were significantly more efficient than those performed during the trawl survey ($p = 0.01$).

During trawl sampling, the 30 mm diameter tube was used to sample all sharks > 740 mm TL, the 25 mm tube was used for three sharks between 690 and 710 mm TL, and the 20 mm tube was used to lavage a single shark that measured 560 mm TL. The 37 mm tube was used for 12 of the 14 sharks sampled during the longline survey, while two sharks < 760 mm TL were lavaged using the 30 mm tube. No captured sharks in either sampling trip were small enough to use the 18 mm tube.

Food items recovered from the sharks made up 26 prey taxa, including a variety of fishes and invertebrates. Among the species recovered were flatfish of the Paralichthyidae and Cynoglossidae families, spotted hake (*Urophycis regia*), northern searobin (*Prionutus carolinus*), darter goby (*Ctenogobius boleosoma*), ctenophores (Ctenophora), bobtail squid (*Rossia* sp.), shrimp (Malacostraca), and sea cucumbers (Holothuroidea). Ctenophores and sand lance (*Ammodytes americanus*) made up the majority of stomach contents observed from the longline samples. Of the prey, 19 out of 29 observed taxa (65.5%) were collected at least once at higher than 50% efficiency (Table 2). Field observations during trawl sampling showed that small flatfish would occasionally complicate stomach content recovery by becoming trapped between the outer surface of the tube and the lining of the stomach. However, flatfish were also present in stomachs in which 100% of the stomach contents were recovered. The only problematic prey item during longline sampling was the head of a large sculpin (*Myoxocephalus* sp.), which became lodged sideways in the end of the tube during lavage. Because of the dismembered and often incomplete nature of the stomach contents, reliable size data were retrieved from only 18 specimens, mostly small fishes.

Overall, lavage efficiency showed a significant negative correlation with total weight of stomach contents, while total length, mouth width, and stomach content weight all correlated significantly and positively (Table 3). Negative correlations between lavage efficiency and all size measurements (TL, MW, and SW) were significant in the trawl samples, with stomach content weight as the best-fitting correlation. In the longline samples, only stomach content weight showed a significant negative correlation with lavage efficiency, and total length and mouth width were the only size measurements to correlate significantly (Table 3).

Plots of lavage efficiency against size measurements showed that the longline samples were more efficient at greater total lengths (Figure 2-A) and mouth width (Figure 2-B). However, efficiency plotted against total stomach content weight showed a similar relationship in both the trawl and longline samples (Figure 2-C).

Tube diameter:total length, tube diameter:mouth width, and mouth width – tube diameter all showed relatively strong, significant correlations, with mouth width – tube diameter correlation negative with the two tube:size ratios (Table 4). Tube diameter:total length and mouth width – tube diameter correlated significantly with lavage efficiency (Table 4). Scatter plots supported the ANOVA results, with tube diameter:mouth width (Figure 3-A) and tube diameter:total length (Figure 3-B) showing weak positive trends with lavage efficiency, while mouth width – tube diameter (Figure 3-C) had a negative relationship with efficiency.

The tube width:total length ratio averaged approximately 0.04:1 for all efficiency groups and t-test results showed that the ratio did not vary significantly between any group (Table 5). The mean difference between mouth width and tube diameter was significantly smaller ($p = 0.01$) in dogfish lavaged at 100% efficiency (15.85 ± 6.87 mm) than those in the ≤ 50% range (22.50 ± 4.77 mm) (Table 5).

Discussion

The results show that acrylic tubes can be an effective method for non-lethally extracting stomach contents from sharks, as long as the size of the tube is appropriate for the size of the shark. Lavage efficiency improved significantly from trawl to longline sampling, and the longline samples were > 90% efficient. The most important predictive variable was the difference between mouth width and tube diameter; a difference range of 9.5-22.2 mm provided 51-100% efficiency (Table 5), and can reasonably be expected to remove 100% of spiny dogfish stomach contents. In the field, selecting a tube diameter within 10-20 mm of the shark's mouth width will likely provide the best lavage efficiency.

The overall high lavage efficiency suggests that dogfish gut morphology alone does not play a significant role in limiting the efficiency of stomach content removal. Prey morphology also does not appear to be a major confounding factor. Prey groups such as flatfish, which were expected to be difficult to extract because of morphology, were capable of being recovered at 100% efficiency. Larger species were usually present in the stomach contents in dismembered pieces small enough to fit through the tube. In fact, the lowest efficiencies were found in smaller, more fusiform fishes from the stomachs of larger sharks (Table 1).

As in Cailteux et al. (1990), the size of the fish was the most important factor influencing efficiency. The precipitous decline in efficiency at TL 785 mm in the trawl-caught sharks suggests that a tube of 30 mm diameter is insufficient to efficiently remove stomach contents from spiny dogfish >785 mm TL (Figure 2-A). Efficiency improved from 69.65% to 93.01% with the use of a tube diameter of 37 mm, which may have been better matched to sharks > 785 mm TL. Total length and mouth width ceased to be significantly correlated with lavage efficiency in sample populations that included the 37 mm tube (Table 3, Figures 2-A and 2-B), suggesting that this tube size was well-matched to sharks in the size range captured during the longline survey. While total body length does appear to correlate significantly with lavage efficiency, the difference between mouth and tube width was the most significant driver of lavage efficiency (Table 5), with higher differences resulting in lower efficiency (Table 4, Figure 3-C). Total stomach content weight remains a significant influence on lavage efficiency (Table 3, Figure 2-C), and may potentially be overcome by flushing the stomach with greater pressure.

The difference in collection method should be addressed as a potential influence on lavage efficiency. Gear used to capture sharks can significantly affect the amount and type of food recovered during diet sampling (Wetherbee and Cortés 2004). Generally longline sampling tends to capture sharks with relatively empty stomachs, but the longline-captured dogfish had a higher mean total stomach content weight than the trawl-captured dogfish (Table 1). In this study, differences in survey methods did not appear to influence stomach content weight, but could potentially affect lavage efficiency and should always be assessed as a possible confounding factor.

Ease of use is a major advantage of this method. The minimum of equipment required makes the stomach tube method appropriate aboard crowded research and fishing vessels where space and time may be limited. This method was easiest with a two-person team: one researcher handling the shark, inserting the tube, and performing the flushes while the other held the bag open and recorded data, but this method is feasible with one person. There was some concern over possible injury from the shark's teeth, but the tubes used for this survey were of sufficient length to keep hands a safe distance from the mouth during insertion and retrieval. Because this method involves directly handling the sharks, it is best used on juveniles or species with a maximum total length of 1-1.2 m, such as those in the dogfish and small coastal shark complex.

It is difficult for any nonlethal method of collecting stomach contents to be as effective as sacrifice and dissection. However, increased sensitivity towards shark conservation may eventually require the use of nonlethal methods. The results of this assessment suggest that flushed tubes may be an effective means of sampling the diets of sharks in the field, but the efficiency of the method is dependent on selecting the appropriate tube width for the mouth width of the shark. Pre-measuring the shark's mouth width and selecting the tube width within 10-20 mm of that measurement will likely provide the highest possible lavage efficiency, and should be standard procedure whenever this method is performed.

References

Barnett, A., K. S. Redd, S.D. Frusher, J. D. Stevens, and J. M. Semmens. 2010. Non-lethal method to obtain stomach samples from a large marine predator and the use of DNA analysis to improve dietary information. Journal of Experimental Marine Biology and Ecology 393: 188-192.

Brunnschweiler, J. M., P. L. R. Andrews, E. J. Southall, M. Pickering, and D. W. Sims. 2005. Rapid voluntary stomach eversion in a free-living shark. Journal of the Marine Biological Association of the United Kingdom 85: 1141-1144.

Bush, A. 2003. Diet and diel feeding periodicity of juvenile scalloped hammerhead sharks, *Sphyrna lewini*, in Kane'ohe Bay, Oahu, Hawaii. Environmental Biology of Fishes 67: 1-11.

Cailteux, R. L., W. F. Porak, and S. Crawford. 1990. Reevaluting the use of acrylic tubes for collection of largemouth bass stomach contents. Proceedings of the Annual Conference of the Southeast Association of Fish and Wildlife Agencies 44: 126-132.

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

Foster, J. R. 1977. Pulsed gastric lavage: an efficient method of removing the stomach contents of live fish. The Progressive Fish Culturist 39: 166-169.

Gilbert, S. G. 1973. Pictorial anatomy of the dogfish. University of Washington Press, Seattle.

Gilliland, E. R., C. W. Kleinholz, and M. D. Clady. 1981. The efficiency of removing food items from fish with glass tubes. Proceedings of the Texas Chapter of the American Fisheries Society 4: 95-100.

Hannan, K. 2009. Determination of gastric evacuation rate for immature spiny dogfish. Pages 253-258 *in* V.F. Gallucci, G.A. McFarlane, and G.G. Bargman, editors. Biology and management of dogfish sharks. American Fisheries Society, Bethesda, Maryland.

Hartleb, C. F., and J. R. Moring. 1995. An improved gastric lavage device for removing stomach contents from live fish. Fisheries Research 24: 261-265.

Heupel, M. R. and C. A. Simpfendorfer. 2010. Science or slaughter: the need for lethal sampling of sharks. Conservation Biology 24: 1212-1218.

Kamler, J. F. and K. L. Pope. 2001. Nonlethal methods of examining fish stomach contents. Reviews in Fisheries Science 9: 1-11.

Quist, M. C., C. S. Guy, R. J. Bernott, and J. L. Stephen. 2002. Efficiency of removing food items from walleye using acrylic tubes. Journal of Freshwater Ecology 17: 179-184.

Van Den Avyle, M. J. and J. E. Roussel. 1980. Evaluation of a simple method for removing food items from live black bass. The Progressive Fish Culturist 42: 222-223.

Waters, D. S., T. J. Kwak, J. B. Arnott, and W. E. Pine III. 2004. Evaluation of stomach tubes and gastric lavage for sampling diets from blue catfish and flathead catfish. North American Journal of Fisheries Management 24: 258-261.

Wetherbee, B. M. and E. Cortés. 2004. Food consumption and feeding habits. Biology of Sharks and their Relatives. Pages 223-235 *in* J.C. Carrier, J.A. Musick, and M.R. Heithaus, editors. Biology of sharks and their relatives. CRC Press, Boca Raton, FL.

White, H. C. 1930. Some observations on the eastern brook trout (*S. fontinalis*) on Prince Edward Island. Transactions of the American Fisheries Society 60: 101-108.

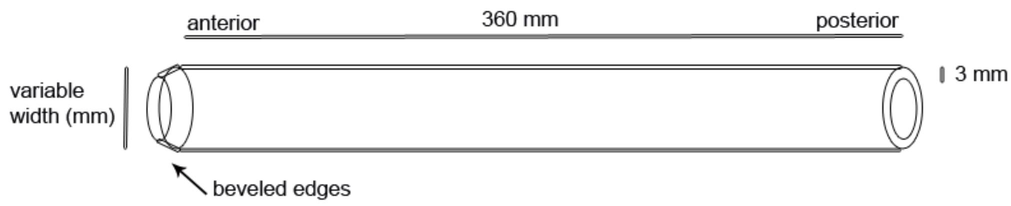


Figure 1-1. General design for acrylic tubes used to remove stomach contents from spiny dogfish in this survey.

Table 1-1. Mean total length, mouth width, stomach content weight, and lavage efficiency ± standard deviation (SD) for spiny dogfish sampled by trawl and longline.

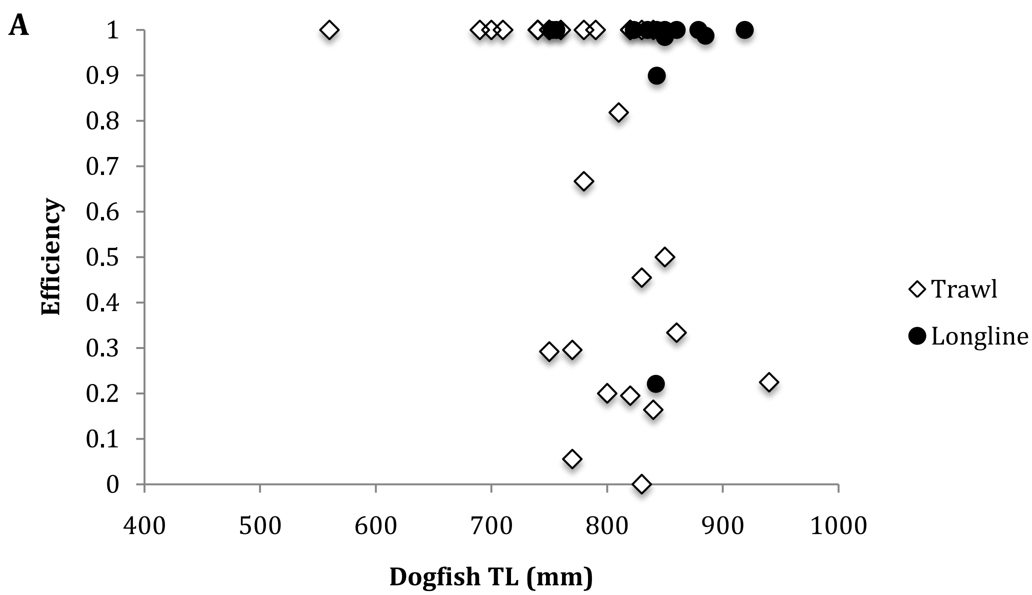
	Mean ± SD	
Variable	Trawl	Longline
n	29	13
Total length (mm)	782.07 ± 68.89	841.31 ± 46.1
Mouth width (mm)	49.60 ± 5.83	47.88 ± 5.96
Stomach weight (g)	18.76 ± 23.45	21.23 ± 23.19
Lavage efficiency (%)	69.65 ± 37.00	93.01 ± 21.00

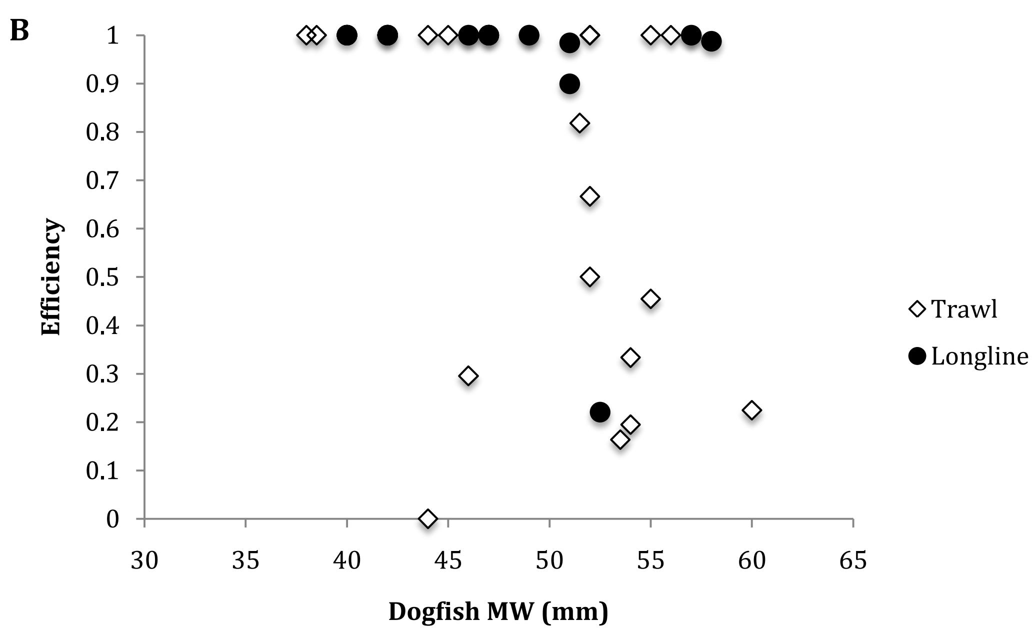
Table 1-2. Number of occurrences grouped by lavage efficiency range (≤50%, 51-99%, 100%), mean total length (mm) of all prey taxa, and mean total length (mm) of all sharks containing each prey taxa.

Prey taxon	Occurrences per efficiency range			**Mean prey TL (mm) (*n*)**	**Mean shark TL (mm)**
	≤ 50%	51% - 99%	100%		
Algae/Detritus	1	-	1	-	770
Animal remains	1	-	1	-	810
Ctenophora	-	-	5	-	840
Clypeasteroida	-	1	-	-	780
Holothuroidea	-	-	2	-	835
Polychaeta	-	1	1	-	800
Malacostraca	1	-	2	47 (1)	810
Stomatopoda	1	-	-	-	840
Euphausiidae	-	-	2	-	745
Portunidae	1	-	-	-	850
Decapoda	1	-	1	-	835
Rossia sp.	1	-	-	24 (1)	825
Euspira heros	-	-	1	-	879
Bivalva	-	1	1	-	780
Unclassified invertebrate	-	-	1	-	790
Ammodytes americanus	-	-	3	-	811
Ctenogobius boleosoma	2	1	-	30.33 (3)	817
Ophidion sp.	1	-	-	-	860
Urophycis regia	2	-	-	89 (1)	830
Urophycis sp.	-	1	-	-	810
Polymixia lowei	1	-	-	-	860
Brevoortia tyrannus (gizzards)	1	-	-	-	840
Syngnathidae	1	-	-	130 (1)	830
Prionutus carolinus	2	1	1	53.33 (6)	840
Myoxocephalus sp.	1	-	-		842
Cynoglossidae	2	-	-	143 (2)	795
Paralichthyidae	-	-	1	49 (1)	780
Citharichthys arctifrons	-	1	-	56 (2)	780
Unclassified teleost	5	1	3	-	826

Table 1-3. Pearson correlation coefficients between percent efficiency of stomach content removal and total length (TL), mouth width (MW), and total stomach content weight (SW) for all spiny dogfish and each sampling area. Correlations marked with an asterisk (*) are significant at the 0.05 level.

R	Efficiency	TL	MW	SW
		Overall		
Efficiency	1			
TL	-0.221	1		
MW	-0.320	0.598*	1	
SW	-0.522*	0.413*	0.383*	1
		Trawl		
Efficiency	1			
TL	-0.466*	1		
MW	-0.423*	0.878*	1	
SW	-0.572*	0.542*	0.358	1
		Longline		
Efficiency	1			
TL	-0.0119	1		
MW	-0.2662	0.8015*	1	
SW	-0.6142*	0.0598	0.3167	1


A
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
Efficiency
400
500
600
700
800
900
1000
Dogfish TL (mm)
Trawl
Longline


B
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
Efficiency
30
35
40
45
50
55
60
65
Dogfish MW (mm)
Trawl
Longline

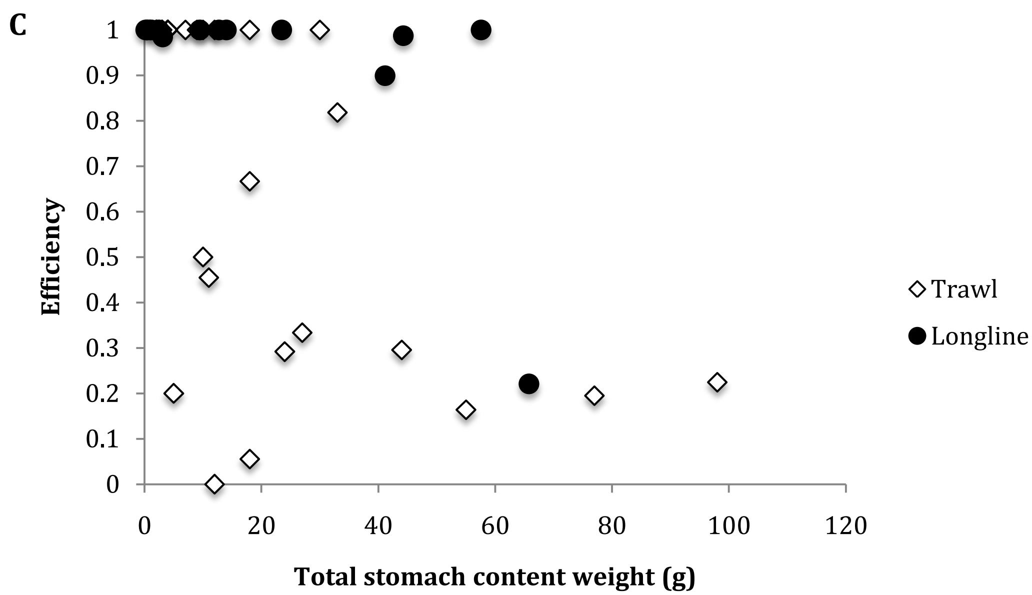
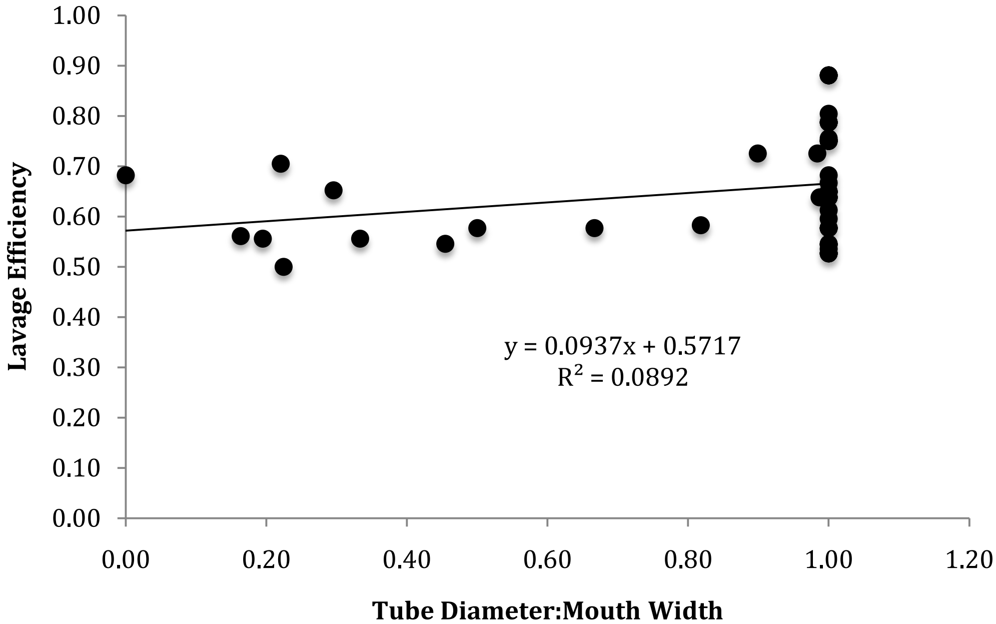


Figure 1-2. Percent efficiency of stomach content removal by stomach tube lavage plotted against A.) total length (mm), B.) mouth width (mm), and C.) total stomach content weight (g) for spiny dogfish sampled by trawl (n=29) and longline (n=13).

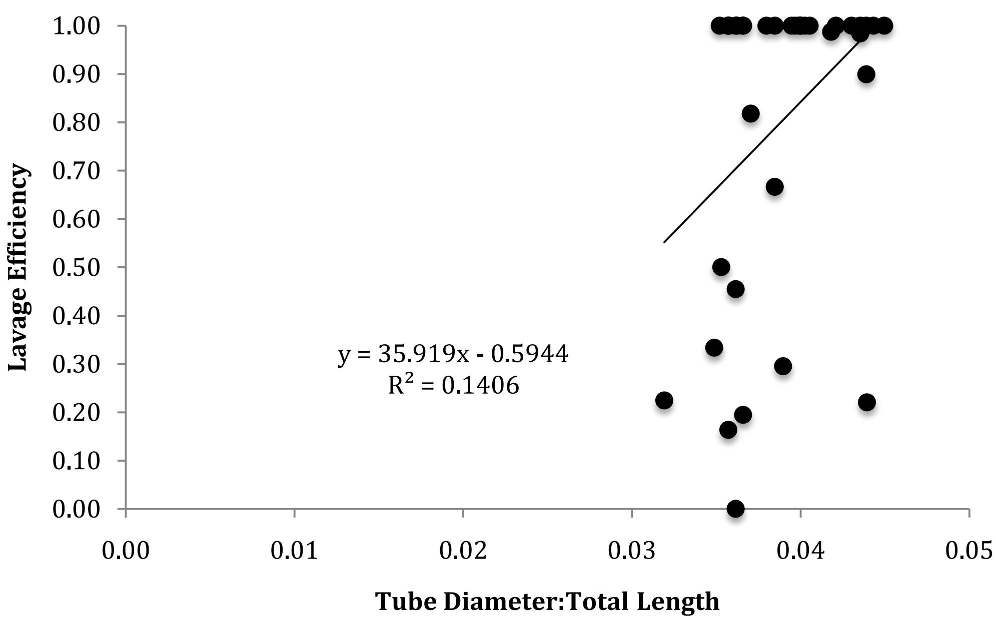
Table 1-4. Pearson correlation coefficients between percent efficiency of stomach content removal, ratio of tube diameter:mouth width (Tube/MW), tube diameter:total length (Tube/TL), and the difference between tube width and mouth width (MW-Tube) for all spiny dogfish. Correlations marked with an asterisk (*) are significant at the 0.05 level.

R	Tube/MW	Tube/TL	MW-Tube	Efficiency
Tube/MW	1			
Tube/TL	0.797*	1		
MW-Tube	-0.944*	-0.673*	1	
Efficiency	0.230	0.375*	-0.353*	1

A


1.00
0.90
0.80
0.70
0.60
0.50
0.40
0.30
0.20
0.10
0.00
Lavage Efficiency
y = 0.0937x + 0.5717
R² = 0.0892
0.00
0.20
0.40
0.60
0.80
1.00
1.20
Tube Diameter:Mouth Width

B


1.00
0.90
0.80
0.70
0.60
0.50
0.40
0.30
0.20
0.10
0.00
Lavage Efficiency
y = 35.919x - 0.5944
R² = 0.1406
0.00
0.01
0.02
0.03
0.04
0.05
Tube Diameter:Total Length

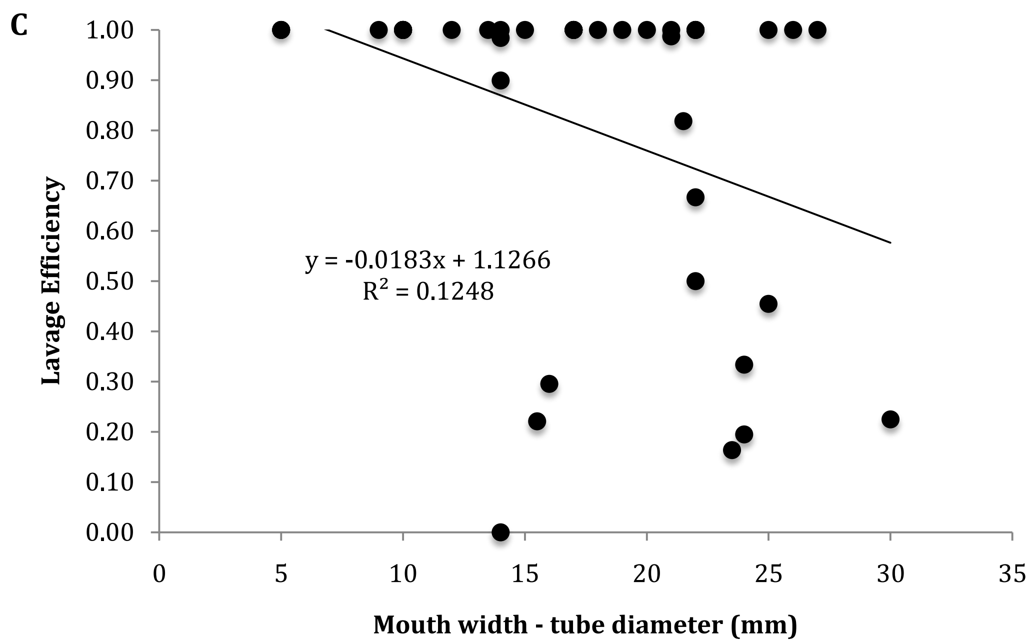


Figure 1-3. Lavage efficiency plotted against A.) tube width:total length, B.) tube width:mouth width, and C.) mouth width – tube width, for all lavaged spiny dogfish, with linear correlation equations.

Table 1-5. Mean and standard deviation values for tube diameter:total length ratio (Tube/TL) and difference between mouth and tube diameter (MW-Tube) for dogfish lavaged at 100%, 99-51%, and ≤ 50% efficiency, with t-test results comparing mean values for both variables between the different efficiency ranges.

	Mean ± SD		
Var/Efficiency	100%	99-51%	≤50%
n	23	6	8
Tube/TL	0.039 ± 0.003	0.040 ± 0.003	0.037 ± 0.004
MW-Tube	15.85 ± 6.37	17.75 ± 4.12	22.50 ± 4.77
	T-test results (α = 0.05)		
Var/Test	100% vs 99-51%	100 % vs ≤50%	99-51% vs ≤50%
Tube/TL	0.61	0.38	0.63
MW-Tube	0.50	0.01	0.07

2. Demographic and environmental variation in the diet of spiny dogfish (*Squalus acanthias*) off the coast of North Carolina

Abstract

Size and sex play a role in both the habitat use and diet of spiny dogfish (*Squalus acanthias*). To determine how habitat use by different demographics of may affect feeding habits, spiny dogfish were sampled in North Carolina waters during the 2010 NOAA/NMFS spring bottom trawl survey. Depth, surface and bottom temperature, and surface and bottom salinity were recorded at each station, as well as the total number of male and female spiny dogfish caught. Stomach contents were collected from 10-15 spiny dogfish at each station, and total length, fork length, and sex were recorded for each dogfish. Prey were identified to the lowest possible taxa and grouped into broad taxonomic categories for analysis. Mean values for all environmental factors were compared between male and female dogfish using Student's t-tests. Measured spiny dogfish were divided into 50-mm size ranges and the mean of each environmental factor was calculated for each size range. For each demographic, percent weight and percent Index of Relative Importance were calculated for each prey taxa and category, and Bray-Curtis analysis was used to determine dietary overlap between males, females, and different size classes. Pearson correlations and PCA were used to describe the relationships between the relative importance of prey categories and environmental factors. Overall, males occupied significantly deeper depths, higher temperatures, and greater salinities than females. The diet of female dogfish was dominated by teleost fishes, while crustaceans were more important in the male diet. Size analysis showed that an apparently ontogenetic shift occurs at 600-650 mm total length, when dogfish move to shallower, cooler, less saline habitats and switch from an invertebrate-based diet to one comprised mostly of teleosts. Prey taxa in the teleost and crustacean categories showed opposing correlations with environmental factors, providing more evidence for an ontogenetic shift from crustacean to fish prey with increasing size in spiny dogfish.

Introduction

Sharks show significant ontogenetic shifts in diet and habitat utilization despite limited ontogenetic changes in morphology (Grubbs 2010). Because sharks develop directly rather than going through metamorphosis like most teleost fishes, habitat may have more influence on ontogenetic shifts in diet than morphology. Many sharks occupy restricted nursery areas as juveniles, which can result in significantly different foraging habits and energetic intake in comparison to adults of the same species (Heithaus 2007).

Most well-studied shark species utilize enclosed, inshore habitats such as lagoons and estuaries as nursery areas (Heithaus 2007). The spiny dogfish, *Squalus acanthias*, differs in that parturition occurs in offshore overwintering grounds (Nammack et al. 1985, Hanchet 1988, Burgess 2002). This species is highly k-selected; age and length at maturity are 12 years and 79.9 cm for females and 6 years and 59.5 cm for males (Nammack et al. 1985). Spiny dogfish range from 20-33 cm at birth to 60-90 cm for males and 76-107 cm for females, with reported maximum lengths of 100 cm and 124 cm for males and females, respectively (Burgess 2002).

Spiny dogfish segregate by size and sex, with large females occurring in shallow nearshore waters while males and juveniles are more abundant offshore (Shepherd et al. 2002, Methratta and Link 2007, Stehlik 2007). In the Scotian Shelf and Bay of Fundy, male and juvenile dogfish occupy significantly deeper and more saline habitats than females (Shepherd et al. 2002). In Georges Bank, dogfish size is strongly related to depth, with neonatal to 50 cm dogfish occurring at the shelf break (Methratta and Link 2007). NEFSC trawl survey data also supports the pattern of segregation; the majority of juvenile dogfish are found at depths below 50 m in spring and below 40 m in autumn (Stehlik 2007).

In the northwestern Atlantic Ocean, spiny dogfish are highly migratory, occupying waters from southern New England to the Gulf of Maine and Scotian Shelf in the summer and overwintering off of North Carolina to Cape Hatteras (Burgess 2002, Stehlik 2007). Though considered rare south of Cape Hatteras, large aggregations of dogfish have been found overwintering in North Carolina waters south of Cape Hatteras (Rulifson and Moore 2009) and along the coast of South Carolina (Bearden 1965, Ulrich et al. 2007).

The diet of the spiny dogfish has received much attention due to its role as the dominant piscivore in the northwestern Atlantic ecosystem after the collapse of Atlantic cod (*Gadus morha*) in the 1980s (Fogarty and Murawski 1998, Link and Garrison 2002). The rapid niche expansion of spiny dogfish in the 1970s and 1980s was attributed to competitive release from overfished groundfish species (Fogarty and Murawski 1998), with which adult spiny dogfish occupy the same feeding guild, suggesting significant dietary overlap (Garrison and Link 2000). Predation by dogfish on commercially-important groundfish such as gadids and flatfishes has been suspected of preventing those species from recovering from overfishing, but Link et al. (2002) found that the level of predation on these species by dogfish was not sufficient to explain their low abundance. Spiny dogfish also show high dietary overlap with thornback rays (*Raja clavata*) in the Black Sea (Demirhan et al. 2007) and narrowmouth catsharks (*Schroederichthys bivius*) in the Falkland Islands (Laptikhovsky et al. 2001) though in both cases the generalist diet of the spiny dogfish allows it to avoid direct competition for prey.

Spiny dogfish are opportunistic feeders and their diet is highly varied, but teleost fishes make up the most significant portion (Burgess 2002, Stehlik 2007). Fishes made up 53.7% of the diet by weight of spiny dogfish sampled during NEFSC trawl and longline surveys from 1963-1984 (Bowman et al. 2000). Teleosts made up 80.8% of the diet of spiny dogfish sampled in the northeast Atlantic Ocean (Ellis et al. 1996). Other important prey groups from these surveys included squid (17.8%), crustaceans (4.3%) and other invertebrates (24.2%) in the northweast Atlantic (Bowman et al. 2000) and crustaceans (12.0%), ctenophores (3.5%) and mollusks (2.8%) in the northeast Atlantic (Ellis et al. 1996).

Generally, teleost species preyed upon by spiny dogfish tend to be smaller species or juveniles of larger species (Stehlik 2007) though dogfish may be capable of dismembering and consuming prey larger than themselves (Burgess 2002). Ellis et al. (1996) noted that dogfish feed mainly on pelagic and epibenthic species, with Atlantic herring (*Clupea harengus*) making up 11.8% of the diet. In the Northwest Atlantic, spiny dogfish are among the most important predators of herring, though the importance of herring in the diet of spiny dogfish varies with prey abundance (Overholtz and Link 2007). Fish species consumed by spiny dogfish vary over time and by geographical area, but the overall proportion of fish in the diet has remained a relatively consistent majority (Smith and Link 2010).

Spiny dogfish undergo an ontogenetic shift in diet from gelatinous zooplankton such as ctenophores to teleost prey with increased size (Smith and Link 2010). The importance of ctenophores in the diet of spiny dogfish less than 60 cm in length has caused small and medium-sized dogfish to be grouped as part of the planktivore feeding guild in the Georges Bank ecosystem (Garrison and Link 2000, Auster and Link 2009). Frequency of ctenophores in the spiny dogfish diet has increased since the 1980s, which may be indicative of an increase in the abundance of ctenophores (Link and Ford 2006). Ctenophores remain an important prey resource even after spiny dogfish reach maturity and their diet becomes dominated by fish (Smith and Link 2010). In contrast, Ellis et al. (1996) found evidence that crustaceans were the most important prey of spiny dogfish less than 60 cm in length, though ctenophores were still the third most important food category overall. However, the importance of ctenophore prey in sharks may have been underestimated due to the generally rapid rate of digestion for gelatinous organisms and the fact that many common methods for preserving stomach contents may fail in preserving ctenophores and cnidarians (Arai 2005).

Differences in diet through ontogeny may also reflect differences in habitat use. Alonso et al. (2002) observed the common shift from gelatinous zooplankton to fish with increased size, but also compared the environment of the prey species consumed by spiny dogfish in Argentinian waters. Immature dogfish tended to feed on pelagic species, while both mature males and mature females fed primarily on fish species inhabiting the demersal environment (Alonso et al. 2002).

The goal of this study was to determine if the feeding habits of spiny dogfish overwintering in North Carolina waters are significantly affected by size, sex, and environmental factors, and to describe these relationships in a fisheries management context. Because the feeding habits of spiny dogfish are related to habitat use, sex, and ontogeny, these factors may be important in assessing the potential predatory impact of these sharks on economically-important species. Understanding these relationships may also be of use in developing a fishery targeting a specific demographic of spiny dogfish..

Methods

Stomach contents were sampled from 145 spiny dogfish captured in North Carolina waters during the 2010 NOAA/NMFS spring bottom-trawl survey. The survey was conducted aboard the NOAA/NMFS R/V *Henry B. Bigelow* and consisted of approximately 20-minute tows at each station. The survey included 40 stations in North Carolina waters, which were towed from March 4-8 (Figure 1). Station selection and sampling protocols were conducted as per the Northeast Fisheries Science Center (NEFSC) standard operating procedures for groundfish bottom trawl surveys (Stauffer 2004). Surface and bottom temperature were recorded using a ship-board Conductivity, Temperature, and Depth sensor (CTD) at each sampling station. Average depth at each station was calculated using the starting and ending depths for each tow.

The abundance in both number (N) and biomass (kg) were recorded for spiny dogfish at each station, and were classified by sex. A subsample of no more than 17 dogfish of each sex was randomly selected from each catch for stomach content sampling. If less than 20 spiny dogfish total were captured in one tow, then stomach content analysis was performed on all dogfish captured at that station. Total length (TL, mm), fork length (FL, mm) and sex were recorded for each subsampled dogfish.

Stomach contents were collected using acrylic tube lavage, as described by Van den Avyle and Roussel (1980). To accomplish this, each dogfish was held upside-down to induce tonic immobility, and an acrylic tube of the largest diameter that would fit through the shark's esophagus was chosen. The tube was inserted through the mouth and esophagus until it felt as though it would go no further, then was pulled out slightly to prevent it from pressing against the posterior end of the stomach. The tube was then flushed with water using the hose available at each workstation in the wet lab aboard the *Bigelow*. The dogfish would then be lifted so the mouth and tube were angled downward and stomach contents were captured in a mesh bag at the end of the tube. This procedure was repeated until no stomach contents were observed exiting the tube after three consecutive flushes. In the final flush the dogfish was held vertically as the tube was removed, and the mouth was visually inspected for the presence of any remaining stomach contents. Every fifth dogfish was sacrificed and dissected to determine the efficiency of the tube lavage method by comparing the weight (g) of stomach contents removed by the flushed tube with the total weight of the stomach contents, including any recovered by dissection.

Stomach contents were placed on ice until all dogfish from that station had been sampled, then were transferred to 10% buffered formalin solution for transport back to the laboratory. In the laboratory, prey items were identified to the lowest possible taxa, and number, total weight (g) and frequency of occurrence were recorded for each prey taxa. If number could not be positively determined, it was assumed to be one individual. For analysis, positively identified prey taxa were classified into six prey categories based on taxonomy; Teleost, Elasmobranch, Mollusc, Crustacean, Ctenophore, and Other Invertebrate. Prey items too damaged or digested for positive identification were classified as Unidentified, and inorganic and plant matter was classified as Detritus.

All spiny dogfish were grouped by sex and size. Size classes were determined by grouping all spiny dogfish total lengths by 50-mm increments. If diet and environmental data showed a major shift over any size increment, dogfish were divided into two major size classes; those with TL greater than and those with TL less than or equal to the maximum TL in that size increment.

For each subgroup of dogfish, the percent Index of Relative Abundance (% IRI) (Cortés 1997) was calculated for each prey taxa and for each prey category, using the percentage by number, weight, and frequency. Differences in diet composition between sexes and size classes were determined by calculating Bray-Curtis Index of Similarity (BCIS) (Bray and Curtis 1957) between males and females, and size classes.

Average depth and temperature were calculated for each subgroup, and a Student's t-test was used to determine significant differences between males and females and immature and mature dogfish. Pearson Correlations were calculated between spiny dogfish total length, average depth, bottom temperature, and surface temperature, and one-way ANOVAs were used to verify the significance of those correlations. This procedure was also used to determine if the proportions of prey categories present in the dogfish diet by number and weight correlated with average depth, surface and bottom temperature, and surface and bottom salinity.

Using Arc-GIS, surface and bottom temperature were plotted by station. The percentage of male and female dogfish was determined for each station and expressed visually using Arc-GIS, as well as the percentage of immature and mature dogfish. Spatial overlap between male and female dogfish and immature and mature dogfish was determined by dividing the number of stations with one demographic present by the number stations containing both demographics (Link et al. 2002). Because size classes were based on TL, only those dogfish that were subsampled and measured were used for analyses comparing those subgroups. Analyses comparing males and females used the relative percent of the total catch data from each station.

Principle component analysis (PCA) was used to describe the relationships between prey categories by number, weight, and frequency of occurrence, total dogfish length, depth, and surface and bottom temperatures.

Results

Of the 145 dogfish sampled, 25 (17.2%) had empty stomachs. Not including unidentified animal remains and detritus, a total of 54 prey taxa were identified from the stomach contents of spiny dogfish sampled for this study (Table 1). The Teleost category included the highest number of prey taxa, though most prey taxa in the Ctenophore and Other Invertebrate categories could only be identified to a broad taxonomic level.

Stomach contents were recovered from 105 female spiny dogfish. All identified prey taxa were present in the diet of female dogfish, with unidentified fish (63.93% IRI) as the most important, followed by polychaetes (8.84% IRI) and unidentified shrimp (4.68% IRI) (Table 2). The Teleost category dominated the diet of female spiny dogfish with an 81.01% IRI, followed by Other Invertebrates (8.54% IRI) (Table 2). The diet of female spiny dogfish could be described as piscivorous, with Teleost prey making up the majority of the diet by both weight (Figure 2) and relative importance (Figure 3).

Of the 30 males sampled, 16 contained prey items in their stomachs. Seven identified taxa were included in the diet of male spiny dogfish, as well as small amounts of detritus and plant matter. Euphausiids were the most important prey taxa in the male diet (66.56% IRI), followed by unidentified fish (22.38% IRI) and ctenophores (5.21% IRI) (Table 3). Crustaceans were the most important prey category for male spiny dogfish (79.88% IRI), followed by Teleosts (14.78% IRI) (Table 3). Teleosts dominated the male diet by weight (Figure 4), but Crustacean prey showed the highest relative importance (Figure 5). No prey taxa within the Elasmobranch, Mollusc, and Other Invertebrate categories were found in the stomach contents of male dogfish.

Female dogfish were significantly larger than males, with a mean TL of 785.3 mm compared to 726.7 mm TL in males. Male dogfish were found at stations with a higher mean depth, surface temperature, bottom temperature, and surface and bottom salinity than those where female dogfish were captured. Student's t-test results showed that the differences in all three environmental variables were significant between the sexes (Table 4).

Females made up the majority of the spiny dogfish catch at stations on the continental shelf, though relative abundance decreased along the continental slope (Figure 6). Males were largely absent from the northern areas of the continental shelf, and made up only up to 5% of the spiny dogfish catch in areas north of Cape Hatteras. However, the relative abundance of males increased at the shelf break and males made up over 96% of the dogfish catch at three of the shelf break stations (Figure 7). No spiny dogfish of either sex were found at any stations south of the Hatteras Bight.

Spiny dogfish showed a sudden shift in both feeding habits and environmental preferences at between 601 and 650 mm TL. The Crustacean and Other Invertebrate prey categories dominated the diet by % IRI in dogfish 650 mm or less in total length, but Teleost prey rapidly becomes the most important prey category in dogfish greater than 650 mm TL (Figure 8). This size range also marks a dramatic shift in environmental preferences; all size ranges greater than 650 mm TL occupy consistently shallower depths (Figure 9-A), lower mean temperatures (Figure 9-B) and lower mean salinities (Figure 9-C) than those 650 mm TL or less. Student's t-test results showed significant differences in depth, surface temperature, and bottom salinity between dogfish > 650 mm and those ≤ 650 mm TL (Table 5). Due to the apparent and significant shift in diet and habitat use, all dogfish were grouped as either ≤ 650 mm TL or > 650 mm TL for size-based analysis.

Stomach contents were recovered from 132 dogfish > 650 mm TL, and included all identified prey taxa and categories. Unidentified fish were the prey taxa with the highest relative abundance (65.32% IRI), followed by polychaetes (5.87% IRI) and euphausiids (4.62% IRI) (Table 6). Teleosts were the most important prey category (81.06% IRI) followed by Crustaceans (8.36% IRI) (Table 6). Teleost prey dominated the diet of dogfish > 650 mm TL, both by weight (Figure 10) and relative importance (Figure 11).

Of the 12 spiny dogfish grouped as ≤ 650 mm TL, seven contained prey items in their stomachs. Dogfish in this size class consumed 10 identified prey taxa, of which polychaetes (50.73% IRI), euphausiids (28.38% IRI) and ctenophores (9.17% IRI) were the most important (Table 7). The Crustacean category showed the highest relative importance in the diet of dogfish ≤ 650 mm TL (55.68% IRI), followed by Other Invertebrates (38.31% IRI) (Table 7). Prey taxa in the Other Invertebrate category made up 51.96% of the diet by weight, followed by the Crustaceans (32.65%) (Figure 12). By relative importance, the diet of dogfish ≤ 650 mm TL was dominated by Crustaceans (Figure 13). No prey from the Elasmobranch and Mollusc categories were found in the diet of Immature-sized dogfish.

Dietary overlap was generally low between females and males, and mature and immature dogfish (Table 8, Figure 14). Female dogfish diet overlapped the least with males (31.95%) and the most with dogfish > 650 mm TL (96.17%) (Table 8). Male dogfish did not overlap strongly (> 60%) with any other demographic, and dogfish ≤ 650 mm TL were the only demographic with a higher than 40% overlap with males (54.00%). Dogfish ≤ 650 mm TL also showed weak dietary overlap with other demographics (Table 8).

Spiny dogfish total length showed significant negative correlations with depth surface temperature, and bottom salinity, with depth showing the strongest significant correlation (R=-0.494) (Table 9). All environmental factors showed significant positive correlations with each other, with the exception of surface temperature and bottom salinity. The strongest correlation occurred between depth and surface temperature (R=0.720) (Table 9).

Surface and bottom temperature varied geographically. The highest surface temperatures were observed at stations along the shelf break south of Cape Hatteras, and the lowest were in the shallow areas of the continental shelf north of Cape Hatteras. In general, higher surface temperatures were found in deeper stations along the shelf break and continental slope (Figure 15). Bottom temperature followed a similar pattern, with the lowest temperatures recorded at shallow, inshore stations north of Cape Hatteras and higher temperatures occurring along the shelf break. However, bottom temperatures were warmer than surface temperatures at stations south of Cape Hatteras (Figure 16). Salinity showed similar trends, with less saline water present closer inshore and north of Cape Hatteras at both surface (Figure 17) and bottom (Figure 18) depths.

Correlation analysis between the proportion of identified prey categories in the diet of spiny dogfish and size and environmental factors revealed some significant relationships. By weight, the percentage of the diet made up of prey from the Mollusc, Other Invertebrate, and Teleost categories showed significant negative correlations with depth, surface temperature, and both surface and bottom salinity, while Crustacean prey showed a significant positive correlation with those factors (Table 10). The proportion by weight of Teleost prey in the diet correlated positively with total length, but total length and the Ctenophore category had a significantly negative relationship. Ctenophores did have a significant positive relationship with depth (Table 10). Elasmobranchs were not included in the analysis due to only occurring once in the spiny dogfish diet during this study.

By number, Teleost prey showed the same relationships with size and environmental factors, showing a significant positive correlation with dogfish total length and significant negative correlations with depth, surface temperature, and both salinity measurements (Table 11). Prey in the Other Invertebrate category correlated negatively and significantly with depth, surface temperature, and salinity, and Crustacean prey showed significant positive relationships with those environmental variables. Ctenophores and Molluscs did not show significant correlations with any factors by number (Table 11).

PCA analysis supported the relationships between prey categories, demographic, and environmental factors and was driven by total length and depth (Figure 19). Principle Component 1 was negatively correlated with total length and positively correlated with all other factors, while Principle Component 2 was negatively correlated with depth and positively related to all other factors. For prey categories measured by frequency of occurrence (% O), components 1 and 2 explained approximately 70% of variance. The majority of the variance in prey categories measured by number and weight were informed by more than four principle components and these were not plotted.

Crustacean prey grouped with empty stomachs, showing a positive relationship with depth and a negative relationship with total length. Teleost, Mollusc, and Other Invertebrate prey grouped with larger total lengths and shallower depths, and Ctenophore prey were centrally grouped, overlapping with both Crustaceans and Teleosts (Figure 19-A). Crustacean prey grouped in the same areas as male and immature-sized dogfish, while Teleosts and other prey categories overlapped with female dogfish in the mature size class (Figure 19-A-C).

Discussion

This study confirms that size and sex are important factors determining habitat use by spiny dogfish. Differences in size and habitat selection also influence the diet of spiny dogfish. Generally, these findings support the findings of previous studies establishing that male and immature dogfish inhabit deeper habitats while large females inhabit shallow, inshore areas (Shepherd et al. 2002, Methratta and Link 2007). The relationship between prey selectivity and size is also supported, showing an ontogenetic shift from invertebrate to teleost prey with increasing total length. This shift appears to occur between 600 and 650 mm TL. Diet data also correlate significantly with environmental factors, particularly depth and surface temperature, suggesting that habitat use may play as important a role as size in determining the broad feeding habits of spiny dogfish.

The increased abundance of smaller dogfish and males with increasing depth may also be connected to the reproductive cycle of the spiny dogfish. It is known that spiny dogfish use offshore waters as nursery grounds (Nammack et al. 1985, Hanchet 1988). However, mature males are also generally found further offshore than females (Shepherd et al. 2002). Jones and Ugland (2001) noted that embryonic development is likely influenced by the environmental preferences of female dogfish, which may occupy shallower, warmer waters to encourage the growth of their pups. Once the pups are near-term, the females return to deeper waters to give birth and mate (Nammack et al. 1985, Hanchet 1988, Jones and Ugland 2001). Because the males have no need of warm water to aid in the development of young, they may remain in deeper water.

The results of this study match the observations of previous studies in terms of depth, but found that male and immature dogfish are more abundant at higher temperatures. This is counterintuitive to the typical relationship between shark demographics and environmental factors, where smaller, juvenile sharks are more likely to occur in warm, shallow water (Heithaus 2007). However, the combined influence of local currents and the geography of the North Carolina continental shelf, which reverses the typical relationship between temperature and depth. Stefánsson et al. (1971) found that the near-shore waters north of Cape Hatteras were strongly influenced by colder, lower salinity water from the Chesapeake Bay, while warmer Caribbean water traveled north along the shelf break in the Gulf Stream. Their observations closely match the distribution of surface (Figure 15) and bottom (Figure 16) temperature and surface (Figure 17) and bottom (Figure 18) salinity measurements in this study, demonstrating that outflow from Chesapeake Bay exerts a strong influence on environmental gradients in coastal North Carolina waters.

What remains unclear is whether differences in diet between sexes and size classes are reflections of habitat use or ontogeny. Ellis et al. (1996) found that spiny dogfish in U.K. waters shifted from crustacean to fish prey with increasing size, though in the Northwest Atlantic gelatinous zooplankton may be more important in the diet of immature dogfish (Smith and Link 2010). However, our results suggest that sex may play a role in diet selectivity as well. Males showed low dietary overlap with female or large (> 650 mm TL) dogfish and only moderate dietary overlap with smaller dogfish (≤ 650 mm TL) (Table 8, Figure 14). Since male spiny dogfish inhabit the same habitats as immature dogfish, their diet may be influenced more by prey availability than ontogeny. The high proportion of empty stomachs in both male and small dogfish may indicate that these demographics feed more intermittently than larger females, but may also be a result of more rapid digestion of their preferred prey. Either of these factors may explain why empty stomachs group closely with Crustacean prey in PCA analysis (Figure 19-A). However, dietary differences between the sexes may be an artifact of males having a shorter mean total length than females, and may instead reflect the influence of size rather than sex.

The shift from a diet of crustaceans and benthic invertebrates to piscivory seems to occur in dogfish 600-650 mm TL (Figure 8). This corresponds with previous studies on spiny dogfish feeding habits. Bowman et al. (2000) showed teleost prey making up less than 50% of the diet by weight in spiny dogfish less than 610 mm in length in the Northwest Atlantic. In U.K. waters, crustacean prey made up approximately 42% of the diet of dogfish in the smallest size class (< 600 mm TL), then dropped to 4.4% in the next size class, while teleost prey increased from 47% in the smallest dogfish to 89% in dogfish greater than 600 mm in length and remained above 80% in all subsequent size classes (Ellis et al. 1996). The 601-650 mm TL size range also marks significant shifts in environmental factors (Figure 9-A-C, Table 5), suggesting that an ontogenetic shift in habitat use also occurs within this size range. Methratta and Link (2007) showed that the majority of spiny dogfish in the small (< 400 mm TL) and medium (400-600 mm TL) size classes occupy areas around the shelf break on Georges Bank, and a similar trend appears to occur off of North Carolina. Overall, significant ontogenetic shifts are occurring between 600 and 650 mm TL, though this may represent multiple years of growth due to the slow growth rate of spiny dogfish (Nammack et al. 1985). Further research with a greater sample size of small dogfish should more precisely determine the size at which these shifts occur.

The data used in this study represent only one year of intense sampling, and may be limited in their ability to explain long-term trends in spiny dogfish feeding habits in North Carolina waters. Though female dogfish and the larger size classes were well represented, low sample sizes of both male and small spiny dogfish may be a source of bias. The importance of taxa such as euphasiids and ctenophores may have been underestimated due to the rapid digestion of these small, soft-bodied prey (Arai 2005). The results of this study reveal some significant relationships between diet, size, and environmental factors that are supported by previous literature, but thorough sampling of all spiny dogfish demographics over multiple years will be needed to determine if these findings are useful to long-term understanding of their trophic relationships in North Carolina waters.

Ontogenetic shifts in diet may be facilitated by shifts in habitat use and allow mature and immature conspecifics to specialize in utilizing different resources. Therefore ontogenetic shifts may be important in reducing intraspecific competition in shark species (Grubbs 2010). Habitat use by spiny dogfish is closely related to sex (Shepherd et al. 2002) and size (Methratta and Link 2007) and feeding habits are also related to these demographic factors (Alonso et al. 2002, Smith and Link 2010). By lessening the opportunity for intraspecific competition, the relationships between size, sex, habitat selection, and diet may be key to the adaptive success of spiny dogfish.

References

Alonso, M.K., E.A. Crespo, N.A. Garcia, S.N. Pedraza, P.A. Mariotti, and N.J. Mora. 2002. Fishery and ontogenetic driven changes in the diet of the spiny dogfish, *Squalus acanthias*, in Patagonian waters, Argentina. Environmental Biology of Fishes 63: 193-202.

Arai, M.N. 2005. Predation on pelagic coelenterates: a review. Journal of the Marine Biological Association of the United Kingdom 85: 523-536.

Auster, P.J. and J.S. Link. 2009. Compensation and recovery of feeding guilds in a northwest Atlantic shelf fish community. Marine Ecology Progress Series 382: 163-172.

Bearden, C.M. 1965. Occurrence of spiny dogfish, *Squalus acanthias*, and other elasmobranchs in South Carolina coastal waters. Copeia 1965: 378-378.

Bowman, R.E., C.E. Stillwell, W.L. Micheals, and M.D. Grosslein. 2000. Food of Atlantic fishes and two common species of squid. NOAA Technical Memorandum NMFS-NE-155. NOAA, Woods Hole, Massachusetts.

Bray, J.R. and J.T. Curtis. 1957. An ordination of the upland forest communities of southern Wisconsin. Ecological Monographs 27: 325-349.

Burgess, G.H. 2002. Spiny dogfish/*Squalus acanthias* Linneaus 1785. Pages 54-57 *in* B.B. Collette and G. Klein-MacPhee, editors. Bigelow and Schroeder's fishes of the Gulf of Maine, 3rd edition. Smithsonian Institution Press, Washington, D.C.

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

Demirhan, S.A., K. Seyhan, and N. Basuta. 2007. Dietary overlap in spiny dogfish (*Squalus* *acanthias*) and thornback ray (*Raja clavata*) in the southeastern Black Sea. Ekoloji 62: 1-8.

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

Fogarty, M.J. and S.A. Murawski. 1998. Large-scale disturbance and the structure of marine systems: fishery impacts on Georges Bank. Ecological Applications 8: S6-S22.

Garrison, L.P., and J.S. Link. 2000. Dietary guild structure of the fish community in the Northeast United States continental shelf ecosystem. Marine Ecology Progress Series 202: 231-240.

Grubbs, R.D. 2010. Ontogenetic shifts in movements and habitat use. Pages 319-342 *in* J.C. Carrier, J.A. Musick, and M.R. Heithaus, editors. Sharks and their relatives II: biodiversity, adaptive physiology, and conservation. CRC Press, Boca Raton, Florida.

Hanchet, S. 1988. Reproductive biology of *Squalus acanthias* from the east coast, South Island, New Zealand. New Zealand Journal of Marine and Freshwater Research 22: 537-549.

Heithaus, M.R. 2007. Nursery areas as essential shark habitats: a theoretical perspective. Pages 3-13 *in* C.T. McCandless, N.E. Kohler, and H.L. Pratt, editors. Shark nursery grounds of the Gulf of Mexico and the east coast of the United States. American Fisheries Society, Symposium 50, Bethesda, Maryland.

Jones, T.S. and K.I. Ugland. 2001. Reproduction of female spiny dogfish, *Squalus acanthias*, in the Oslofjord. Fishery Bulletin 99: 685-690.

Laptikhovsky, V.V., A.I. Arkhipkin, and A.C. Henderson. 2001. Feeding habits and dietary overlap in spiny dogfish *Squalus acanthias* (Squalidae) and narrowmouth catshark

Schroederichthys bivius (Scyliorhinidae). Journal of the Marine Biological Association of the United Kingdome 81: 1015-1018.

Link, J.S. and M.D. Ford. 2006. Widespread and persistent increase of Ctenophora in the continental shelf ecosystem off NE USA. Marine Ecology Progress Series 320: 153-159.

Link, J.S. and L.P. Garrison. 2002. Changes in piscivory associated with fishing induced changes in the finfish community on Georges Bank. Fisheries Research 55: 71-86.

Link, J.S., L.P. Garrison, and F.P. Almeida. 2002. Ecological interactions between elasmobranchs and groundfish species on the Northeastern U.S. contintental shelf. I. Evaluating predation. North American Journal of Fisheries Managament 22: 550-562.

Methratta, E.T. and J.S. Link. 2007. Ontogenetic variation in habitat association for four groundfish species in the Gulf of Maine – Georges Bank region. Marine Ecology Progress Series 338: 169-181.

Nammack, M.F., J.A. Musick, and J.A. Colvocoresses. 1985. Life history of the spiny dogfish off the Northeastern United States. Transactions of the American Fisheries Society 114: 367-376.

Overholtz, W.J. and J.S. Link. 2007. Consumption impacts by marine mammals, fish and seabirds on the Gulf of Maine-Georges Bank Atlantic herring (*Clupea harengus*) complex during the years 1977-2002. ICES Journal of Marine Science 64: 83-96.

Rulifson, R.A. and T.M. Moore. 2009. Population estimates of spiny dogfish aggregations overwintering south of Cape Hatteras, North Carolina, using an area density method. Pages 133-138 *in* V.F. Gallucci, G.A. McFarlane, and G.G. Bargmann, editors. Biology and management of dogfish sharks. American Fisheries Society, Bethesda, Maryland.

Shepherd, T., F. Page, and B. MacDonald. 2002. Length and sex-specific associations between spiny dogfish (*Squalus acanthias*) and hydrographic variables in the Bay of Fundy and Scotian Shelf. Fisheries Oceanography 11: 78-89.

Smith, B.E. and J.S. Link. 2010. The trophic dynamics of 50 finfish and 2 squid species on the Northeast U.S. continental shelf. NOAA Technical Memorandum NMFS-NE-216, NOAA, Woods Hole, Massachusetts.

Stauffer, G. 2004. NOAA protocols for groundfish bottom trawl surveys of the nation's fishery resources. NOAA Technical Memorandum NMFS-SPO-65. NOAA, Woods Hole, Massachusetts.

Stefánsson, U., L.P. Atkinson, and D.F. Bumpus. 1971. Hydrographic properties and circulation of the North Carolina shelf and slope waters. Deep-Sea Research 18: 383-420.

Stehlik, L.L. 2007. Essential fish habitat source document: spiny dogfish, *Squalus acanthias*, life history and habitat characteristics. NOAA Technical Memorandum NMFS-NE-203, NOAA, Woods Hole, Massachusetts.

Ulrich, G.F., C.M. Jones, W.B. Driggers, III, J.M. Drymon, D. Oakley, and C. Riley. 2007. Habitat utilization, relative abundance, and seasonality of sharks in the estuarine and nearshore waters of South Carolina. Pages 125-139 *in* C.T. McCandless, N.E. Kohler, and H.L. Pratt, editors. Shark nursery grounds of the Gulf of Mexico and the east coast of the United States. American Fisheries Society, Symposium 50, Bethesda, Maryland.

Van Den Avyle, M.J. and J.E. Roussel. 1980. Evaluation of a simple method for removing food items from live black bass. The Progressive Fish Culturist 42: 222-223.

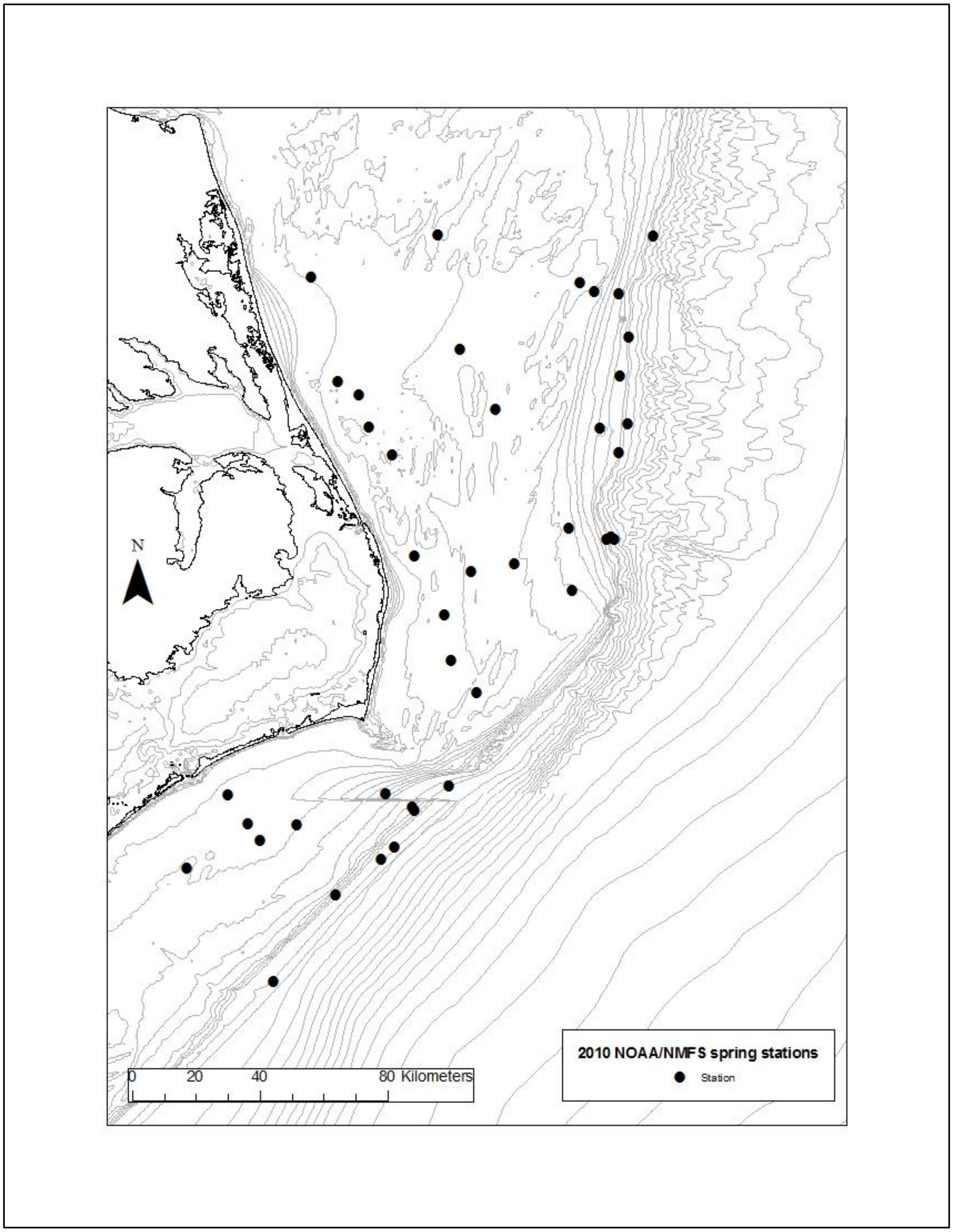


Figure 2-1. Sampling stations in North Carolina waters from the 2010 NOAA/NMFS spring bottom trawl survey.

Table 2-1. All prey taxa collected from spiny dogfish stomach contents during the 2010 NOAA/NMFS spring bottom trawl survey, grouped by category.

Prey taxa/category	Scientific name
Teleost	
Atlantic croaker	*Micropogonias undulatus*
Atlantic menhaden	*Brevoortia tyrannus*
Bay anchovy	*Anchoa mitchilli*
Beardfish	*Polymixia lowei*
Black sea bass	*Centropristis striata*
Butterfish	*Peprilus triacanthus*
Cusk eel sp.	Ophidiidae
Darter Goby	*Ctenogobius boleosoma*
Flounder left-eye	Paralichthyidae
Goby sp.	Gobiiae
Gulf Stream Flounder	*Citharichthys arctifrons*
Hake sp.	*Urophycis* sp.
Lantern fish sp.	Phosichtheyidae
Northern Searobin	*Prionotus carolinus*
Pipefish sp.	*Sygnathus* sp.
Red hake	*Urophycis chuss*
Sand Lance	*Ammodytes americanus*
Searobin sp.	*Prionotus* sp.
Smallmouth Flounder	*Etropus microstomus*
Snake Eel	*Ophichthus cruentifer*
Snake Mackerel	Gempylidae
Spotted Hake	*Urophycis regia*
Tonguefish sp.	Cynoglossidae
Unidentified fish	Teleostii
Unidentified flatfish	Pleuronectiformes
Wenchman	*Pristipomoides aquilonaris*
Windowpane Flounder	*Scopthalamus aquosus*
Wrasse sp.	Labridae
Elasmobranch	
Unidentified skate	Rajidae
Crustacean	
Amphipods	Amphipoda
Cancer crab	*Cancer* sp.
Decapod	Decapoda
Euphausiid	Euphausiidae
Hermit Crab	Paguroidea
Jonah Crab	*Cancer borealis*

Lobster sp.	Nephropidae
Mantis shrimp sp.	Stomatopoda
Penaeid shrimp	*Penaeus* sp.
Portunid crab	Portunidae
Unidentified crab	Brachyura
Unidentified crustacean	Crustacea
Unidentified shrimp	Malacostraca
Mollusc	
Bivalve	Bivalva
Bobtail Squid	*Rossia* sp.
Gastropod	Gastropoda
Loligo squid	*Loligo pealeii*
Octopus	*Octopus vulgaris*
Unidentified mollusc	Mollusca
Unidentified squid	Teuthoidea
Ctenophore	
Comb jelly	Ctenophora
Other Invertebrate	
Polychaete	Polychaeta
Sand Dollar	Clypeasteroidea
Sea Cucumber	Holothuroidea
Unidentified invertebrate	-
Unidentified worm	-

Table 2-2. Percent weight, number, frequency of occurrence, and Index of Relative Importance for all prey taxa and prey categories included in the diet of female spiny dogfish (n = 105).

	Prey	%N	%W	%O	%IRI
Prey Taxa	Unidentified fish	15.95	26.23	45.71	63.93
	Polychaete	9.20	4.80	19.05	8.84
	Unidentifed shrimp	7.06	1.66	16.19	4.68
	Sea Cucumber	5.21	6.58	9.52	3.72
	Ctenophore	3.07	4.85	9.52	2.50
	Euphausiid	7.06	0.25	9.52	2.31
	Northern Searobin	5.52	2.55	8.57	2.29
	Tonguefish sp.	1.23	11.41	3.81	1.60
	Animal Remains	2.76	2.05	8.57	1.37
	Spotted Hake	2.76	2.92	5.71	1.08
	Unidentified invertebrate	2.15	2.54	6.67	1.04
	Loligo squid	1.84	4.14	4.76	0.94
	Atlantic menhaden	3.37	1.22	5.71	0.87
	Bivalve	1.53	3.25	4.76	0.76
	Bobtail Squid	1.53	1.20	4.76	0.43
	Wrasse sp.	1.53	3.59	1.90	0.32
	Algae/Detritus	1.53	0.46	4.76	0.32
	Gulf Stream Flounder	1.23	1.78	2.86	0.28
	Darter Goby	1.84	0.21	3.81	0.26
	Decapod	1.23	0.62	3.81	0.23
	Hake sp.	1.23	0.47	3.81	0.21
	Searobin sp.	1.23	0.36	3.81	0.20
	Flounder left-eye	0.92	0.84	2.86	0.17
	Unidentified worms	1.23	0.28	2.86	0.14
	Unidentified squid	0.92	0.56	2.86	0.14
	Croaker Atlantic	0.61	1.09	1.90	0.11
	Octopus	1.23	0.42	1.90	0.10
	Bay anchovy	1.23	0.40	1.90	0.10
	Hermit Crab	0.61	0.83	1.90	0.09
	Smallmouth Flounder	0.92	0.34	1.90	0.08
	Unidentified mollusc	0.61	1.84	0.95	0.08
	Butterfish	0.61	1.66	0.95	0.07
	Unidentified flatfish	0.92	0.16	1.90	0.07
	Wenchman	0.61	1.49	0.95	0.07
	Mantis Shrimp sp.	0.61	0.37	1.90	0.06
	Beardfish	0.61	0.32	1.90	0.06
	Unidentified skate	0.31	1.53	0.95	0.06
	Red hake	0.31	1.30	0.95	0.05
	Pipefish sp.	0.61	0.08	1.90	0.04
	Lobster sp.	0.31	0.87	0.95	0.04

	Lantern fish	0.61	0.13	0.95	0.02
	Black sea bass	0.31	0.43	0.95	0.02
	Goby sp.	0.31	0.38	0.95	0.02
	Jonah crab	0.31	0.28	0.95	0.02
	Peneaid shrimp	0.31	0.17	0.95	0.02
	Sand lance	0.31	0.16	0.95	0.01
	Cusk eel	0.31	0.15	0.95	0.01
	Snake Eel	0.31	0.15	0.95	0.01
	Portunid crab	0.31	0.15	0.95	0.01
	Windowpane Flounder	0.31	0.13	0.95	0.01
	Unidentified crab	0.31	0.12	0.95	0.01
	Cancer Crab	0.31	0.06	0.95	0.01
	Amphipods	0.31	0.04	0.95	0.01
	Gastropod	0.31	0.04	0.95	0.01
	Sand dollar	0.31	0.03	0.95	0.01
	Unidentified crustacean	0.31	0.01	0.95	0.01
	Snake mackerel	0.31	0.00	0.95	0.01
Category	Teleost	46.63	59.94	112.38	81.01
	Other Invertebrate	18.10	14.23	39.05	8.54
	Crustacean	19.02	5.45	40.95	6.78
	Mollusc	7.98	11.43	20.95	2.75
	Ctenophore	3.07	4.85	9.52	0.51
	Unidentified	2.76	2.05	8.57	0.28
	Detritus	2.15	0.53	6.67	0.12
	Elasmobranch	0.31	1.53	0.95	0.01

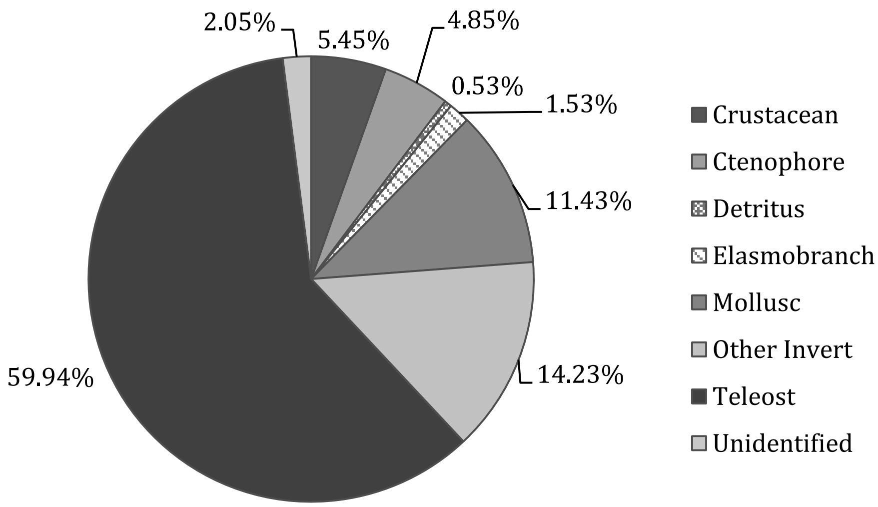


Figure 2-2. Percentage by weight (g) of each prey category in the diet of female spiny dogfish (n=105).

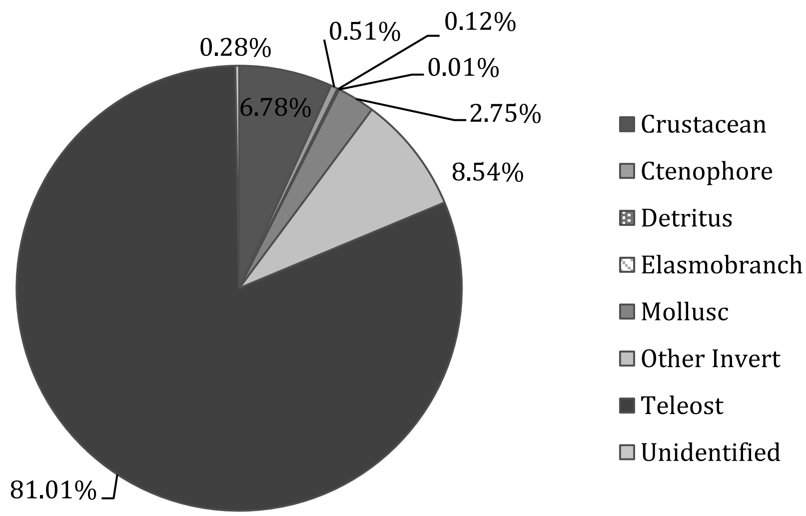


Figure 2-3. Percentage by relative importance (% IRI) of each prey category in the diet of female spiny dogfish (n=105).

Table 2-3. Percent weight, number, frequency of occurrence, and Index of Relative Importance for all prey taxa and prey categories included in the diet of male spiny dogfish (n = 16).

	Prey	%N	%W	%O	%IRI
Prey Taxa	Euphausiid	48.00	9.27	62.50	66.56
	Unidentified fish	12.00	84.29	12.50	22.38
	Ctenophore	12.00	2.94	18.75	5.21
	Animal Remains	8.00	2.41	12.50	2.42
	Unidentified crustacean	8.00	0.45	12.50	1.96
	Decapod	4.00	0.38	6.25	0.51
	Unidentified shrimp	4.00	0.26	6.25	0.50
	Algae/Detritus	4.00	0.00	6.25	0.46
Category	Crustacean	64.00	10.36	87.50	79.88
	Teleost	12.00	84.29	12.50	14.78
	Ctenophore	12.00	2.94	18.75	3.44
	Unidentified	8.00	2.41	12.50	1.60
	Detritus	4.00	0.00	6.25	0.31

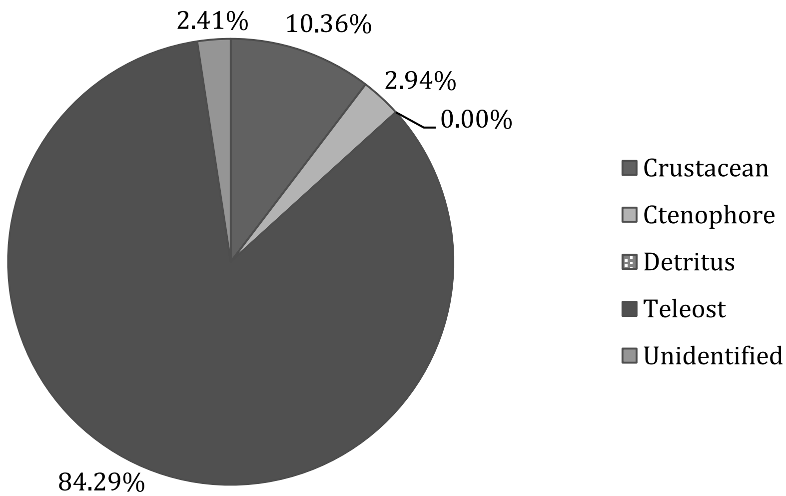


Figure 2-4. Percentage by weight (g) of each prey category in the diet of male spiny dogfish (n=16).

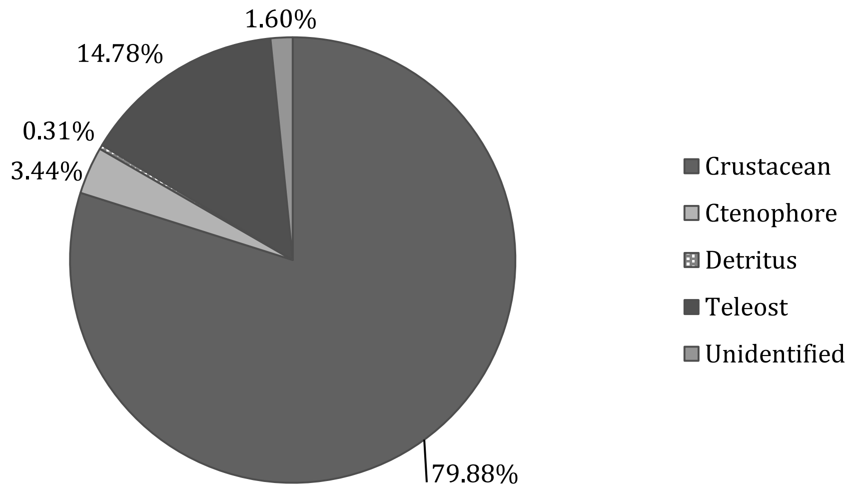


Figure 2-5. Percentage by relative importance (% IRI) of each prey category in the diet of male spiny dogfish (n=16).

Table 2-4. Mean total length, depth, surface and bottom temperature, and surface and bottom salinity ± standard error (SE) for female and male spiny dogfish, and Student's t-test results (*p*) comparing each measurement between the sexes (α=0.05).

Measurement	Female	Male	*p*
n	116	30	-
Total length (mm)	785.30 ± 7.38	729.70 ± 15.61	0.0005
Avg. Depth (m)	54.02 ± 5.16	185.70 ± 13.58	<0.0001
Surface Temp (°C)	5.76 ± 0.10	7.30 ± 0.13	<0.0001
Bottom Temp (°C)	7.13 ± 0.34	9.11 ± 0.22	0.0044
Surface Salinity (ppm)	32.99 ± 0.12	34.12 ± 0.04	<0.0001
Bottom Salinity (ppm)	33.64 ± 0.06	34.64 ± 0.05	<0.0001

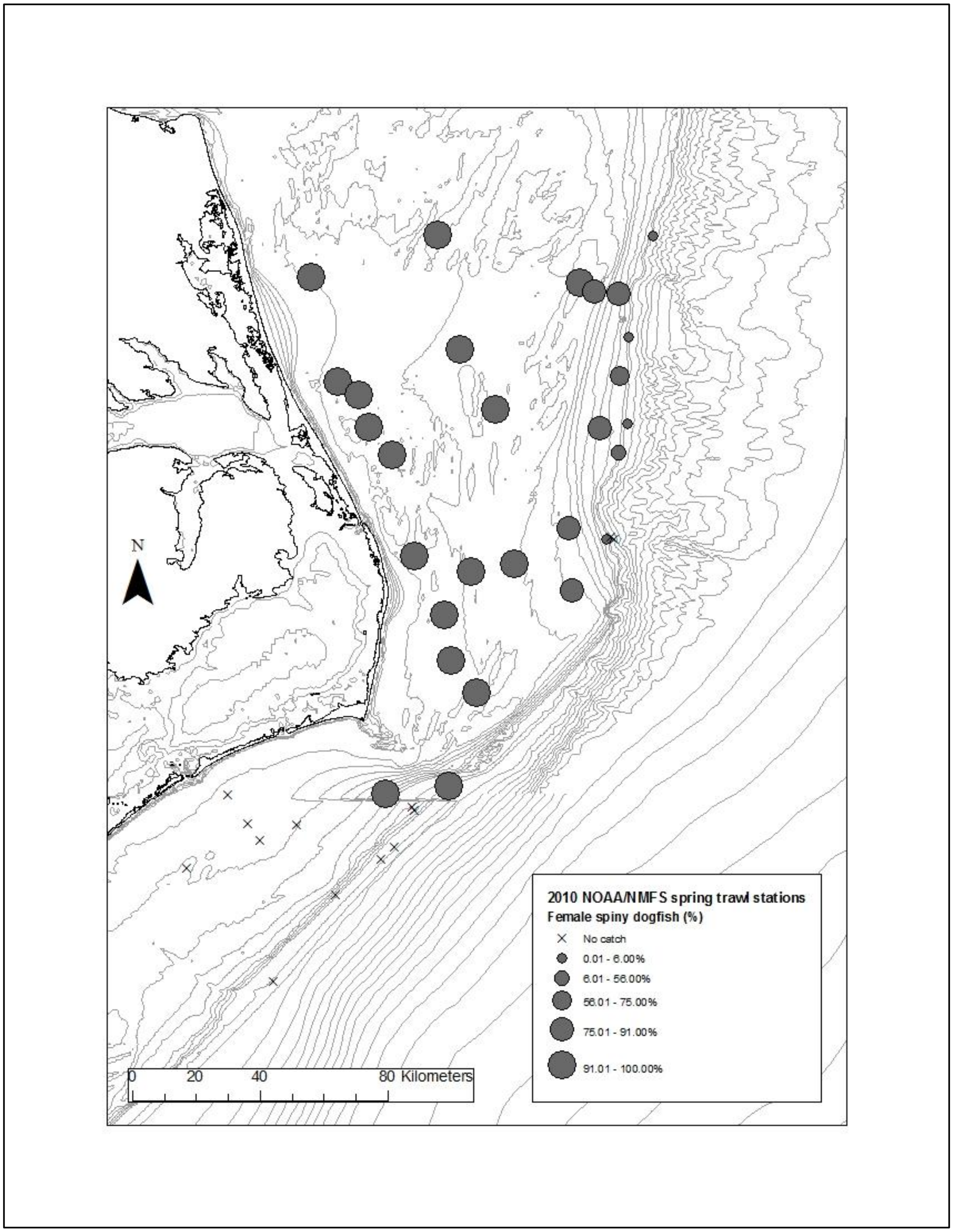


Figure 2-6. Percentage of spiny dogfish catch by number made up of females at stations sampled during the 2010 NOAA/NMFS spring bottom trawl survey.

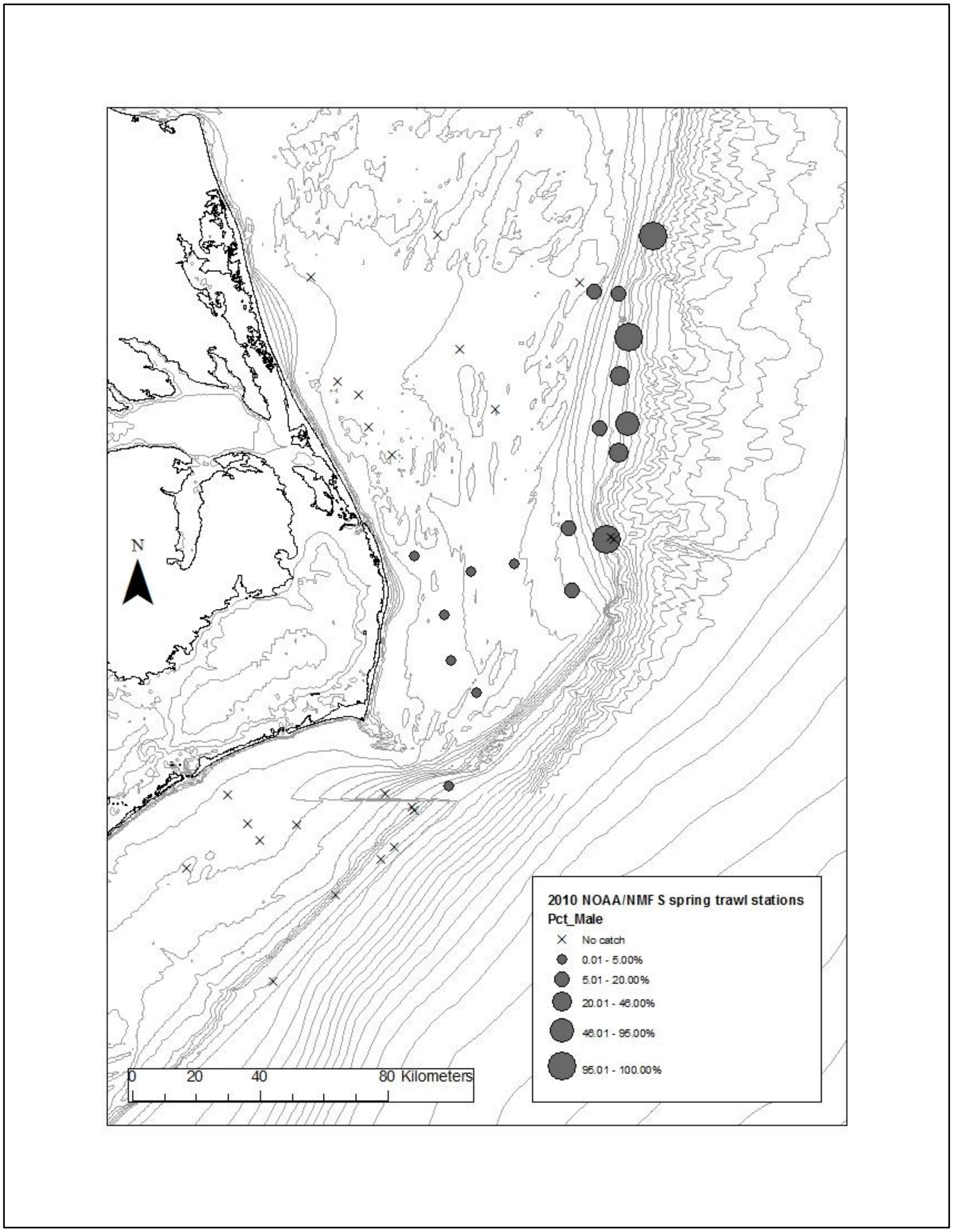


Figure 2-7. Percentage of spiny dogfish catch by number made up of males at stations sampled during the 2010 NOAA/NMFS spring bottom trawl survey.

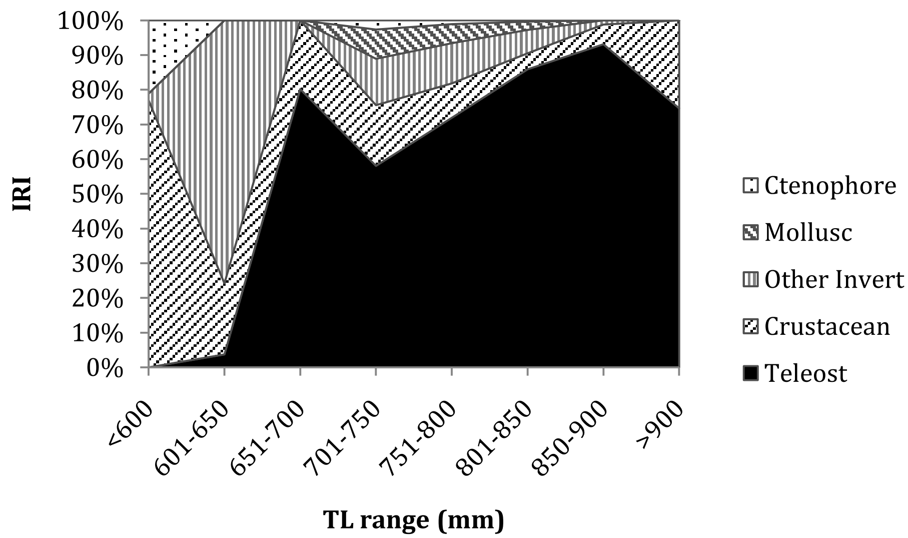


Figure 2-8. Relative importance (% IRI) of prey categories in the diet of spiny dogfish over 50 mm increments of total length.

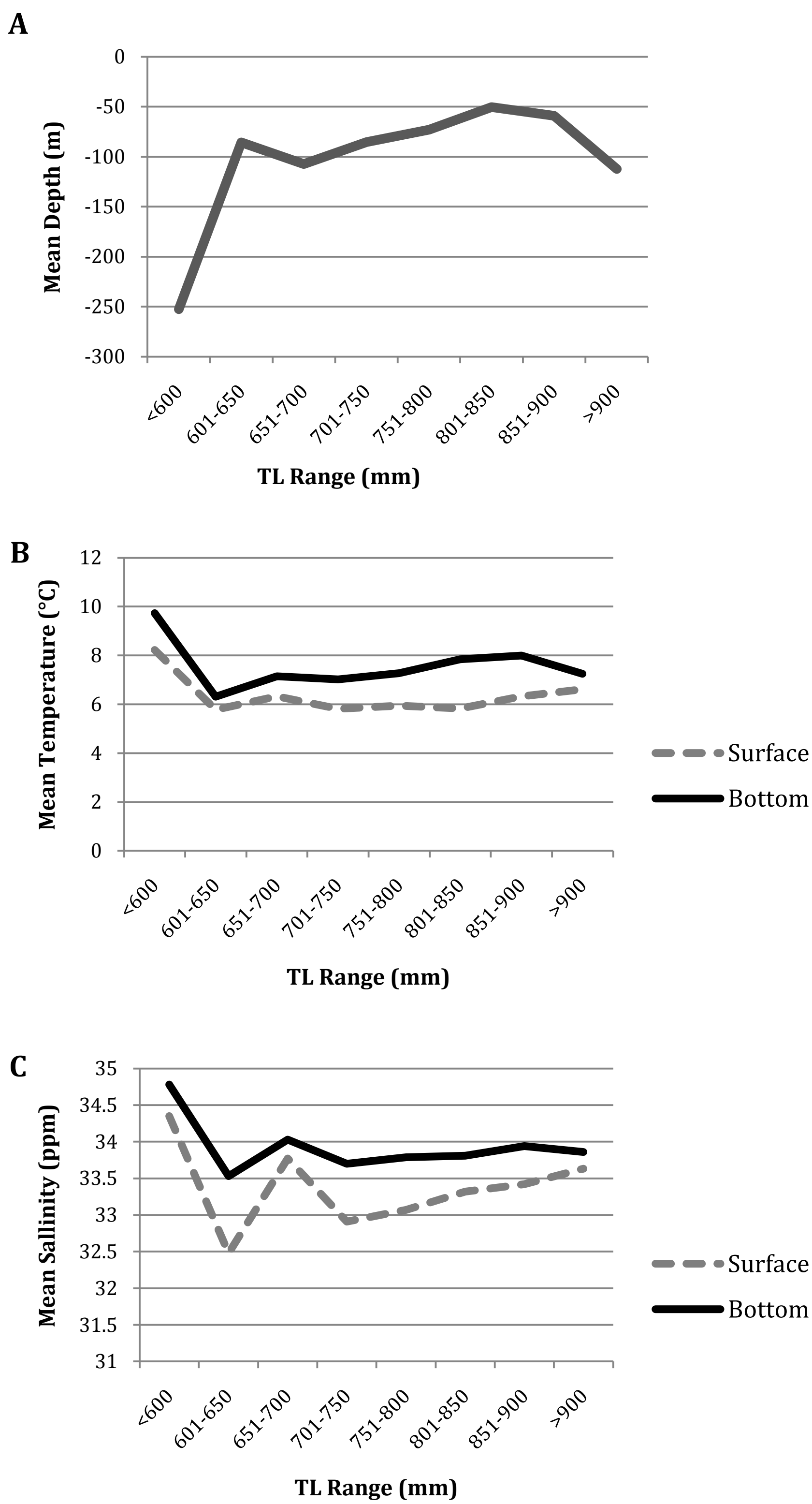


Figure 2-9. Trends in mean depth (A) mean temperature (B) and mean salinity (C) measurements over 50 mm increments of spiny dogfish total length.

Table 2-5. Mean depth, surface and bottom temperature, and surface and bottom salinity ± standard error (SE) for spiny dogfish ≤ 650 mm and > 650 mm TL, and Student's t-test results (*p*) comparing each measurement between the size classes (α=0.05).

Measurement	≤ 650	> 650	p
n	12	152	-
Avg. Depth (m)	196.80 ± 29.05	70.70 ± 6.00	<0.0001
Surface Temp (°C)	7.41 ± 0.47	5.96 ± 0.09	<0.0001
Bottom Temp (°C)	8.59 ± 0.59	7.44 ± 0.30	0.2669
Surface Salinity (ppm)	33.73 ± 0.39	33.18 ± 0.11	0.1538
Bottom Salinity (ppm)	34.36 ± 0.22	33.80 ± 0.06	0.0094

Table 2-6. Percent weight, number, frequency of occurrence, and Index of Relative Importance for all prey taxa and prey categories included in the diet of spiny dogfish > 650 mm TL (n = 132).

	Prey Taxa	%N	%W	%O	%IRI
Prey Taxa	Unidentified fish	16.22	28.11	37.12	65.32
	Polycheate	7.51	3.98	12.88	5.87
	Euphausiid	8.71	0.34	12.88	4.62
	Unidentified shrimp	6.91	1.64	12.88	4.37
	Sea Cucumber	5.11	6.50	7.58	3.49
	Ctenophore	3.30	4.71	8.33	2.65
	Northern Searobin	5.41	2.52	6.82	2.15
	Animal Remains	3.30	2.09	8.33	1.78
	Tonguefish sp.	1.20	11.27	3.03	1.50
	Spotted Hake	2.70	2.88	4.55	1.01
	Loligo squid	1.80	4.09	3.79	0.89
	Atlantic menhaden	3.30	1.20	4.55	0.81
	Unidentified invertebrate	1.80	2.50	4.55	0.78
	Bivalve	1.50	3.21	3.79	0.71
	Algae/Detritus	1.80	0.46	4.55	0.41
	Bobtail Squid	1.50	1.18	3.79	0.40
	Decapod	1.50	0.62	3.79	0.32
	Wrasse	1.50	3.55	1.52	0.30
	Gulf Stream Flounder	1.20	1.76	2.27	0.27
	Darter Goby	1.80	0.21	3.03	0.24
	Hake sp.	1.20	0.46	3.03	0.20
	Searobin sp.	1.20	0.35	3.03	0.19
	Flounder left-eye	0.90	0.83	2.27	0.16
	Unidentified worms	1.20	0.28	2.27	0.13
	Unidentified squid	0.90	0.55	2.27	0.13
	Atlantic croaker	0.60	1.08	1.52	0.10
	Octopus	1.20	0.41	1.52	0.10
	Bay anchovy	1.20	0.40	1.52	0.10
	Hermit Crab	0.60	0.82	1.52	0.09
	Crustacean	0.90	0.02	2.27	0.08
	Smallmouth Flounder	0.90	0.33	1.52	0.07
	Unidentified mollusc	0.60	1.82	0.76	0.07
	Butterfish	0.60	1.64	0.76	0.07
	Unidentified flatfish	0.90	0.16	1.52	0.06
	Wenchman	0.60	1.47	0.76	0.06
	Beardfish	0.60	0.32	1.52	0.06
	Unidentified skate	0.30	1.51	0.76	0.05
	Red hake	0.30	1.28	0.76	0.05
	Pipefish sp.	0.60	0.08	1.52	0.04
	Lobster	0.30	0.86	0.76	0.03

	Lantern fish	0.60	0.12	0.76	0.02
	Black sea bass	0.30	0.42	0.76	0.02
	Goby sp.	0.30	0.38	0.76	0.02
	Jonah Crab	0.30	0.28	0.76	0.02
	Peneaid shrimp	0.30	0.17	0.76	0.01
	Sand Lance	0.30	0.16	0.76	0.01
	Cusk eel	0.30	0.15	0.76	0.01
	Snake Eel	0.30	0.15	0.76	0.01
	Portunid crab	0.30	0.15	0.76	0.01
	Windowpane Flounder	0.30	0.13	0.76	0.01
	Unidentified crab	0.30	0.12	0.76	0.01
	Mantis Shrimp sp.	0.30	0.11	0.76	0.01
	Bird	0.30	0.05	0.76	0.01
	Amphipods	0.30	0.04	0.76	0.01
	Gastropod	0.30	0.04	0.76	0.01
	Sand Dollar	0.30	0.03	0.76	0.01
	Snake Mackerel	0.30	<0.01	0.76	0.01
Category	Teleost	46.25	61.41	90.15	81.06
	Crustacean	20.72	5.18	38.64	8.36
	Other Invert	15.92	13.29	28.03	6.84
	Mollusc	7.81	11.29	16.67	2.66
	Ctenophore	3.30	4.71	8.33	0.56
	Unidentified	3.30	2.09	8.33	0.38
	Detritus	2.40	0.52	6.06	0.15
	Elasmobranch	0.30	1.51	0.76	0.01

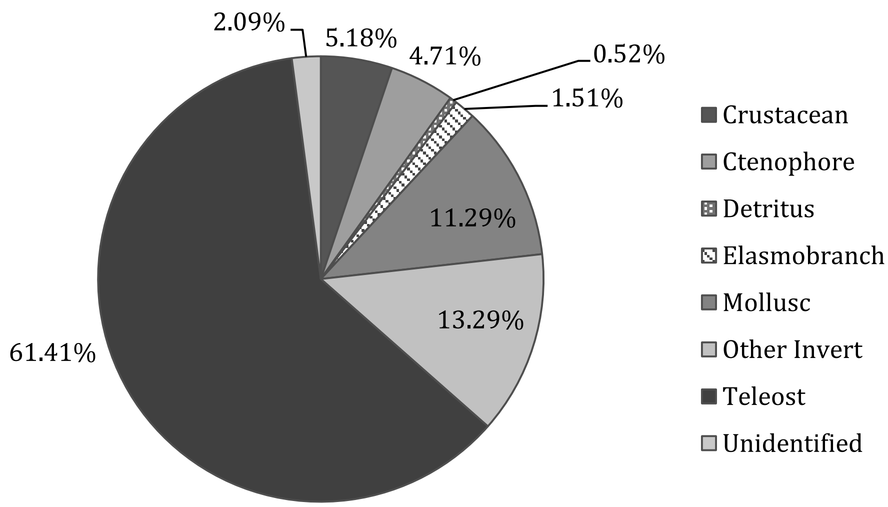


Figure 2-10. Percentage by weight (g) of each prey category in the diet of spiny dogfish > 650 mm TL (n=132).

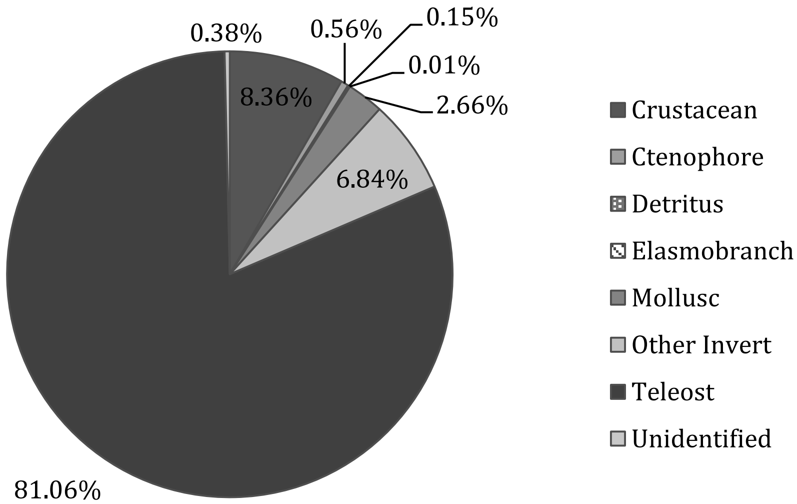


Figure 2-11. Percentage by relative importance (% IRI) for each prey category in the diet in spiny dogfish > 650 mm TL (n=132).

Table 2-7. Percent weight, number, frequency of occurrence, and Index of Relative Importance for all prey taxa and prey categories included in the diet of spiny dogfish ≤650 mm TL (n = 7).

	Prey	%N	%W	%O	%IRI
Prey Taxa	Polychaete	27.78	51.48	42.86	50.73
	Euphausiid	33.33	11.00	42.86	28.38
	Ctenophore	11.11	10.38	28.57	9.17
	Mantis Shrimp sp.	5.56	17.32	14.29	4.88
	Unidentifed fish	5.56	5.02	14.29	2.26
	Cancer sp.	5.56	3.85	14.29	2.01
	Unidentified invertebrate	5.56	0.48	14.29	1.29
	Unidentifed shrimp	5.56	0.48	14.29	1.29
Category	Crustacean	50.00	32.65	85.71	55.68
	Other Invert	33.33	51.96	57.14	38.31
	Ctenophore	11.11	10.38	28.57	4.83
	Teleost	5.56	5.02	14.29	1.19

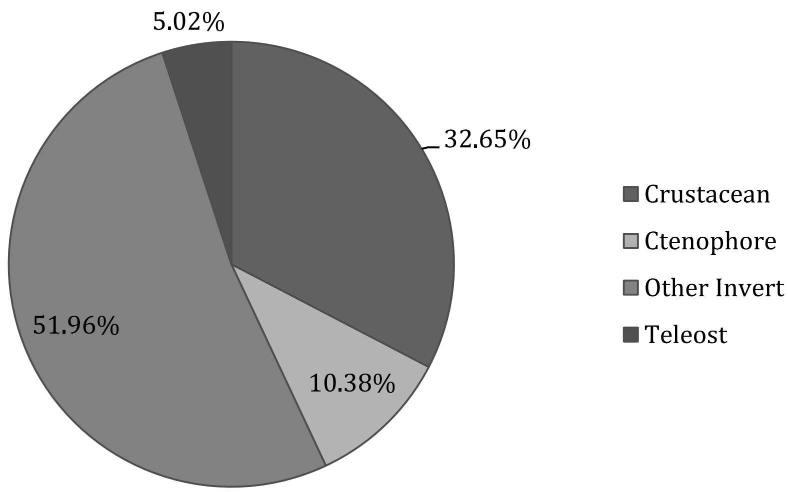


Figure 2-12. Percentage by weight (g) of each prey category in the diet of spiny dogfish ≤ 650 mm TL (n=12).

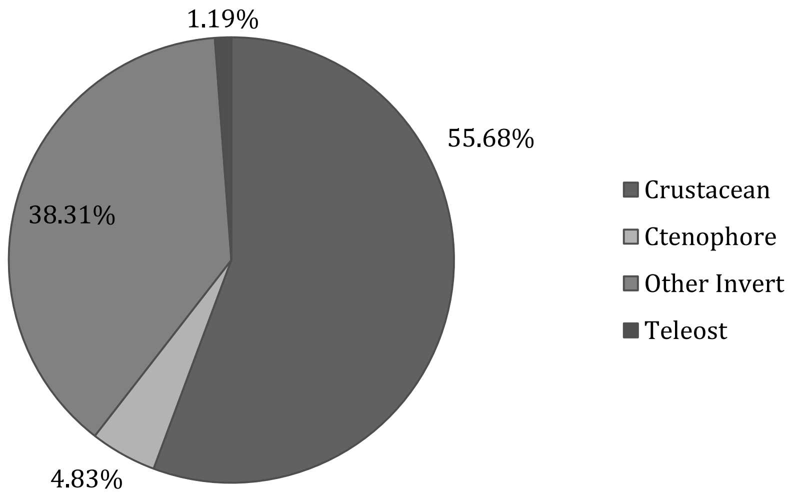


Figure 2-13. Percentage by relative importance (% IRI) of each prey category in the diet of spiny dogfish in the Immature size class (≤700 mm TL) (n=12).

Table 2-8. Dietary overlap expressed as Bray-Curtis Index of Similarity (% BCIS) values between spiny dogfish in the Female, Male, > 650 mm TL, and ≤ 650 mm TL demographics.

BCIS	Females	Males	> 650 mm	≤ 650 mm
Females	100.00			
Males	31.95	100.00		
> 650 mm	96.17	35.52	100.00	
≤ 650 mm	33.50	54.00	32.73	100.00

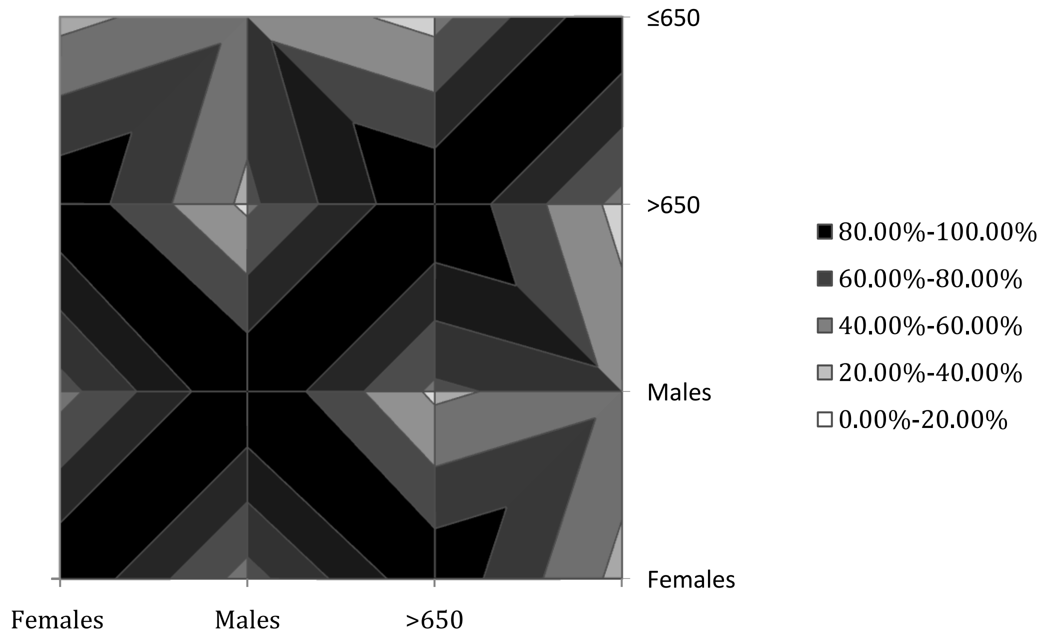


Figure 2-14. Dietary overlap (% BCIS) between male, female, large (> 650 mm TL), and small (≤ 650 mm TL) spiny dogfish.

Table 2-9. Pearson correlations (R) between spiny dogfish total length (TL, mm), average depth (m), surface temperature (°C), and bottom temperature (°C) from the 2010 NOAA/NMFS spring bottom trawl survey.

R	TL (mm)	Avg. Depth (m)	Surface Temp (°C)	Bottom Temp (°C)	Surface Sal (ppm)	Bottom Sal (ppm)
TL (mm)	1					
Avg. Depth (m)	-0.494*	1				
Surface Temp (°C)	-0.248*	0.720*	1			
Bottom Temp (°C)	-0.091	0.505*	0.382*	1		
Surface Sal (ppm)	-0.097	0.386*	0.693*	-0.019	1	
Bottom Sal (ppm)	-0.182*	0.736*	0.865*	0.515*	0.757*	1

* = significant at $\alpha = 0.05$

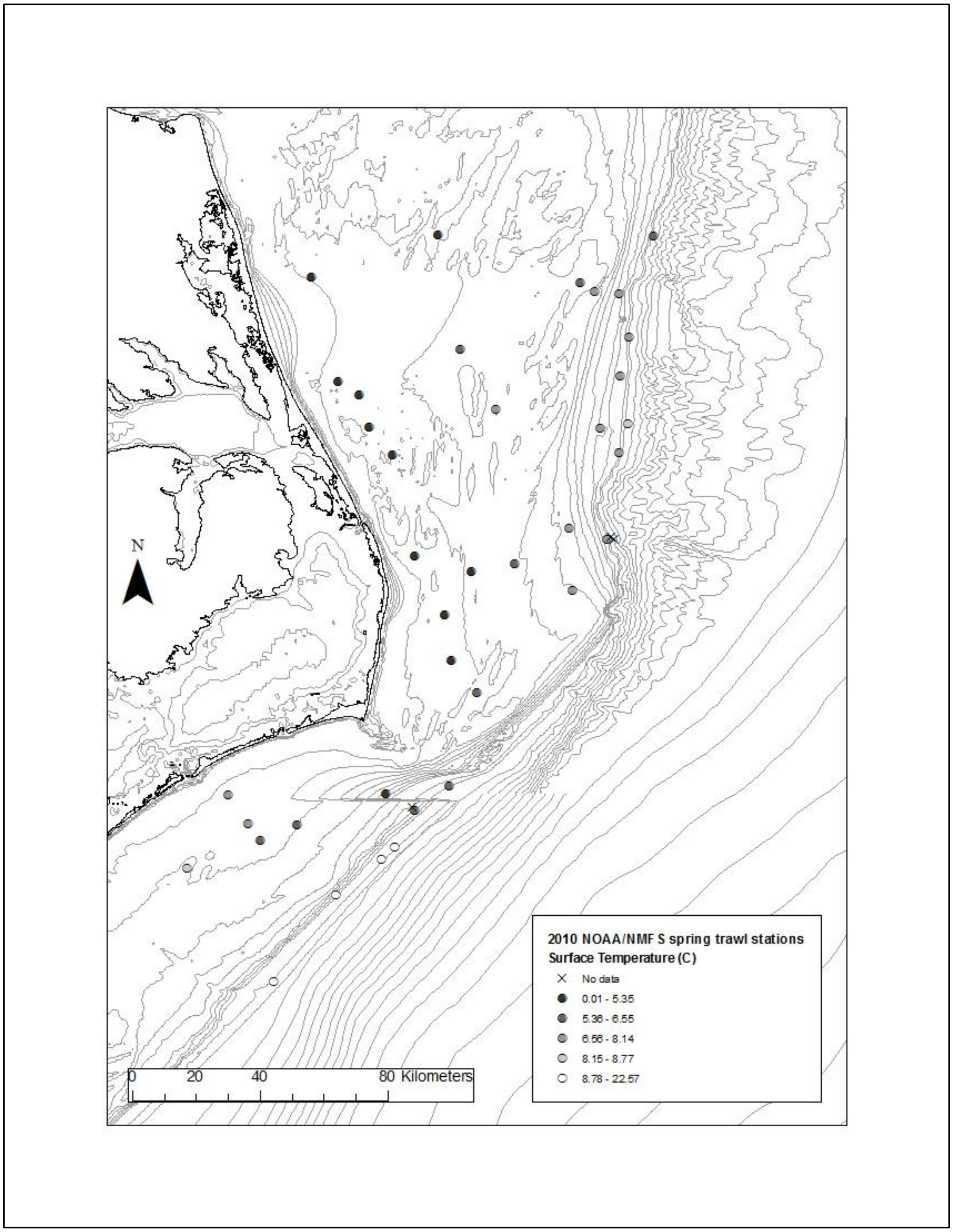


Figure 2-15. Surface temperature (°C) at stations in North Carolina waters sampled during the 2010 NOAA/NMFS spring bottom trawl survey.

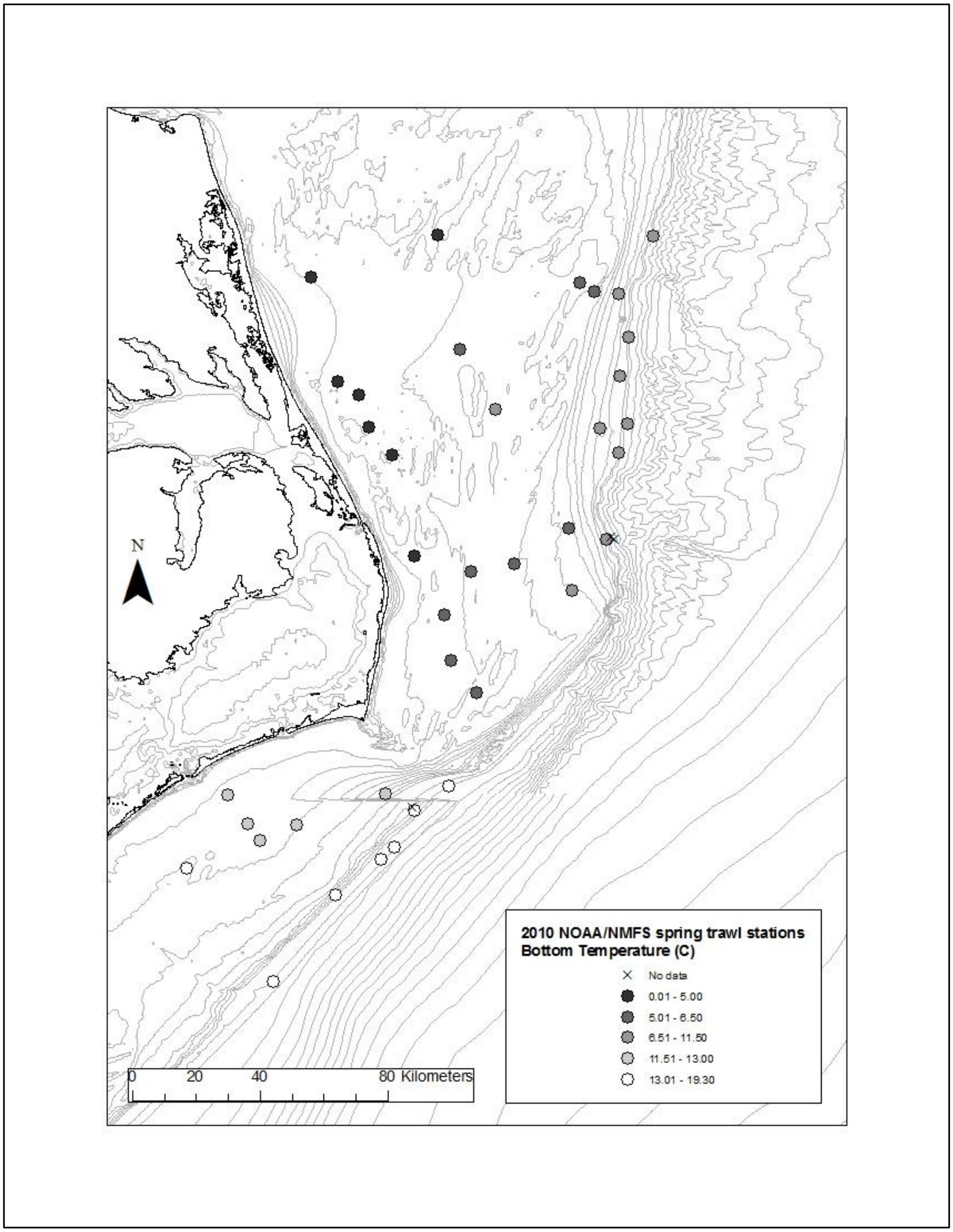


Figure 2-16. Bottom temperature (°C) at stations in North Carolina waters sampled during the 2010 NOAA/NMFS spring bottom trawl survey.

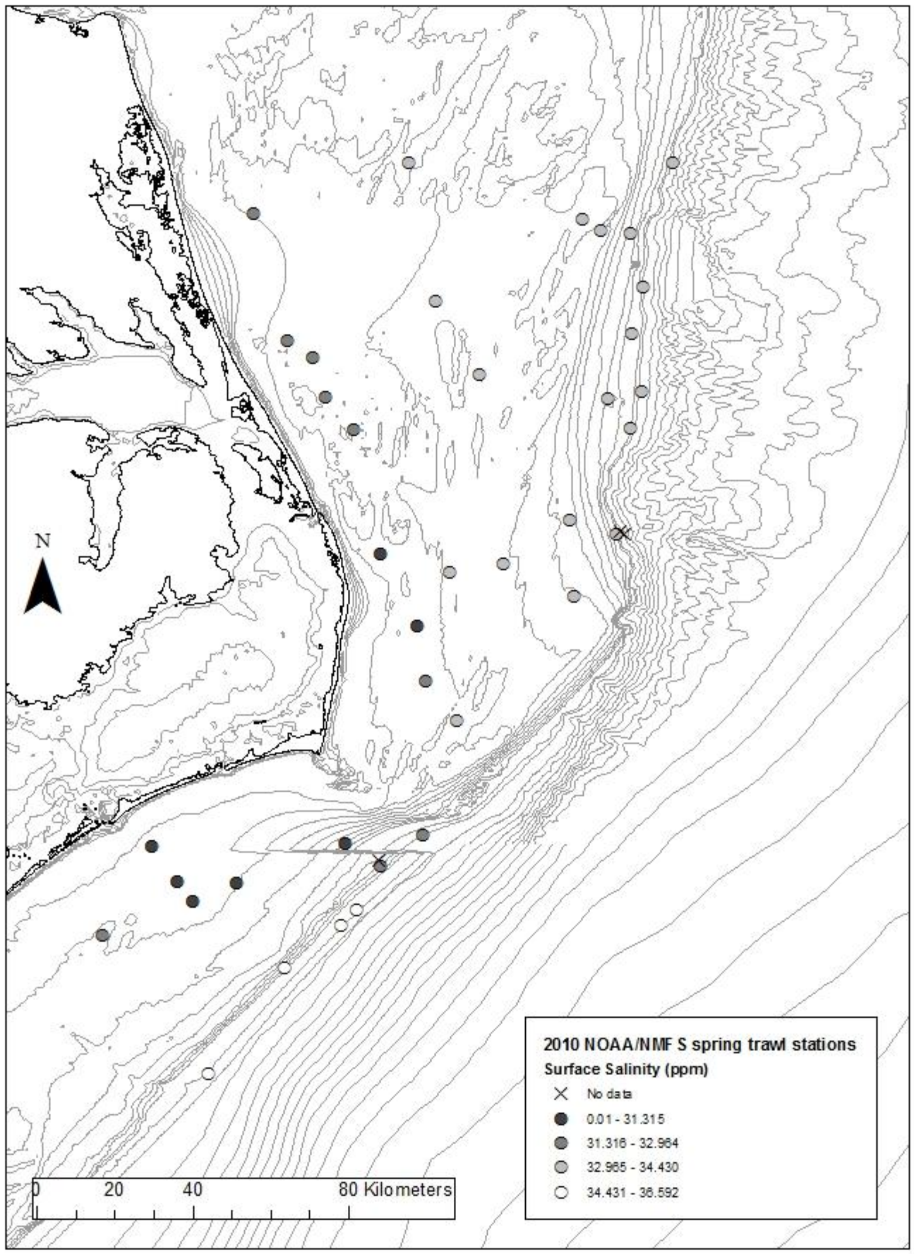


Figure 2-17. Surface salinity (ppm) at stations in North Carolina waters sampled during the 2010 NOAA/NMFS spring bottom trawl survey.

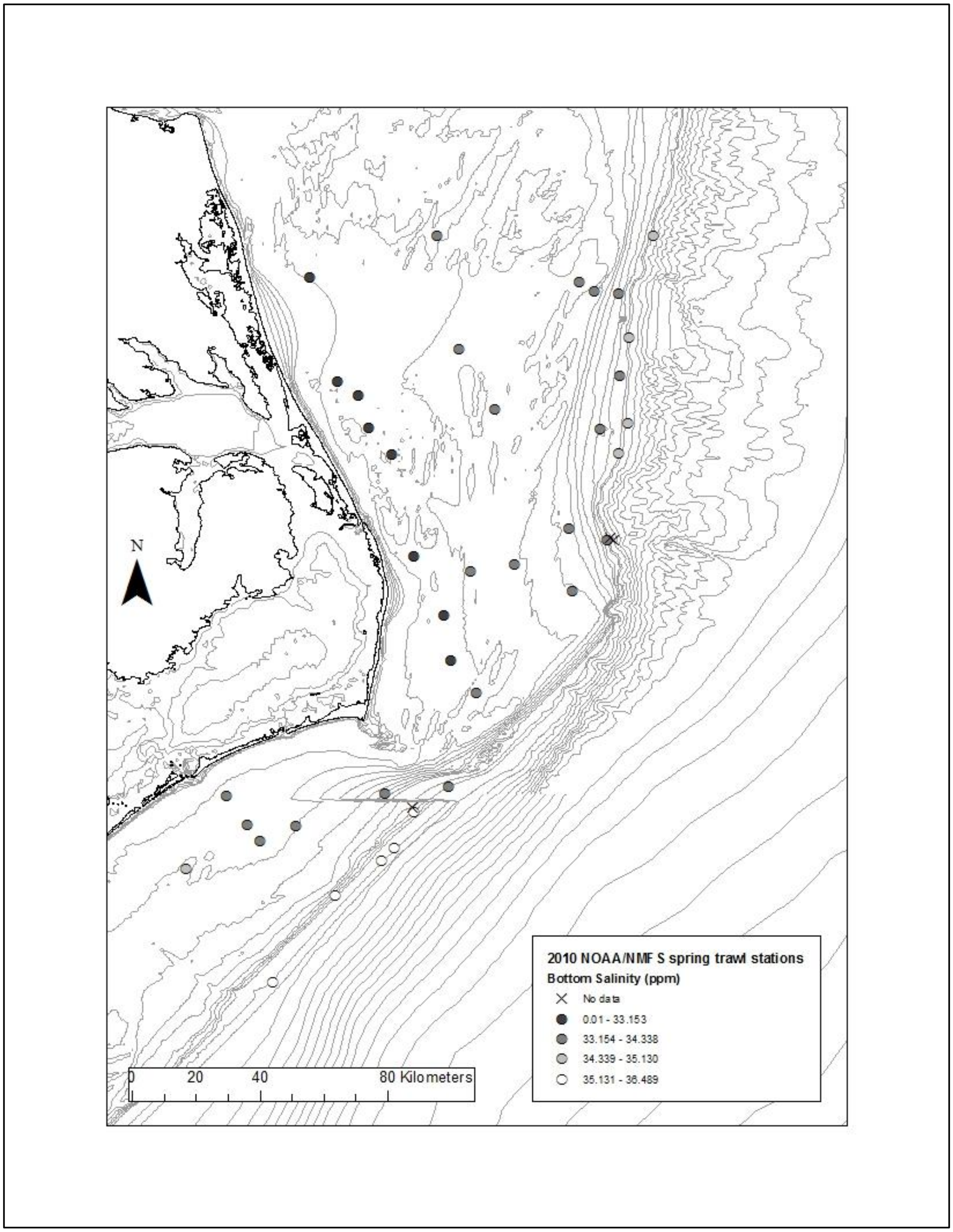


Figure 2-18. Bottom salinity (ppm) at stations in North Carolina waters sampled during the 2010 NOAA/NMFS spring bottom trawl survey.

Table 2-10. Pearson correlation coefficients (R) between the percentage by weight (g) of each prey category and total length (mm), average depth (m), surface temperature (°C), and bottom temperature (°C).

R	Crustacean	Ctenophore	Mollusc	Other Invert	Teleost
TL (mm)	-0.066	-0.194*	0.078	0.065	0.267*
Avg. Depth (m)	0.295*	0.222*	-0.164*	-0.252*	-0.330*
Surface Temp (°C)	0.302*	0.106	-0.174*	-0.240*	-0.236*
Bottom Temp (°C)	0.003	0.029	-0.023	-0.080	0.024
Surface Sal (ppm)	0.205*	0.092	-0.164*	-0.201*	-0.177*
Bottom Sal (ppm)	0.189*	0.133	0.174*	-0.208*	-0.186*

* = significant at α = 0.05

Table 2-11. Pearson correlation coefficients (R) between the percentage by number of each prey category and total length (mm), average depth (m), surface temperature (°C), and bottom temperature (°C).

R	Crustacean	Ctenophore	Mollusc	Other Invert	Teleost
TL (mm)	-0.059	-0.120	0.077	0.006	0.266*
Avg. Depth (m)	0.317*	0.157	-0.139	-0.246*	-0.406*
Surface Temp (°C)	0.317*	-0.022	-0.132	-0.243*	-0.318*
Bottom Temp (°C)	-0.007	-0.017	0.080	-0.093	-0.011
Surface Sal (ppm)	0.269*	0.157	-0.065	-0.222*	-0.226*
Bottom Sal (ppm)	0.211*	-0.022	-0.086	-0.230*	-0.263*

* = significant at $\alpha = 0.05$

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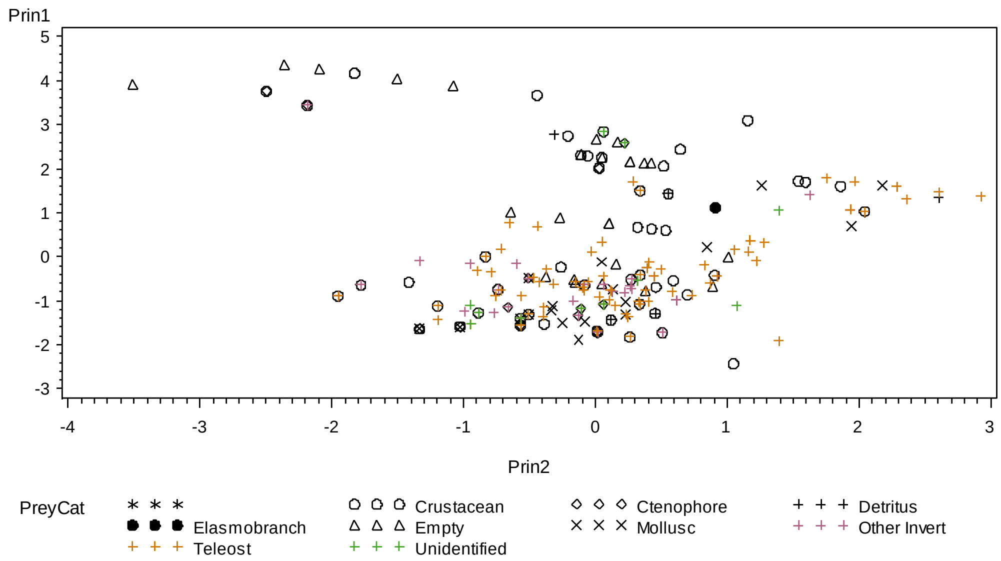
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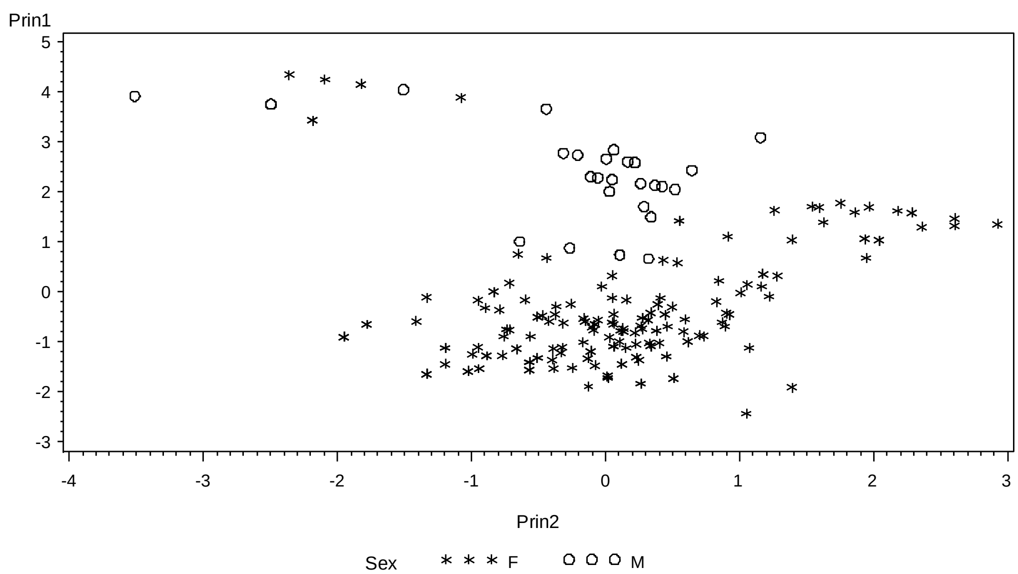
2
3
Prin2
PreyCat
Elasmobranch
Teleost
Crustacean
Empty
Unidentified
Ctenophore
Mollusc
Detritus
Other Invert

B.


Prin1
5
4
3
2
1
0
-1
-2
-3
-4
-3
-2
-1
0
1
2
3
Prin2
Sex
F
M

C.

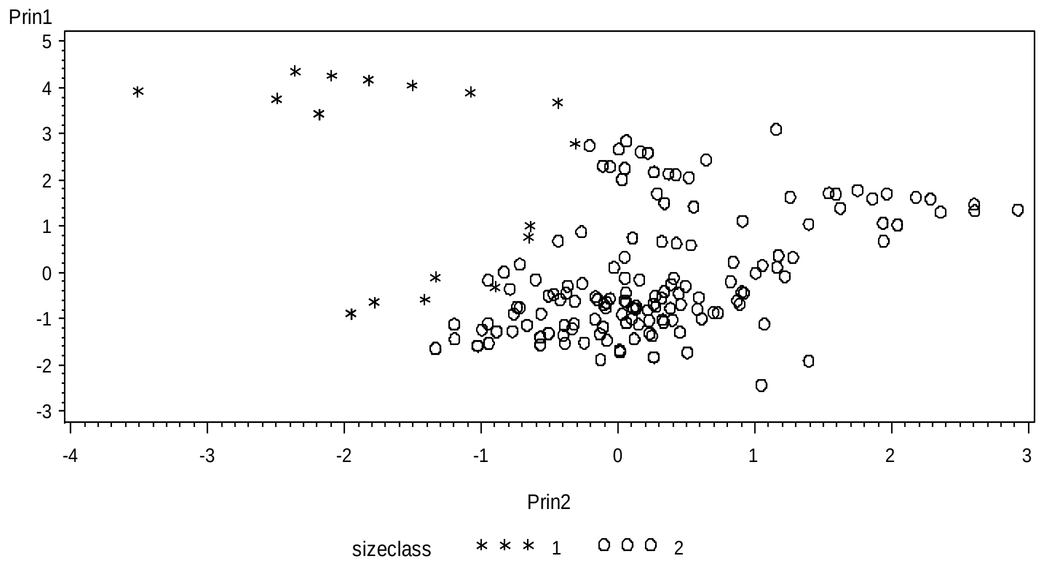


Figure 2-19. PCA analysis of relationships between percent frequency of occurrence, depth, surface temperature, bottom temperature, and total dogfish length by prey category (A), sex (B), and size class (C) (1=Immature, 2=Mature). Total length decreases along Prin1 and depth decreases along Prin2, while all other factors increase along both axes.

3. Feeding habits and predatory impacts of spiny dogfish (*Squalus acanthias*) overwintering in North Carolina waters

Abstract

There has been much interest in the feeding habits of spiny dogfish (*Squalus acanthias*) due to the perceived impact of predation by this shark on species important to commercial and recreational fisheries. Stomach contents were collected from 399 spiny dogfish captured during trawl surveys in North Carolina state waters during February and March, 2010. Prey categories were identified to the lowest possible taxa and grouped into broad taxonomic categories. Predator and prey size data were compared to determine the prey sizes most vulnerable to predation. Prey importance was expressed as percent weight and percent Index of Relative Importance. The biomass of select prey taxa consumed during the study period was estimated and compared to landings and abundance data for those taxa. Teleost fishes dominated the diet in both February and March, though crustacean taxa were secondarily important in March. Atlantic menhaden (*Brevoortia tyrannus*) and bay anchovy (*Anchoa mitchilli*) were the most important prey species in February, while unidentified teleosts were the dominant prey taxa in March, followed by polychaetes and euphausiids. Predator/prey size comparison showed that spiny dogfish were capable of consuming prey up to 45% of their total body length by dismembering larger prey. Predation by spiny dogfish in February may account for the equivalent of 14.08% of commercial landings for Atlantic menhaden, and between 3.59% of the spawning stock of that species. However, Atlantic menhaden are nearly absent from the spiny dogfish diet in March. This study suggests that Atlantic menhaden may be heavily preyed-upon by spiny dogfish during a short-term feeding event in February. This event may be ecologically significant and an important concern in managing the Atlantic menhaden stock.

Introduction

In general, sharks are considered to be apex predators in the marine environment (Heithaus 2004, Wetherbee and Cortés 2004, Heithaus et al. 2010). Most predatory sharks are tertiary consumers (trophic level > 4), occupying the same trophic level as marine mammals and surpassing that of seabirds and the majority of bony fishes (Cortés 1999). Shark feeding habits, particularly those of smaller "mesopredator" species, are of interest to fisheries managers because of recent increases in abundance, possibly due to fishery-induced release from predation (Myers et al. 2007) and competition (Fogarty and Murawski 1998).

The feeding habits of spiny dogfish (*Squalus acanthias*) have been of particular concern due to their long history as a pest species to commercial fishermen and the recent recovery of the Northwest Atlantic stock from overfishing (Rago and Sosebee 2010). Spiny dogfish are a secondary-tertiary consumer; Cortés (1999) calculated a trophic level of 3.9 for the species. As a high-level predator, spiny dogfish feed on a wide variety of fishes and invertebrates, showing an ontogenetic shift from crustaceans and gelatinous zooplankton to teleost fishes with increasing size (Ellis et al. 1996, Smith and Link 2010). This species is highly migratory, spending the summer months in New England waters and overwintering off of North Carolina (Burgess et al. 2002, Stehlik 2007, Rulifson and Moore 2009). Though traditionally thought to be a demersal species, recent evidence suggests that spiny dogfish may occupy midwater depths and make active vertical movements in the water column (Sulikowski et al. 2010).

Spiny dogfish have been suspected of negatively impacting the abundance of economically-important species through either direct predation or competition for shared prey (Link et al. 2002). Adult spiny dogfish are highly piscivorous, occupying similar feeding guild to several heavily exploited teleost species, particularly Atlantic cod (*Gadus morha*) (Garrison and Link 2000, Auster and Link 2009). After the crash of groundfish stocks in the 1990s, spiny dogfish replaced Atlantic cod as the most abundant piscivore in the Georges Bank ecosystem (Link and Garrison 2002, Auster and Link 2009), suggesting that fishery-induced competitive release had allowed spiny dogfish to invade the predatory niche of Atlantic cod (Fogarty and Murawski 1998). Further, predation by dogfish may be detrimental to the recovery of the overfished species (Link et al. 2002).

However, Link et al. (2002) found little evidence that direct predation is sufficient to significantly impact cod and other groundfish species at a population level. Instead, spiny dogfish seem to prey primarily on pelagic forage species such as squid, scombrids, and clupeids (Ellis et al. 1996, Link et al. 2002, Smith and Link 2010). Though dominated by teleosts, the diet of spiny dogfish is highly generalized and the exact prey species vary geographically and temporally (Smith and Link 2010). Among the clupeids, Atlantic herring (*Clupea harengus*) are of particular importance, though Atlantic menhaden (*Brevoortia tyrannus*) become prevalent in the diet at the southern end of the spiny dogfish range (Bearden 1965, Smith and Link 2010). Spiny dogfish feeding habits often reflect prey abundance, and this is especially apparent on a temporal scale (Moustahfid et al. 2010). The level of dogfish predation on Atlantic herring, sand lance (*Ammodytes* sp.), and various squid species has fluctuated over time in response to the relative abundance of those forage species, with Atlantic herring becoming the most prevalent after declines in other prey species in the 1980s (Overholtz et al. 2000, Overholtz and Link 2007). Though spiny dogfish generally prey upon small fishes or juveniles of larger species (Link et al. 2002, Stehlik 2007, Smith and Link 2010), there is anecdotal evidence of dogfish attacking and consuming larger prey (Burgess et al. 2002) and they are biomechanically capable of dismembering prey items too large to fit down the esophagus (Huber and Motta 2004).

Due to the regular seasonal presence of spiny dogfish in North Carolina waters, the feeding habits of this species may have significant ecological impacts on the marine community and fisheries of this region. As a preliminary measure of the predator impact of spiny dogfish in North Carolina waters, the goals of this study are to identify which species occur most often in the diet and to quantify the potential impact of predation on economically-important species.

Methods

Spiny dogfish stomach contents were collected from two bottom trawl surveys during the months of February and March 2010. The first was the U.S. Fish and Wildlife Service-led Cooperative Winter Tagging Cruise (CWTC), which occurred February 18-24 aboard the NOAA/NMFS R/V *Cape Hatteras* and towed 200 stations between Cape Hatteras and the Virginia state line. Samples were also collected on Leg 1 of the NOAA/NMFS spring bottom trawl survey (SBTS), which utilized the NOAA/NMFS R/V *Henry B. Bigelow* and towed 40 stations in North Carolina waters from March 4-8. The CWTC was designed primarily to sample striped bass and stations were chosen based on the likelihood of capturing that species. Tow times ranged from 10-30 minutes depending on sampling needs. In contrast, stations towed during the SBTS were chosen using a stratified-random sampling design and were sampled with standardized 20-minute tows, as described by Stauffer (2004).

At each station, stomach contents were sampled from no more than 20 spiny dogfish of each sex. If less than 20 were captured, then all dogfish were sampled. Total length (mm), fork length (mm), and sex were recorded for each sampled dogfish. During the CWTC, whole stomachs were removed by dissection. Stomach contents aboard the SBTS were sampled using acrylic tube lavage (Van den Ayvle and Roussel 1980) with every fifth shark sacrificed and dissected to verify the efficiency of the lavage method. In both cases stomach contents were placed in a 10% buffered formalin solution for transport back to the laboratory.

In the laboratory, prey items were identified to the lowest possible taxa. Number and total weight in grams (g) were recorded for each prey taxa, and frequency of occurrence was recorded as the number of stomachs containing at least one individual of that taxa. Prey items were also grouped in to broad categories based on taxonomy; Teleost, Elasmobranch, Mollusc, Crustacean, Ctenophore, and Other Invertebrate. Prey items that were obviously animal remains but were too damaged or digested for further identification were classified as Unidentified, and inorganic matter and plant fragments were classified as Detritus. Size data were recorded for intact prey; total length (mm) for fish and crustacean prey and mantle length (mm) for cephalopods. For especially numerous prey taxa, total lengths were measured for a 10% subsample and averaged for that stomach. Total length was estimated for some non-intact fish prey by calculating the proportion of the fish TL to the length of portions of the fish that were commonly missing. Size was also estimated by counting growth rings on scales recovered from non-intact fish prey and referring to published size-at-age measurements for that species.

Percent number (%N), weight (%W), and frequency of occurrence (%O) were calculated for each prey taxa and prey category. These values were used to calculate the index of relative importance for each prey taxa and category, which was expressed as a percentage (%IRI) as suggested by Cortés (1997). The percentage by number (%N) was used to calculate the Bray-Curtis similarity index (Bray and Curtis 1957) between the diets of dogfish sampled in February during the CWTC and those sampled in March during the SBTS.

To determine which age classes were vulnerable to predation by spiny dogfish, prey TL was plotted against dogfish TL and Pearson correlation analysis was used to determine the relationship between prey and predator size. This procedure was performed for all measured prey items combined and for selected prey species of particular ecological or economic importance. For prey species appearing in the diet more than once, the ratio of prey to predator TL was calculated and Pearson correlations were determined between prey:predator ratio and predator TL for the most common prey.

Consumption during the study period was calculated using estimates of annual ration (Jones and Geen 1977, Brett and Blackburn 1978) and the most current estimate of the total spiny dogfish stock biomass (Rago and Sosebee 2010). These estimates were used to create Equation (1).

(1)

In equation (1), total consumption (C) of species i is determined by multiplying the annual ration (R) by the total spiny dogfish stock biomass (S) then multiplying that number by the percent total diet weight ($\%W$) of species i found in the diet data for this study. The calculation was performed using the annual ration calculated by Brett and Blackburn (1978) (1.5 times the dogfish body weight at 10°C) and Jones and Geen (1977) (2.5 times the dogfish body weight at 10°C). Consumption within the sampling period of this study was estimated by dividing C_i by 365 to represent daily consumption, then multiplying that by the number of days in the months during which species i occurred in the diet. Diet data from the CWTC were assumed to represent the entire month of February, while data collected from the SBTS represented March. Total consumption was calculated over both months for prey species occurring in the spiny dogfish diet in both surveys.

Because it is unlikely that the entire spiny dogfish stock is present off of North Carolina at any given time, a sensitivity analysis was used to determine the predatory impact of 100%, 75%, 50%, and 25% of the dogfish stock biomass. In addition, Register

(2006) estimated that approximately 61.92% of the spiny dogfish stock overwinters in North Carolina waters, and consumption by that proportion of the dogfish stock was estimated. These estimates were compared with current landings and stock biomass data for the east coast of the United States. Commercial landings data were taken from NMFS (2010) and were combined with recreational landings data (NMFS Fisheries Statistics Division, personal communication) for species of particular importance to recreational fisheries.

Results

A total of 255 dogfish were sampled from the CWTC, and 146 were sampled from the SBTS. Of the CWTC samples, 53 (22.92%) were empty, and a further 13 (5.14%) failed to preserve and were too deteriorated for analysis. The SBTS samples included 25 (17.20%) empty stomachs. A total of 31 prey taxa were identified in the stomach contents of dogfish sampled during the CWTC (Table 1) and 54 prey taxa were identified from the SBTS samples (Table 2).

Spiny dogfish sampled during the CWTC were highly piscivorous, with Teleost as the dominant prey category by importance (99.52 %IRI) and weight (94.16 %W) (Table 3, Figure 1). Atlantic menhaden (*Brevoortia tyrannus*) were the most important prey species (57.33 %IRI) followed by bay anchovy (*Anchoa mitchilli*) (31.79 %IRI) and unidentified fish (8.88 %IRI) (Table 3).

Teleost prey made up the majority of the diet of dogfish sampled during the SBTS (79.19 %IRI, 60.85 %W), followed in importance by Crustaceans (9.19 %IRI), Other Invertebrates (7.93 %IRI), and Molluscs (2.53 %IRI) (Table 4, Figure 2). Unidentified fishes were the most important prey taxa (61.43 %IRI), followed by polychaetes (7.99 %IRI) and euphausiids (6.87 %IRI) (Table 4). Bray-Curtis analysis showed only a 13.18% dietary overlap between spiny dogfish sampled during the CWTC and the SBTS.

Total length measurements were taken from 138 individuals belonging to 28 prey taxa (Table 5). Atlantic menhaden were both the largest and most variable prey taxa in terms of individual size, ranging from 85 to 408 mm in total length. In addition, scales were recovered from striped bass (*Morone saxatilis*) remains in two stomachs and an age of 12 years was determined for both fish, which would correspond to approximately 850 mm TL for the prey fish (Boyd, personal communication).

Prey taxa consumed by dogfish were an average of 9% of the predator's total length. Atlantic menhaden were the largest prey relative to predator size, averaging 21% of the total length of dogfish consuming them and ranging from 11-45% of predator TL (Table 6). Of the menhaden, 14% were found dismembered, usually missing the head or bitten in half. The next most common prey taxa, bay anchovy and Atlantic croaker (*Micropogonias undulatus*), both showed a mean prey:predator TL ratio of 7% (Table 6). The two dogfish with striped bass in their stomachs were 751 and 785 mm TL, giving an estimated prey:predator ratio of 113% and 108%, respectively.

Pearson correlation analysis revealed significant positive linear relationships between dogfish TL and both prey TL and prey:predator ratio for all prey taxa combined (Table 7). Atlantic menhaden TL also showed a significant positive correlation with dogfish TL, while the other most common prey items (bay anchovy and Atlantic croaker) did not correlate strongly or significantly with predator size (Table 7). Length measurements for other prey taxa were not sufficient in number for adequate analysis.

Scatter plots illustrated the relatively weak correlations between dogfish and prey TL (Figure 3-A) and dogfish TL and prey:predator ratio (Figure 3-B), despite the significant relationship between those prey and predator size measurements. Atlantic menhaden, the only prey taxa to show a significant relationship between prey and predator length, showed a slightly closer exponential than linear relationship with dogfish TL (Figure 4).

Annual consumption by the Atlantic spiny dogfish stock was estimated at 541,560 mt assuming an annual ration of 1.5 x body weight (Brett and Blackburn 1978) or 902,600 mt assuming a ration of 2.5 x body weight (Jones and Geen 1977). As expected from the relative importance of Teleosts in the diet, fish prey showed the highest amount of consumption during the months of February and March 2010, with 67,106.41 – 16,776.60 mt consumed assuming an annual ration of 1.5 x body weight and 111,844.01 – 27,961.00 mt under a ration of 2.5 x body weight (Table 8). Taxa in the Other Invertebrates category made up the second highest consumption weight, at 6,576.62 – 1,644.15 mt at 1.5 x body weight, or 10,961.03 – 2,740.26 mt at 2.5 x body weight (Table 8).

Several species of ecological and economic concern were important prey for spiny dogfish in February and March 2010 (Table 9). Assuming an annual ration of 1.5 x body weight, dogfish consumed the equivalent of 9.47-2.37% of Atlantic croaker landings and 8.98-2.25% of squid landings in 2009 (NMFS 2010), with the estimated overwintering population consuming 5.86% of croaker landings and 5.56% of squid landings. These estimates increased to 14.68-3.67% of croaker landings and 14.97-3.74% of squid landings assuming an annual ration of 2.5 x dogfish body weight, with the overwintering population consuming 9.10% and 9.27% of croaker and squid landings, respectively. Though not commercially landed, bay anchovy and ctenophores were consumed in relatively high amounts (Table 9).

Atlantic menhaden and striped bass were present in the dogfish diet in February (Table 3). During that month, a biomass of menhaden equivalent to 13.64-3.41% of the total coast-wide landings of that species (NMFS 2010) were consumed under the estimated annual ration of 1.5 x body weight, while under an annual ration of 2.5 x body weight the equivalent of 22.73-5.68% of menhaden landings were consumed (Table 10). Of the measured menhaden, 14% were within the size range of fish age 3 or older, which are considered part of the spawning stock biomass (SSB) (ASMFC 2011). Assuming that this proportion of mature fish was consistent across all menhaden consumed, in February the amount of mature menhaden fed upon by spiny dogfish would have accounted for 3.48-0.87% of the SSB under a ration of 1.5 x body weight, or 5.80-1.45% of the SSB under a ration of 2.5 x body weight (Table 10). The North Carolina overwintering population would have consumed an equivalent of 8.44% of commercial landings and 2.15% of menhaden SSB at the 1.5 x body weight ration, or 14.08% of landings and 3.59% of the SSB at 2.5 x body weight (Table 10). Striped bass were comparatively less important in the diet, and under the maximum estimated consumption rate spiny dogfish predation in February would have claimed the equivalent of less than 10% of combined commercial and recreational landings (NMFS, personal communication) and less than 1.5% of the stock biomass (ASMFC 2009).

Discussion

Spiny dogfish overwintering in North Carolina waters feed mainly on fish prey and Atlantic menhaden are of particularly high importance in the diet. However, there were considerable differences in diet between dogfish sampled in February and those sampled in

March, resulting in only 13.18% similarity in feeding habits between the two months. Two species, Atlantic menhaden and bay anchovy, dominated the spiny dogfish diet in February, while in March the sharks fed upon a wide variety of teleost and invertebrate species. Differences in sampling design between the CWTC and the SBTS likely contribute significantly to the low dietary overlap between the two months, but the extent of the differences in diet suggest that dogfish foraging habits may shift dramatically from February to March.

This study supports the findings of previous surveys of spiny dogfish predatory habits, which demonstrate that midwater forage species are more important and consumed at a higher rate than larger-bodied, economically-important piscivores. Jones and Geen (1977) found that the importance of various Pacific salmon species in the diet of spiny dogfish in British Columbia waters was dwarfed by the importance of Pacific herring (*Clupea pallasii*). In the northwest Atlantic, Atlantic herring and Atlantic mackerel (*Scomber scombrus*) were consumed in amounts approaching the amounts taken by commercial fishermen, while more highly-valued groundfish species were consumed at comparatively insignificant levels (Link et al. 2002). In this study, forage species were the most dominant prey taxa while larger predators such as striped bass and paralichthyid flounder were only marginally present in the spiny dogfish diet. Striped bass were the most common large piscivore fed upon by spiny dogfish in February, but consumption only amounted to a potential maximum of 1.45% of striped bass population biomass. It is highly unlikely that direct predation by spiny dogfish is a significant source of mortality among striped bass in North Carolina waters. Generally, cannibalism is the largest source of predation mortality among pisicivorous fishes; Tsou and Collie (2001) found this to be the case in the Georges Bank groundfish complex, even among species preyed upon by spiny dogfish.

Spiny dogfish are an important predator of Atlantic menhaden in coastal North Carolina, with a maximum consumption estimate equivalent to 22.73% of coast-wide commercial landings in 2009 (NMFS 2010). That this amount is consumed within the month of February alone suggests an extremely high level of predatory pressure exerted on the menhaden stock by spiny dogfish, but by early March menhaden were only present in dogfish stomach contents as well-digested remains. From this observation, it appears that spiny dogfish prey heavily on Atlantic menhaden during the month of February before switching to a more generalist foraging strategy in March. Large-scale diet studies based on NMFS bottom-trawl survey data (Bowman et al. 2000, Smith and Link 2010) show Atlantic menhaden only appearing as a large portion of the dogfish diet in the Mid-Atlantic and Southern regions, where the sharks are present during the winter months (Stehlik 2007). These observations combined with the results of this survey provide evidence that high-level predation on menhaden may be a short-term event even within the span of dogfish residence in southern waters. Spiny dogfish are adept at exploiting short-term feeding opportunities; Beamish et al. (1992) found that the appearance of large aggregations of spiny dogfish at the mouth of the Big Qualicum River in British Columbia coincided with the release of smolts from the hatchery upstream. Predation on menhaden in North Carolina waters may only occur over the course of weeks, but may involve large numbers of dogfish drawn in by some environmental or behavioral cue. Sampling for the entire winter over multiple years will be needed to definitively prove or disprove this hypothesis.

The ability of spiny dogfish to dismember and consume relatively large prey was illustrated by analysis of prey intact enough for size measurements. Prey TL and relative prey:predator TL both increased significantly with increasing predator TL, suggesting that larger dogfish were capable of consuming proportionally larger prey (Table 7, Figure 3). This was strikingly illustrated by two striped bass that, based on TL back-calculated from aged scales, were larger than the dogfish that consumed them. However, these two prey items were left out of the correlation calculations due to the uncertainty of the back-calculated size. Of the other prey taxa, only Atlantic menhaden showed a significant correlation between prey and predator size (Table 7). Interestingly, the relationship between prey and predator TL in menhaden appeared to be stronger as an exponential relationship than a linear one (Figure 4). Menhaden were proportionally much larger than all other prey taxa, making up a mean of 21% and a range of 7-45% of predator length (Table 6). Aside from demonstrating that dogfish can attack and consume proportionally large prey, these data show that all age classes of menhaden are vulnerable to spiny dogfish predation. Assuming that the 14% of measured menhaden within the size class for age 3+ fish is consistent across all consumed menhaden, spiny dogfish may remove up to 5.80% of the spawning stock biomass of Atlantic menhaden through direct predation (Table 10).

Assessing the predatory pressure on Atlantic menhaden is of interest to fisheries managers because this forage species is a major food source for many piscivorous predators in the Chesapeake Bay region (Hartman and Brandt 1995). The most recent stock assessment shows that this forage species is currently experiencing overfishing (ASMFC 2011). Accurate estimates of predation mortality are needed to aid in determining the true health of the stock, and spiny dogfish are almost certainly an important predator of this species during the winter.

It is unlikely that the entire spiny dogfish stock is present in the coastal waters of North Carolina in February and March. Register (2006) estimated the proportion of the dogfish stock overwintering in North Carolina waters to be approximately 62% of the U.S. Atlantic stock, but interannual variation in the overwintering population is possible. If this estimate is not constant, consumption estimates corresponding to 75-50% of the stock (Tables 8-10) may also be appropriate for determining the predatory impact of spiny dogfish in the southern extent of their range.

The consumption estimates calculated in this study require several assumptions. Both estimates of annual ration (Jones and Geen 1977, Brett and Blackburn 1978) were derived from spiny dogfish in the North Pacific population, which has distinct life history characteristics from other dogfish populations and has recently been classified as a separate species, *Squalus suckleyi* (Ebert et al. 2010). Additionally, both estimates of annual ration were calculated at a constant temperature of 10°C (Jones and Geen 1977, Brett and Blackburn 1978). Spiny dogfish metabolism may be affected by ambient water temperature, and the temperature ranges of both trawl surveys differ significantly from 10°C. The consumption estimates in this study assume that food intake requirements for *Squalus suckleyi* are similar to those of *Squalus acanthias*, and that metabolic requirements calculated at 10°C are comparable to those at the temperatures observed at the trawl stations. Given that the Atlantic species is faster growing than the Pacific species, the higher annual ration estimated by Jones and Geen (1977) may be the most appropriate of the two for use with *Squalus acanthias* in the Atlantic. However, an estimate of feeding ration for the Northwest Atlantic population will be needed in order to provide the most accurate estimate of predatory impact.

This study provides a snapshot of spiny dogfish feeding habits during the winter of

2010. Though these data only encompass two months of sampling, they provide a jumping-off point for illuminating the predatory behavior of overwintering dogfish in North Carolina waters. These sharks may exert ecologically significant influences over prey and other pisciviores during their seasonal residence, particularly in the case of Atlantic menhaden. Multiple years of sampling over the entire winter season should further clarify the ecological role of spiny dogfish off of North Carolina, and in turn will also clarify the influence of these capable predators on fisheries interests.

References

ASMFC. 2009. 2009 stock assessment report for Atlantic striped bass. Atlantic States Marine Fisheries Commission, Arlington, VA.

ASMFC. 2011. Atlantic menhaden stock assessment and peer review reports. Stock Assessment Report No. 10-02. Atlantic States Marine Fisheries Commission, Arlington, VA.

Auster, P.J. and J.S. Link. 2009. Compensation and recovery of feeding guilds in a northwest Atlantic shelf fish community. Marine Ecology Progress Series 382: 163-172.

Beamish, R.J., B.L. Thomson, and G.A. McFarlane. 1992. Spiny dogfish predation on chinook and coho salmon and the potential effects on hatchery-produced salmon. Transactions of the American Fisheries Society 121: 444-455.

Bearden, C.M. 1965. Occurrence of spiny dogfish, *Squalus acanthias*, and other elasmobranchs in South Carolina coastal waters. Copeia 1965: 378-378.

Bowman, R.E., C.E. Stillwell, W.L. Micheals, and M.D. Grosslein. 2000. Food of Atlantic fishes and two common species of squid. NOAA Technical Memorandum NMFS-NE-155. NOAA, Woods Hole, Massachusetts.

Bray, J.R. and J.T. Curtis. 1957. An ordination of the upland forest communities of southern Wisconsin. Ecological Monographs 27: 325-349.

Brett, J.R. and J.M. Blackburn. 1978. Metabolic rate and energy expenditure of the spiny dogfish, *Squalus acanthias*. Journal of the Fisheries Research Board of Canada 35: 816-821.

Boyd, J., personal communication. North Carolina Department of the Environment and Natural Resources, Division of Marine Fisheries.

Burgess, G.H. 2002. Spiny dogfish/*Squalus acanthias* Linneaus 1785. Pages 54-57 *in* B.B.

Collette and G. Klein-MacPhee, editors. Bigelow and Schroeder's fishes of the Gulf of Maine, 3rd edition. Smithsonian Institution Press, Washington, D.C.

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

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

Ebert, D.A., W.T. White, K.J. Goldman, L.J.V. Compagno, T.S. Daly-Engel, and R.D. Ward. 2010. Resurrection and redescription of *Squalus suckleyi* (Girard, 1854) from the North Pacific, with comments on the *Squalus acanthias* subgroup (Squaliformes: Squalidae). Zootaxa 2612: 22-40.

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

Fogarty, M.J. and S.A. Murawski. 1998. Large-scale disturbance and the structure of marine systems: fishery impacts on Georges Bank. Ecological Applications 8: S6-S22.

Garrison, L.P., and J.S. Link. 2000. Dietary guild structure of the fish community in the Northeast United States continental shelf ecosystem. Marine Ecology Progress Series 202: 231-240.

Hartman, K.J. and S.B. Brandt. 1995. Trophic resource partitioning, diets, and growth of sympatric estuarine predators. Transactions of the American Fisheries Society 124: 520-537.

Heithaus, M.R. 2004. Predator-prey interactions. Pages 487-521 *in* J.C. Carrier, J.A. Musick, and M.R. Heithaus, editors. Biology of sharks and their relatives. CRC Press, Boca Raton, FL.

Heithaus, M.R., A. Frid, J.J. Vaudo, B. Worm, and A.J. Wirsing. 2010. Unraveling the ecological importance of elasmobranchs. Pages 612-636 *in* J.C. Carrier, J.A. Musick, and M.R. Heithaus, editors. Sharks and their relatives II: biodiversity, adaptive physiology, and conservation. CRC Press, Boca Raton, Florida.

Huber, D.R., and P.J. Motta. 2004. Comparing analysis of methods for determining bite force in the spiny dogfish *Squalus acanthias*. Journal of Experimental Zoology 301A: 26-37.

Jones, B.C. and G.H. Geen. 1977. Food and feeding of spiny dogfish (*Squalus acanthias*) in British Columbia waters. Journal of the Fisheries Research Board of Canada 34: 2067-2078.

Link, J.S. and L.P. Garrison. 2002. Changes in piscivory associated with fishing induced changes in the finfish community on Georges Bank. Fisheries Research 55: 71-86.

Link, J.S., L.P. Garrison, and F.P. Almeida. 2002. Ecological interactions between elasmobranchs and groundfish species on the Northeastern U.S. contintental shelf. I. Evaluating predation. North American Journal of Fisheries Managament 22: 550-562.

Moustahfid, H., M.C. Tyrrell, J.S. Link, J.A. Nye, B.E. Smith, and R.J. Gamble. 2010. Functional feeding responses of piscivorous fishes from the northeast U.S. continental shelf. Oceologia 163: 1059-1067.

Myers, R.A., J.K. Baum, T.D. Shepherd, S.P. Powers, and C.H. Peterson. 2007. Cascading effects and the loss of apex predatory sharks from a coastal ocean. Science 315: 1846-1850.

NMFS Fisheries Statistics Division, personal communication. Silver Spring, MD. http://www.st.nmfs.noaa.gov/st1/index.html.

NMFS. 2010. Fisheries of the United States, 2009. National Marine Fisheries Service

Fisheries Statistics Division. Silver Spring, MD.

Overholtz, W.J., and J.S. Link. 2007. Consumption impacts by marine mammals, fish, and seabirds on the Gulf of Maine-Georges Bank Atlantic herring (*Clupea harengus*) complex during the years 1977-2002. ICES Journal of Marine Science 64: 83-96.

Overholtz, W.J., J.S. Link, and L.E. Suslowicz. 2000. Consumption of important pelagic and squid by predatory fish in the northeastern USA shelf ecosystem with some fishery comparisons. ICES Journal of Marine Science 57: 1147-1159.

Rago, P.J. and K.A. Sosebee. 2010. Biological reference points for spiny dogfish. Northeast Fisheries Science Center Document 10-06. NOAA, Woods Hole, Massachusetts.

Register, K. E. 2006. Population estimation and female reproductive state of spiny dogfish (*Squalus acanthias*) overwintering in North Carolina coastal waters. Master's thesis. East Carolina University, Greenville, North Carolina.

Rulifson, R.A. and T.M. Moore. 2009. Population estimates of spiny dogfish aggregations overwintering south of Cape Hatteras, North Carolina, using an area density method. Pages 133-138 *in* V.F. Gallucci, G.A. McFarlane, and G.G. Bargmann, editors. Biology and management of dogfish sharks. American Fisheries Society, Bethesda, Maryland.

Smith, B.E. and J.S. Link. 2010. The trophic dynamics of 50 finfish and 2 squid species on the Northeast U.S. continental shelf. NOAA Technical Memorandum NMFS-NE-216, NOAA, Woods Hole, Massachusetts.

Stauffer, G. 2004. NOAA protocols for groundfish bottom trawl surveys of the nation's fishery resources. NOAA Technical Memorandum NMFS-SPO-65. NOAA, Woods Hole, Massachusetts.

Stehlik, L.L. 2007. Essential fish habitat source document: spiny dogfish, *Squalus acanthias*, life history and habitat characteristics. NOAA Technical Memorandum NMFS-NE-203, NOAA, Woods Hole, Massachusetts.

Sulikowski, J.A., B. Galuardi, W. Bubley, N.B. Furey, W.B. Driggers, III, G.W. Ingram Jr., and P.C.W. Tsang. 2010. Use of satellite tags to reveal the movements of spiny dogfish *Squalus acanthias* in the western North Atlantic Ocean. Marine Ecology Progress Series 418: 249-254.

Tsou, T.S. and J.S. Collie. 2001. Predation-mediated recruitment in the Georges Bank fish community. ICES Journal of Marine Science 58: 994-1001.

Van Den Avyle, M.J. and J.E. Roussel. 1980. Evaluation of a simple method for removing food items from live black bass. The Progressive Fish Culturist 42: 222-223.

Wetherbee, B.M. and E. Cortés. 2004. Food consumption and feeding habits. Pages 223-235 *in* J.C. Carrier, J.A. Musick, and M.R. Heithaus, editors. Biology of sharks and their relatives. CRC Press, Boca Raton, FL.

Table 3-1. Common and scientific names of all prey taxa collected from spiny dogfish stomach contents during the 2010 CWTC survey, grouped by category.

Prey taxa/category	Scientific name
Teleost	
Atlantic croaker	*Micropogonias undulatus*
Atlantic menhaden	*Brevoortia tyrannus*
Bay anchovy	*Anchoa mitchilli*
Blueback herring	*Alosa aestivalis*
Butterfish	*Peprilus triacanthus*
Hake sp.	*Urophycis* sp.
Paralicthyid flounder	*Paralicthyes* sp.
Seahorse	*Hippocampus* sp.
Striped bass	*Morone saxatilis*
Tonguefish sp.	Cynoglossidae
Unidentified eel	Anguilliformes
Unidentified fish	Teleostii
Unidentified flatfish	Pleuronectiformes
Unidentified Herring	Cupleidae
Elasmobranch	
Unidentified elasmobranch	Elasmobranchii
Crustacean	
Decapod	Decapoda
Hermit crab sp.	Paguroidea
Isopod	Isopoda
Lady crab	*Ovalipes ocellatus*
Mantis Shrimp sp.	Stomatopoda
Mole crab	Hippoidea
Unidentified shrimp	Malacostraca
Mollusc	
Bivalve	Bivalva
Loligo squid	*Loligo paelii*
Unidentified mollusc	Mollusca
Unidentified squid	Teuthida
Ctenophore	
Comb jelly	Ctenophora
Other Invertebrate	
Brittle star	Echinodermata
Nematode	Nematoda
Polycheate	Polychaeta
Unidentified worm	-

Table 3-2. All prey taxa collected from spiny dogfish stomach contents during the 2010 NOAA/NMFS spring bottom trawl survey, grouped by category.

Prey taxa/category	Scientific name
Teleost	
Atlantic croaker	*Micropogonias undulatus*
Atlantic menhaden	*Brevoortia tyrannus*
Bay anchovy	*Anchoa mitchilli*
Beardfish	*Polymixia lowei*
Black sea bass	*Centropristis striata*
Butterfish	*Peprilus triacanthus*
Cusk eel sp.	Ophidiidae
Darter Goby	*Ctenogobius boleosoma*
Flounder left-eye	Paralichthyidae
Goby sp.	Gobiiae
Gulf Stream Flounder	*Citharichthys arctifrons*
Hake sp.	*Urophycis* sp.
Lantern fish sp.	Phosichtheyidae
Northern Searobin	*Prionotus carolinus*
Pipefish sp.	*Sygnathus* sp.
Red hake	*Urophycis chuss*
Sand Lance	*Ammodytes americanus*
Searobin sp.	*Prionotus* sp.
Smallmouth Flounder	*Etropus microstomus*
Snake Eel	*Ophichthus cruentifer*
Snake Mackerel	Gempylidae
Spotted Hake	*Urophycis regia*
Tonguefish sp.	Cynoglossidae
Unidentified fish	Teleostii
Unidentified flatfish	Pleuronectiformes
Wenchman	*Pristipomoides aquilonaris*
Windowpane Flounder	*Scopthalamus aquosus*
Wrasse sp.	Labridae
Elasmobranch	
Unidentified skate	Rajidae
Crustacean	
Amphipods	Amphipoda
Cancer crab	*Cancer* sp.
Decapod	Decapoda
Euphausiid	Euphausiidae
Hermit Crab	Paguroidea
Jonah Crab	*Cancer borealis*
Lobster sp.	Nephropidae
Mantis shrimp sp.	Stomatopoda

Penaeid shrimp	*Penaeus* sp.
Portunid crab	Portunidae
Unidentified crab	Brachyura
Unidentified crustacean	Crustacea
Unidentified shrimp	Malacostraca
Mollusc	
Bivalve	Bivalva
Bobtail Squid	*Rossia* sp.
Gastropod	Gastropoda
Loligo squid	*Loligo pealeii*
Octopus	*Octopus vulgaris*
Unidentified mollusc	Mollusca
Unidentified squid	Teuthoidea
Ctenophore	
Comb jelly	Ctenophora
Other Invertebrate	
Polychaete	Polychaeta
Sand Dollar	Clypeasteroidea
Sea Cucumber	Holothuroidea
Unidentified invertebrate	-
Unidentified worm	-

Table 3-3. Percent number, weight, frequency of occurrence, and Index of Relative Importance for all prey taxa and prey categories consumed by dogfish sampled during the 2010 CWTC (n = 189)

	Prey	% N	% W	% O	% IRI
Prey Taxa	Atlantic menhaden	6.96	59.82	49.45	57.33
	Bay anchovy	82.51	18.49	18.13	31.79
	Unidentified fish	3.48	10.01	37.91	8.88
	Ctenophore	1.45	2.73	17.58	1.27
	Atlantic croaker	0.95	0.47	6.59	0.16
	Polycheate	0.68	0.27	5.49	0.09
	Bivalve	0.41	1.09	3.30	0.09
	Animal Remains	0.36	0.65	4.40	0.08
	Striped bass	0.14	2.30	1.65	0.07
	Unidentified shrimp	0.50	0.09	6.04	0.06
	Tonguefish sp.	0.18	0.91	2.20	0.04
	Decapod	0.32	0.16	3.85	0.03
	Unidentified worm	0.41	0.15	2.75	0.03
	Unidentified herring	0.18	0.64	1.10	0.02
	Paralicthyid flounder	0.09	0.57	1.10	0.01
	Unidentified eel	0.14	0.16	1.65	0.01
	Mantis shrimp sp.	0.14	0.06	1.65	0.01
	Isopod	0.18	0.01	1.65	0.01
	Unidentified squid	0.14	0.05	1.65	0.01
	Butterfish	0.05	0.43	0.55	<0.01
	Elasmobranch	0.05	0.35	0.55	<0.01
	Unidentified mollusc	0.09	0.06	1.10	<0.01
	Mole crab	0.09	0.05	1.10	<0.01
	Seahorse	0.05	0.16	0.55	<0.01
	Hake sp.	0.05	0.14	0.55	<0.01
	Loligo squid	0.05	0.09	0.55	<0.01
	Nematode	0.14	<0.01	0.55	<0.01
	Blueback herring	0.05	0.03	0.55	<0.01
	Unidentified flatfish	0.05	0.03	0.55	<0.01
	Hermit crab sp.	0.05	0.03	0.55	<0.01
	Brittle star	0.05	0.01	0.55	<0.01
	Lady crab	0.05	<0.01	0.55	<0.01
	Algae/Detritus	0.05	<0.01	0.55	<0.01
Category	Teleost	94.85	94.16	122.53	99.52
	Ctenophore	1.45	2.73	9.34	0.17
	Other Invert	1.27	0.43	17.58	0.13
	Crustacean	1.31	0.40	15.38	0.11
	Mollusk	0.68	1.29	6.59	0.06
	Unidentified	0.36	0.65	4.40	0.02
	Elasmobranch	0.05	0.35	0.55	<0.01
	Detritus	0.05	0.00	0.55	<0.01

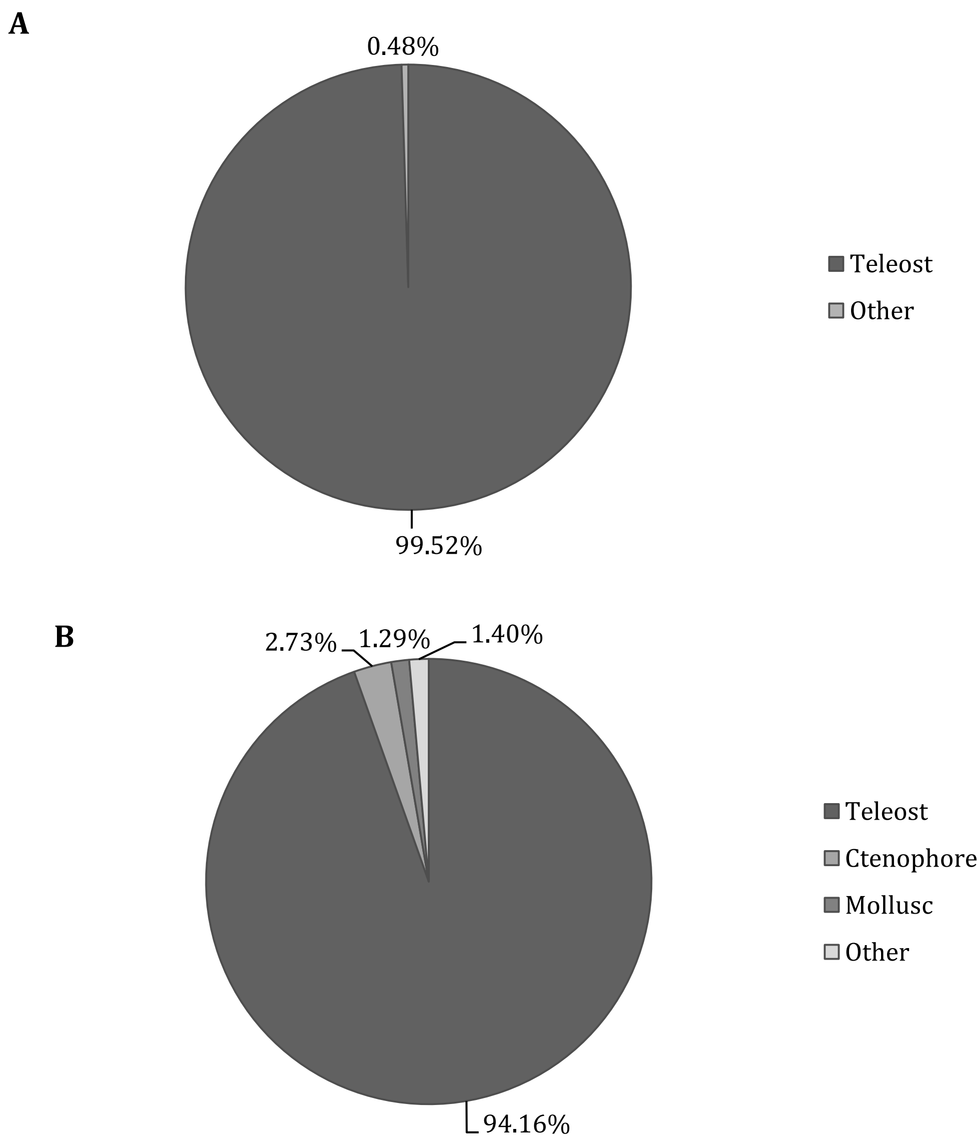


Figure 3-1. Percentage of stomach contents sampled during the 2010 CWTC made up of prey categories by A.) % IRI and B.) % weight (g).

Table 3-4. Percent weight, number, frequency of occurrence, and Index of Relative Importance for all prey taxa and prey categories included in the diet of female spiny dogfish (n = 120).

Prey Taxa

Prey	% N	% W	% O	% IRI
Teleost	15.36	27.53	40.00	61.43
Polycheate	8.70	4.69	16.67	7.99
Euphausiid	10.43	0.53	17.50	6.87
Sea cucumber	4.93	6.43	8.33	3.39
Ctenophore	3.77	4.82	10.83	3.33
Unidentified shrimp	5.51	1.17	13.33	3.19
Northern searobin	5.22	2.49	7.50	2.07
Animal remains	3.19	2.06	9.17	1.72
Tonguefish sp.	1.16	11.15	3.33	1.47
Spotted Hake	2.61	2.85	5.00	0.98
Atlantic menhaden	3.48	1.19	5.83	0.97
Unidentified Invertebrate	2.03	2.48	5.83	0.94
Loligo squid	1.74	4.04	4.17	0.86
Bivalve	1.45	3.18	4.17	0.69
Algae/Detritus	1.74	0.45	5.00	0.39
Bobtail squid	1.45	1.17	4.17	0.39
Hake sp.	1.45	0.82	4.17	0.34
Decapod	1.45	0.62	4.17	0.31
Wrasse	1.45	3.51	1.67	0.30
Gulf Stream flounder	1.16	1.74	2.50	0.26
Darter goby	1.74	0.21	3.33	0.23
Searobin sp.	1.16	0.35	3.33	0.18
Left-eye flounder	0.87	0.82	2.50	0.15
Unidentified worms	1.16	0.28	2.50	0.13
Unidentified squid	0.87	0.54	2.50	0.13
Atlantic croaker	0.58	1.07	1.67	0.10
Octopus	1.16	0.41	1.67	0.09
Bay anchovy	1.16	0.39	1.67	0.09
Hermit crab sp.	0.58	0.81	1.67	0.08
Crustacean	0.87	0.02	2.50	0.08
Smallmouth flounder	0.87	0.33	1.67	0.07
Unidentified mollusc	0.58	1.80	0.83	0.07
Butterfish	0.58	1.63	0.83	0.07
Unidentified flatfish	0.87	0.16	1.67	0.06
Wenchman	0.58	1.45	0.83	0.06
Mantis Shrimp sp.	0.58	0.37	1.67	0.06
Beardfish	0.58	0.32	1.67	0.05
Unidentified skate	0.29	1.49	0.83	0.05
Red hake	0.29	1.27	0.83	0.05
Pipefish	0.58	0.08	1.67	0.04

	Lobster sp.	0.29	0.85	0.83	0.03
	Black sea bass	0.29	0.42	0.83	0.02
	Lantern fish	0.58	0.12	0.83	0.02
	Goby sp.	0.29	0.37	0.83	0.02
	Jonah Crab	0.29	0.28	0.83	0.02
	Peneaid shrimp	0.29	0.17	0.83	0.01
	Sand lance	0.29	0.16	0.83	0.01
	Cusk eel	0.29	0.15	0.83	0.01
	Snake eel	0.29	0.15	0.83	0.01
	Portunid crab	0.29	0.15	0.83	0.01
	Windowpane flounder	0.29	0.13	0.83	0.01
	Unidentified crab	0.29	0.12	0.83	0.01
	Cancer sp.	0.29	0.06	0.83	0.01
	Bird	0.29	0.05	0.83	0.01
	Amphipods	0.29	0.04	0.83	0.01
	Gastropod	0.29	0.04	0.83	0.01
	Sand Dollar	0.29	0.03	0.83	0.01
	Shell	0.29	0.02	0.83	0.01
	Snake Mackerel	0.29	<0.01	0.83	0.01
Category	Teleost	44.93	60.85	100.00	79.19
	Crustacean	21.45	5.18	45.83	9.14
	Other Invert	17.10	13.91	34.17	7.93
	Mollusk	7.25	11.17	18.33	2.53
	Ctenophore	3.77	4.82	10.83	0.70
	Unidentified	3.19	2.06	9.17	0.36
	Detritus	2.32	0.52	6.67	0.14
	Elasmobranch	0.29	1.49	0.83	0.01

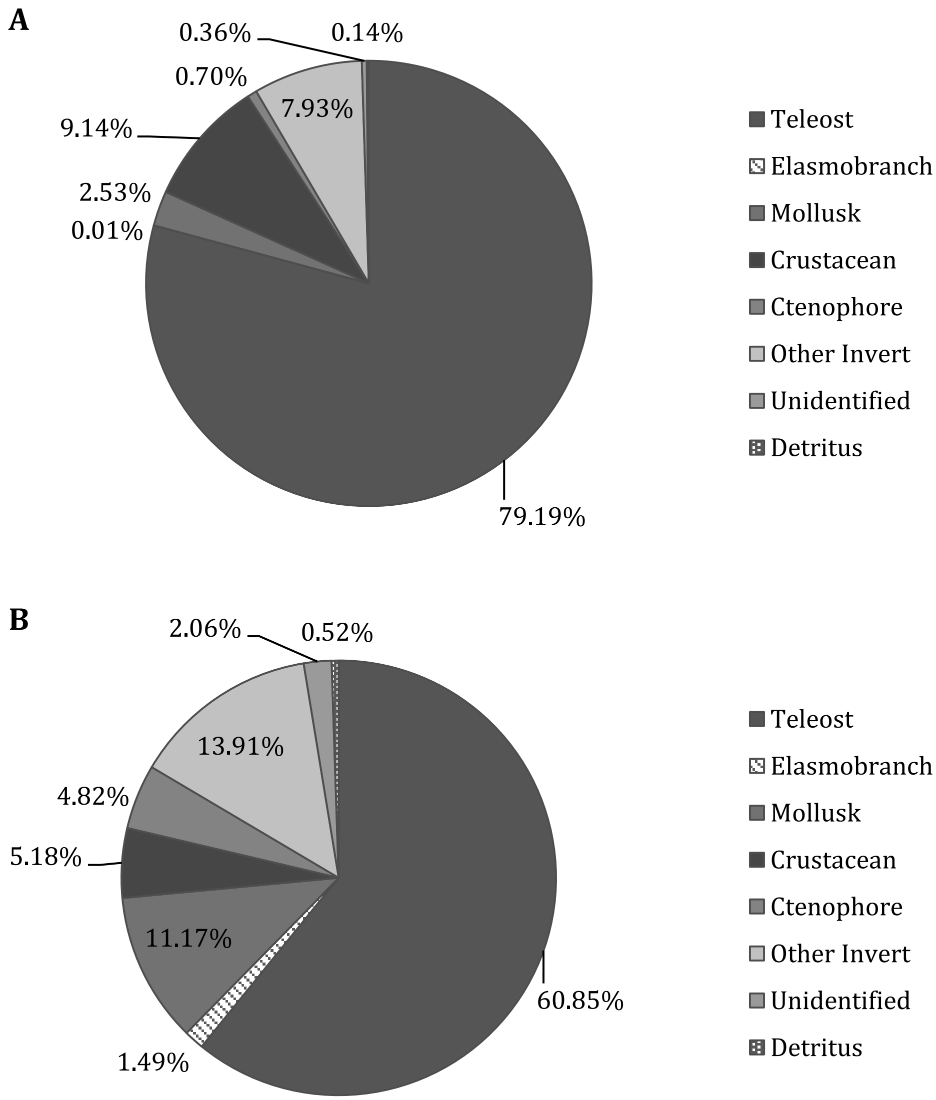


Figure 3-2. Percentage of stomach contents sampled during the 2010 SBTS made up of prey categories by A.) % IRI and B.) % weight (g).

Table 3-5. Mean total length (TL), standard deviation (SD), minimum TL, and maximum TL measurements for all prey taxa.

		Total Length (mm)			
Prey Taxa	*n*	Mean	SD	Min	Max
Atlantic menhaden	41	176.98	63.29	85.00	408.00
Bay anchovy	22*	56.81	7.78	46.75	73.40
Atlantic croaker	13	51.46	14.02	22.00	75.00
Northern searobin	8	42.38	16.41	28.00	76.00
Tonguefish sp.	6	123.33	34.81	60.00	149.00
Unidentified shrimp	5	51.17	3.09	46.85	54.00
Spotted hake	5	59.00	21.27	37.00	89.00
Gulf Stream flounder	4	59.75	30.12	32.00	91.00
Loligo squid	4	46.00	5.35	43.00	54.00
Wrasse	4	90.75	17.35	72.00	113.00
Darter goby	3	30.33	3.06	27.00	33.00
Octopus	3	9.33	2.52	7.00	12.00
Bobtail squid	2	21.50	3.54	19.00	24.00
Butterfish	2	124.00	14.14	114.00	134.00
Smallmouth flounder	2	50.50	13.44	41.00	60.00
Wenchman	2	72.50	2.12	71.00	74.00
Black sea bass	1	50.00	0.00	50.00	50.00
Blueback herring	1	74.00	0.00	74.00	74.00
Cusk eel	1	59.00	0.00	59.00	59.00
Left-eyed flounder	1	47.00	0.00	47.00	47.00
Goby sp.	1	81.00	0.00	81.00	81.00
Hake sp.	1	106.00	0.00	106.00	106.00
Jonah crab	1	25.00	0.00	25.00	25.00
Mantis shrimp sp.	1	40.59	0.00	40.59	40.59
Pipefish	1	130.00	0.00	130.00	130.00
Red hake	1	126.00	0.00	126.00	126.00
Seahorse	1	125.00	0.00	125.00	125.00
Snake eel	1	140.00	0.00	140.00	140.00

* mean from subsamples

Table 3-6. Mean, standard deviation (SD), minimum, and maximum ratio of Prey:Shark TL (% of predator length) for all prey taxa found in more than one stomach.

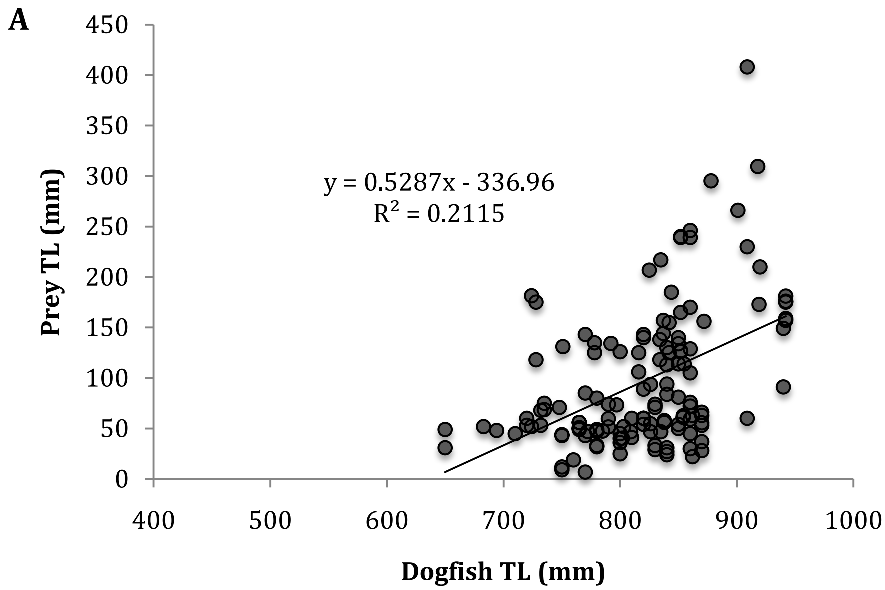
	Prey:Shark TL ratio (% of predator length)				
Prey Taxa	*n*	Mean	SD	Min	Max
Atlantic menhaden	41	0.21	0.07	0.11	0.45
Bay anchovy	22*	0.07	0.01	0.06	0.09
Atlantic croaker	13	0.07	0.02	0.03	0.10
Northern searobin	8	0.05	0.02	0.03	0.09
Tonguefish sp.	6	0.15	0.04	0.08	0.19
Unidentified shrimp	5	0.07	0.01	0.06	0.07
Spotted hake	5	0.07	0.03	0.04	0.11
Gulf Stream flounder	4	0.07	0.03	0.04	0.10
Loligo squid	4	0.06	0.00	0.06	0.07
Wrasse sp.	4	0.11	0.02	0.08	0.13
Darter goby	3	0.04	0.01	0.03	0.04
Octopus	3	0.01	0.00	0.01	0.02
Bobtail squid	2	0.03	0.00	0.03	0.03
Butterfish	2	0.15	0.02	0.13	0.16
Smallmouth flounder	2	0.06	0.02	0.05	0.07
Wenchman	2	0.09	0.00	0.09	0.09

* mean from subsamples

Table 3-7. Pearson correlations (R) between dogfish and prey TL and between dogfish TL and prey:predator TL ratio.

	Dogfish total length (mm)	
R	Prey length	Prey:predator ratio
All prey	0.45993*	0.37662*
Atlantic menhaden	0.41736*	0.2456
Bay anchovy	0.22048	-0.03554
Atlantic croaker	0.02175	-0.21902

* = significant at 0.05



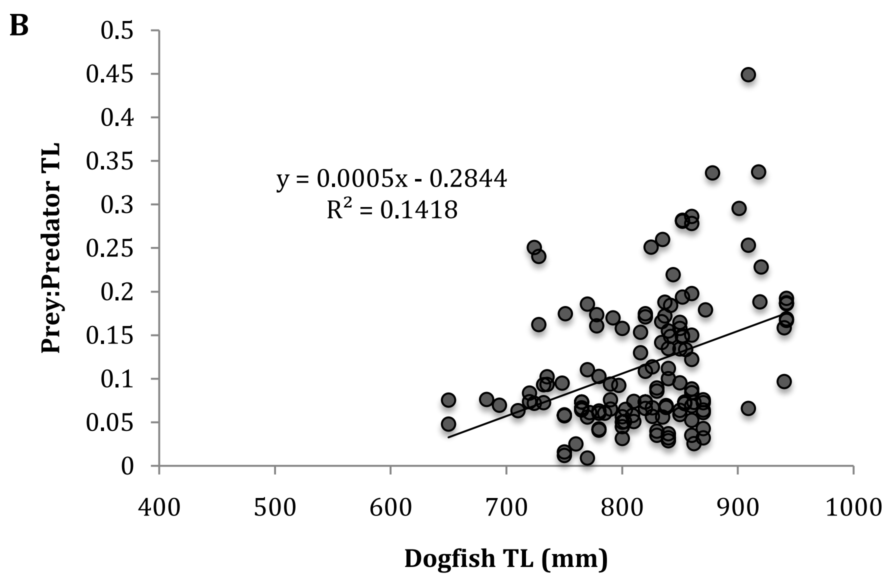


Figure 3-3. Scatter plots of dogfish TL (mm) against A.) prey TL and B.) prey:predator TL ratio.

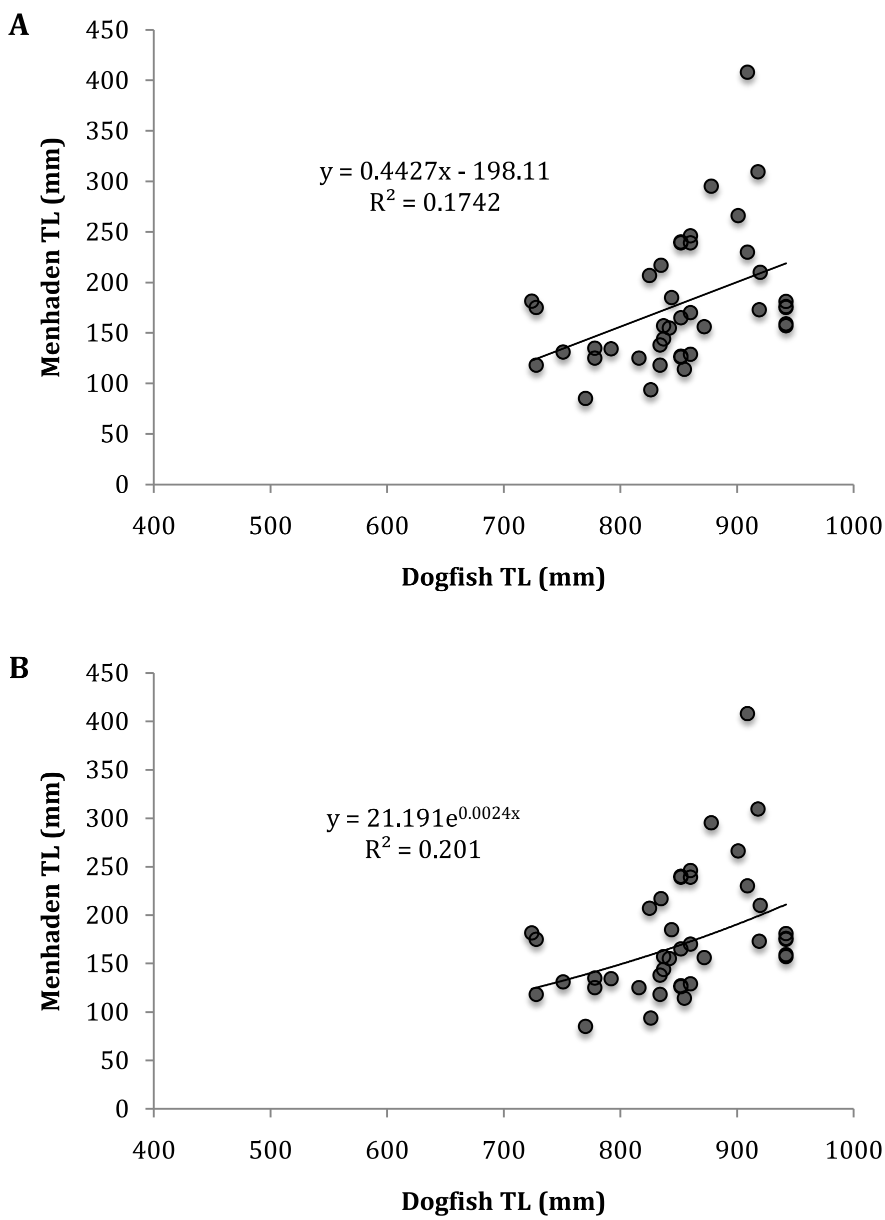


Figure 3-4. Scatter plots of dogfish TL (mm) against Atlantic menhaden TL (mm), showing A.) linear and B.) exponential relationships.

Table 3-8. Estimates of total consumption (mt) of identified prey categories by 100-25% and 61.92% of the spiny dogfish TEB (361,040 mt) (Rago and Sosebee 2010) over the months of February and March 2010, for both estimates of annual ration (1.5 X, Brett and Blackburn 1978) (2.5 X, Jones and Geen 1977).

	% TEB	Teleost	Elasmo	Mollusc	Crustacean	Ctenophore	Other Invertebrate
1.5 X	100	67106.41	830.74	5673.62	2320.89	3351.14	6576.62
	75	50329.80	623.05	4255.21	1740.67	2513.36	4932.46
	50	33553.20	415.37	2836.81	1160.44	1675.57	3288.31
	25	16776.60	207.68	1418.40	580.22	837.79	1644.15
	61.92	*41552.29*	*514.39*	*3513.11*	*1437.09*	*2075.03*	*4072.24*
2.5 X	100	111844.01	1384.56	9456.03	4247.91	5585.24	10961.03
	75	83883.01	1038.42	7092.02	3185.93	4188.93	8220.77
	50	55922.00	692.28	4728.02	2123.95	2792.62	5480.51
	25	27961.00	346.14	2364.01	1061.98	1396.31	2740.26
	61.92	*69253.81*	*857.32*	*5855.18*	*2630.30*	*3458.38*	*6787.07*

Table 3-9. Estimates of total biomass (mt) and percentage of commercial landings consumed of selected prey taxa by 100-25% and 61.92% of the spiny dogfish TEB (361,040 mt) during February - March 2010, assuming annual ration of 1.5 x and 2.5 x body weight.

	Prey	% dogfish biomass	Total consumption (mt)	Landings (mt)	% landings consumed
1.5 X	Bay anchovy	100	9793.63	-	-
		75	5761.16	-	-
		50	3889.35	-	-
		25	1920.52	-	-
		61.92	*6064.22*	-	-
	Atlantic croaker	100	687.41	7262.01	9.47
		75	515.56	7262.01	7.10
		50	343.71	7262.01	4.73
		25	171.85	7262.01	2.37
		61.92	*425.64*	*7262.01*	*5.86*
	Squid	100	2707.50	30143.48	8.98
		75	2030.63	30143.48	6.74
		50	1353.75	30143.48	4.49
		25	676.88	30143.48	2.25
		61.92	*1676.49*	*30143.48*	*5.56*
	Ctenophore	100	3351.14	-	-
		75	2513.36	-	-
		50	1675.57	-	-
		25	837.79	-	-
		61.92	*2075.03*	-	-
2.5 X	Bay anchovy	100	16322.72	-	-
		75	12242.04	-	-
		50	8161.36	-	-
		25	4080.68	-	-
		61.92	*10107.03*	-	-
	Atlantic croaker	100	1066.30	7262.01	14.68
		75	799.73	7262.01	11.01
		50	533.15	7262.01	7.34
		25	266.58	7262.01	3.67
		61.92	*660.26*	*7262.01*	*9.10*
	Squid	100	4512.51	30143.48	14.97
		75	3384.38	30143.48	11.23
		50	2256.25	30143.48	7.49
		25	1128.13	30143.48	3.74
		61.92	*2794.14*	*30143.48*	*9.27*
	Ctenophore	100	68146.30	-	-
		75	51109.73	-	-
		50	34073.15	-	-
		25	17036.58	-	-
		61.92	*42196.19*	-	-

Table 3-10. Biomass consumed (mt), percent landings and percent stock biomass of Atlantic menhaden and striped bass consumed by 100-25% and 61.92% of spiny dogfish TEB in February 2010.

	Prey	Percent dogfish biomass	February consumption (mt)	Total landings (mt)	Percent landings	Stock biomass (mt)	Percent biomass
1.5 X	Atlantic menhaden	100	24851.82	182209.00[a]	13.64	100000[c]	3.48
		75	18638.86	182209.00	10.23	100000	2.61
		50	12425.91	182209.00	6.82	100000	1.74
		25	6212.95	182209.00	3.41	100000	0.87
		61.92	*15388.24*	*182209.00*	*8.44*	*100000*	*2.15*
	Striped bass	100	955.52	16620.14[b]	5.75	108300[d]	0.88
		75	716.64	16620.14	4.31	108300	0.66
		50	477.76	16620.14	2.87	108300	0.44
		25	238.88	16620.14	1.44	108300	0.22
		61.92	*591.66*	*16620.14*	*3.56*	*108300*	*0.55*
2.5 X	Atlantic menhaden	100	41419.70	182209.00	22.73	100000	5.80
		75	31064.77	182209.00	17.05	100000	4.35
		50	20709.85	182209.00	11.37	100000	2.90
		25	10354.92	182209.00	5.68	100000	1.45
		61.92	*25647.08*	*182209.00*	*14.08*	*100000*	*3.59*
	Striped bass	100	1592.53	16620.14	9.58	108300	1.47
		75	1194.40	16620.14	7.19	108300	1.10
		50	796.27	16620.14	4.79	108300	0.74
		25	398.13	16620.14	2.40	108300	0.37
		61.92	*986.10*	*16620.14*	*5.93*	*108300*	*0.91*

[a] Commercial landings 2008 (NMFS 2010)

[b] Combined commercial and recreational landings 2008 (NMFS, personal communication)

[c] Spawning stock biomass (ASMFC 2011)

[d] Stock biomass (ASMFC 2009

4. Ecological interactions between spiny dogfish (*Squalus acanthias*) and striped bass (*Morone saxatilis*) in North Carolina nearshore waters: a case of intraguild predation?

Abstract

Spiny dogfish and striped bass are high-level predators in the Northwest Atlantic ecosystem that have recently recovered from overfishing, and there is interest in their ecological interactions. Striped bass and spiny dogfish abundance, salinity, temperature, and depth data were taken from winter trawl surveys conducted in North Carolina waters from 1996-1998 and 2006-2010. Diet data were collected from striped bass in 2006-2007 and from spiny dogfish in 2006-2007 and 2010. Spatial and dietary overlaps were determined between the two species and the importance of striped bass in the diet of spiny dogfish was assessed. Spatial overlap was consistently high and abundance was more strongly correlated with environmental factors than the abundance of the other predator. Dietary overlap was less than 40% between striped bass and dogfish sampled in 2006-2007 but was over 84% between striped bass and spiny dogfish sampled in 2010. Atlantic menhaden (*Brevoortia tyrannus*) and bay anchovy (*Anchoa mitchilli*) were the most important overlapping prey species. Spiny dogfish in North Carolina waters may have consumed 0.91% of the striped bass stock during the winter. These data suggest that spiny dogfish are intraguild predators of striped bass, but this interaction is insufficient to affect the abundance and distribution of either species.

Introduction

Predators can exert strong top-down control over their environment. The influence of predators can be observed in terms of direct predation and risk effects such as predator avoidance behaviors, both of which are observable in marine ecosystems (Heithaus et al. 2008). Predatory sharks occupy an apex predator role in most marine habitats, and as such may have significant influence over the ecosystem dynamics of those habitats (Heithaus et al. 2010). There is some evidence that sharks may play a keystone role in regulating certain prey species (Myers et al. 2007). However, in environments where other high-level predators such as large teleosts are present, the role of sharks in balancing the community may be diminished due to redundancy in the apex predator niche (Kitchell et al. 2002).

Interspecies competition between predators can strongly influence the distribution and foraging habits of the competing predators and have indirect effects on the trophic dynamics of the entire community. For example, Papastamatiou et al. (2006) found that the distributions of sandbar (*Carcharhinus plumbeus*) and grey reef sharks (*Carcharhinus amblyrynchos*) in the Hawaiian Islands were driven by competition between the two species for similar prey.

An extreme example of interspecies competition is intraguild predation, in which one or both of the competing predators are capable of consuming the other, which conveys the dual benefits of energetic gain from feeding and removal of a potential competitor (Polis et al. 1989). Intraguild predation has been documented between species of sharks (Gallucci and Langseth 2009) and between sharks and marine mammals (Heithaus 2001a). Because the risk involved is higher than that of normal interspecific competition, intraguild predation often results in competitive exclusion of one of the predators from areas that would otherwise be optimal foraging habitat (Heithaus 2001b, Heithaus and Dill 2002, Frid et al. 2008). This may have the indirect effect of lowering the overall predation pressure on some of the prey species in those areas (Dill et al. 2003, Frid et al. 2008).

The spiny dogfish (*Squalus acanthias*) is a relatively small shark common in the Northwest Atlantic Ocean (Burgess 2002). This species has a wide distribution and is highly migratory, occurring in southern New England and the Gulf of Maine during the spring and summer and overwintering in North Carolina waters, occasionally occurring as far south as Georgia (Bearden 1965, Stehlik 2007, Rulifson and Moore 2009). During the winter, approximately 61.92% of the stock may be present off the coast of North Carolina north of Cape Hatteras (Register 2006). Spiny dogfish are the target of a directed fishery in the Northwest Atlantic and showed signs of overexploitation in the 1990s (Rago et al. 1998); by 1998 they were considered overfished (Rago and Sosebee 2009). However, after a decade of conservative management the stock is now considered recovered (Rago and Sosebee 2010).

The trophic relationships of spiny dogfish have been of considerable interest because of interactions between these sharks and commercially important species (Link et al. 2002). Adult dogfish are primarily piscivores, though they will take a variety of prey including other elasmobranchs, ctenophores, cephalopods, benthic and planktonic crustaceans, sea cucumbers, and other invertebrates (Bowman et al. 2000, Burgess 2002, Smith and Link 2010). The amount and species of teleost prey vary by location (Bowman et al. 2000, Stehlik 2007, Smith and Link 2010). In North Carolina waters, fish prey made up 60.4% of the diet by weight of spiny dogfish sampled north of Cape Hatteras, and 92.4% of the diet south of Cape Hatteras (Bowman et al. 2000). Dogfish feed primarily on pelagic and demersal species but will consume benthic species as well (Ellis et al. 1996, Link et al. 2002). Clupeids are of particular importance: spiny dogfish are the main consumer of Atlantic herring (*Clupea harengus*) out of 12 principle piscivores in the Georges Bank ecosystem (Overholtz et al. 2000, Overholtz and Link 2007), and clupeids made up the majority of identified fish prey recorded by the NEFSC trawl survey in North Carolina waters north of Cape Hatteras (Bowman et al. 2000). Aggregations of spiny dogfish feeding on Atlantic menhaden (*Brevoortia tyrannus*) have been observed in the coastal waters of South Carolina during the winter (Bearden 1965).

As high-level piscivores, adult spiny dogfish occupy the same general trophic guild as many economically important species (Garrison and Link 2000). Competitive release has been cited as a possible cause for the dramatic increase in the abundance of dogfish that coincided with the crash of Atlantic cod (*Gadus morha*) and other groundfish species in the 1990s (Fogarty and Murawski 1998), and since then spiny dogfish have become the dominant piscivores in the Northwest Atlantic (Link and Garrison 2002). It has been hypothesized that a combination of competition for prey resources and direct predation by spiny dogfish has contributed to the slow recovery of groundfish stocks on Georges Bank, and groundfish species do appear as juveniles in the diet of spiny dogfish (Link et al. 2002). However, Link et al. (2002) found that groundfish only make up a relatively small portion of the dogfish diet, and that predation by dogfish alone is not sufficient to explain the continued low abundance of those species.

Like spiny dogfish, striped bass (*Morone saxatilis*) are highly piscivorous (Walter et al. 2003) and have successfully recovered from overfishing (Richards and Rago 1999). An anadromous species, striped bass spend most of their life cycle in marine waters and make annual migrations to natal streams to spawn, though some may become freshwater residents (Klein-MacPhee 2002). Migratory striped bass overwinter off of Virginia and North Carolina during their annual ocean migration (Chapoten and Sykes 1961).

Clupeids, particularly Atlantic menhaden, dominate the diet of striped bass (Walter et al. 2003). In the coastal waters of Virginia and North Carolina, menhaden accounted for 67.9% of the striped bass diet by weight from 1994-2007 (Overton et al. 2008), and striped bass selectively feed on clupeids as they move into brackish and fresh water (Ruderhausen et al. 2005). The combination of the successful recovery and voracious feeding habits of striped bass has lead to potential ecological consequences. Between 1997 and 2000, predation by striped bass may have exceeded the availability of menhaden in the Chesapeake Bay, resulting in significant health problems for the predators (Uphoff 2003). The striped bass population of the Hudson River may require more alosine prey than is actually produced by the river, and may be hindering the recovery of declining species such as blueback (*Alosa aestivalis*) and alewife (*Alosa psuedoharengus*) herrings (Hartman 2003).

Spiny dogfish and striped bass both occur in the coastal waters of North Carolina during the winter (Chapoten and Sykes 1961, Stehlik 2007). Both have recently recovered from overfishing (Richards and Rago 1999, Rago and Sosebee 2010). Striped bass and spiny dogfish are both highly piscivorous, and according to NMFS food habits data there is a 40-60% dietary overlap between the two species (Smith and Link 2010). The foraging strategies of the two predators differ: spiny dogfish are opportunistic feeders and shift their diet to reflect the abundance of different prey species (Overholtz and Link 2007, Moustahfid et al. 2010) while striped bass are selective towards menhaden and river herrings throughout their range (Walter et al. 2003). Coincidentally, clupeids also make up a significant portion of the spiny dogfish diet in the southern end of their range (Bearden 1965, Bowman et al. 2000, Smith and Link 2010). Because of the high degree of seasonal co-occurrence and dietary overlap, there is potential for strong competitive interactions between spiny dogfish and striped bass.

Spiny dogfish usually feed on small fishes and juveniles of larger species (Stehlik 2007), but there is anecdotal evidence of dogfish attacking and consuming prey larger than themselves (Burgess 2002). A combination of jaw morphology and prey manipulation behavior makes dogfish capable of dismembering prey too large to swallow (Wilga and Motta 1998, Huber and Motta 2004).

Since spiny dogfish are capable of consuming large prey, they may be a potential intraguild predator of striped bass. Such an interaction would be evident through both the feeding habits of spiny dogfish and the spatial distribution of both species, and could have significant implications for the management of both species and their prey. The goals of this study are to determine if predatory and competitive interactions are occurring between spiny dogfish and striped bass as they overwinter in North Carolina waters, and to provide a preliminary assessment of their potential impacts on the striped bass stock.

Materials and Methods

2010 CWTC Data

Spiny dogfish were sampled aboard the U.S. Fish and Wildlife Service-led Cooperative Winter Tagging Cruise (CWTC). This cruise took place aboard the NSF R/V *Cape Hatteras* from February 18-14, 2010, and sampled 200 stations in North Carolina waters between Cape Hatteras and the Virginia state line. Stations were chosen based on potential for sampling striped bass and tow time varied between 10 and 30 minutes. Latitude, longitude, and time were recorded for the beginning and end of each tow, as well as depth (m), salinity (ppm), air temperature (°C), and water temperature (°C). Catch and abundance data for striped bass, spiny dogfish, and selected other species were also recorded at each station.

Because two species must be in the same location in order to interact, spatial overlap was calculated between the dogfish and striped bass using equation (1), adapted from Link et al. (2002). Spatial overlap (O_{ij}) between species *i* and *j* is equal to the number of stations at which both species are present (n_{ij}) divided by the total number of stations at which species *i* occurs (n_i). The result ranges from 0 (no spatial overlap) to 1.0 (100% spatial overlap) (Link et al. 2002).

— (1)

To determine if the abundance of spiny dogfish and striped bass affected one another, correlations between the abundance of the two species were calculated. Correlations were also calculated between spiny dogfish and striped bass abundance and the environmental measurements recorded at each station, and one-way ANOVAs were used to determine if these correlations were significant. Finally, spiny dogfish and striped bass abundance data were analyzed using ArcGIS to identify any geographical features along the North Carolina coast that may have been associated with the abundance of either species.

No more than 10 spiny dogfish per tow were sampled for diet analysis. If the total catch at a given station was less than 10 dogfish, all dogfish were sampled. Fork length (FL, mm), total length (TL, mm), and sex were recorded for each sampled dogfish, and whole stomachs were removed and preserved in a 10% buffered formalin solution for transport back to the lab. Because net feeding in the trawl can potentially bias feeding habits data, other species landed with dogfish were carefully checked for bites and other signs of attempted predation.

In the lab, stomach contents were identified to the lowest possible taxon, usually species for teleost fishes and crustaceans, and family for most other invertebrates. If prey items were not intact enough for ready identification, hard parts such as scales and bones were saved to aid in classification. Scales were used to calculate the age and size of some large partial specimens, with particular emphasis on striped bass.

Weight (g) and number were recorded for each prey species, which were grouped into five broad categories based on classification: Teleost, Elasmobranch, Crustacean, Mollusc, Ctenophore, and Other Invertebrate. Animal tissue of unknown origin was categorized as Unidentified and sand, rocks, plant matter, and other non-food material were categorized as Detritus. Frequency of occurrence, percent weight, and percent by number were calculated for each prey category across the total spiny dogfish diet, as well as for prey species within each category. These values were used to calculate the index of relative importance (IRI) for each prey species and each prey category. To aid in direct comparison between prey types and categories, IRI was expressed as a percentage (Cortés 1997). Percent IRI for a given prey species or category *i* was calculated using equation (2), adapted from Cortés (1997).

(2)

Previous CWTC Data

CWTC data from previous years (1996-1998 and 2006-2009) were incorporated into the analysis to determine whether any observed ecological interactions between spiny dogfish and striped bass were long-term trends or fluctuate over time. These data were obtained using the same standard operating procedures as the 2010 CWTC, though research vessels and gear deployment methods varied.

Catch data for spiny dogfish and striped bass were obtained from CWTC tows from 1996-1998 and 2006-2009. Because conservative management policies for dogfish came into effect in 2004, the survey years from 1996-1998 were grouped as "Pre-Management" and those from 2006-2010 were considered "Post-Management." The number of stations and dates sampled varied between years: 204 stations from January 24-25 and February 7-12 in 1996, 131 stations from February 1-6 in 1997, 64 stations from January 16-22 in 1998, 302 stations from January 19-28 in 2006, 185 stations from January 18-24 in 2007, 329 stations from January 15-24 in 2008, and 210 stations from 2009. Spatial overlap was calculated for each year, for the 1996-1998 sampling period, the 2006-2010 sampling period, and for all years combined. The catch-per-unit-effort (CPUE) of striped bass and spiny dogfish was calculated as fish/km^2 for the 1996-1998 and 2006-2010 sampling periods and all years combined. Pearson correlations were calculated between CPUE of striped bass and spiny dogfish, as well as depth, temperature, and salinity. Arc-GIS analysis was used to determine if any geographical features along the North Carolina coast were consistently associated with the abundance of either species.

Data on spiny dogfish and striped bass stomach contents were collected during the 2006 and 2007 CWTC. During these surveys no more than five spiny dogfish stomachs were sampled from any given station, and whole stomachs were removed and preserved in

10% normalin solution. Total length (mm) was recorded for intact prey items. Number, weight (g), and frequency of abundance were recorded for each prey species, and prey species were grouped into the same categories as the 2010 data. IRI and % IRI were calculated for each prey species and category.

Dietary overlap was determined by calculating the Bray-Curtis similarity index (Bray and Curtis 1957). This index is considered the most accurate method for determining overlap (Bloom 1981) and is the standard method used in NOAA/NMFS feeding habits models (Smith and Link 2010). Overlap (*B*) is expressed in terms of 0 (no similarity) to 1.0 (100% similarity) and is calculated using equation (3), in which the sum of minimum percent abundance (*X*) for all species *j* between communities *i* and *k* is doubled and divided by the sum of the combined abundance of all species.

(3)

Overlap was determined between spiny dogfish and striped bass diet from 2006-2007, and between both of those diets and spiny dogfish diet from 2010. Percent similarity was also calculated with prey species of less than 1% IRI removed from the spiny dogfish diets to determine if rare prey items may bias the index.

To provide an estimate of the total biomass of striped bass consumed by spiny dogfish, stock biomass estimates determined by Rago and Sosebee (2010) and estimates of the annual ration of prey needed by spiny dogfish for routine metabolism were used to create equation (4).

(4)

In equation (4) the total consumption (*C*) of a given species *i* is equal to the annual food ration (*R*) times the total stock biomass of spiny dogfish (*S*) multiplied by the percent weight (%*W*) of species *i* in the spiny dogfish diet. Consumption was calculated using annual ration requirements found by Jones and Geen (1977) and Brett and Blackburn (1978). Jones and Geen (1977) determined that spiny dogfish require an annual intake of 2.5 times their body weight, while Brett and Blackburn (1978) calculated annual ration at 1.5 times the dogfish body weight. Total consumption was calculated for both the spawning stock biomass (SSB) (163,256 mt) and total exploitable biomass (TEB) (361,040 mt) (Rago and Sosebee 2011). These stock estimates represent the large, mature dogfish that are targeted by the commercial fishery, which are also the dogfish that fit within the piscivore guild in the Northwest Atlantic (Garrison and Link 2000).

It is unlikely that the entire spawning stock of spiny dogfish is present off of North Carolina during the winter, so a sensitivity analysis was performed to estimate consumption by different proportions of the spiny dogfish biomass. Consumption was expressed in kg and calculated for 100%, 75%, 50%, 25%, and 61.92% (Register 2006) of the total spiny dogfish biomass using the percent weight of striped bass from the 2010 dogfish diet. Total estimated biomass of striped bass consumed by spiny dogfish was compared with 2009 striped bass landings (NMFS Fisheries Statistics Division, personal communication) and current data on striped bass spawning stock biomass (NEFSC 2008). Because this study could only verify consumption during the month of February, the annual estimates of consumption were divided by 365 and then multiplied by 28 to estimate striped bass consumption during the sampling period.

Results

Abundance and Spatial Overlap

Within the study period, 1,625 stations were sampled by the CWTC. These stations ranged from the mouth of the Chesapeake Bay to just south of Cape Hatteras, and encompassed Platt Shoals, Wimble Shoals, and Diamond Shoals, which are important geographical features for fishing and navigation. During the 1996-1998 period most sampling stations were south of Oregon Inlet, while from 2006-2010 all stations were north of Cape Hatteras (Figure 1).

The relative frequency of both spiny dogfish and striped bass has changed over time. Overall spiny dogfish occurred in approximately 85 % of tows from 1996-2010, while striped bass occurred in about 51 % of tows within the same period. In general, the percent frequency of spiny dogfish has increased since 1996, while the frequency of striped bass has decreased (Figure 2). Peak striped bass frequency occurred in 1997, with bass occurring in over 80 % of tows, while the lowest frequency occurred in 2009, with striped bass appearing in only 14 % of tows. Conversely, the lowest frequency of dogfish occurred in 1997 (57 % of tows) and the highest occurred in 2007, when dogfish were present in over 98 % of tows (Table 1).

Spatial overlap between striped bass and spiny dogfish was above 60 % for the entire study period, and striped bass co-occurred with spiny dogfish in over 96 % of tows each year since 2008 (Figure 3). Conversely, spatial overlap between spiny dogfish and striped bass has decreased over time as dogfish appear in more tows that do not contain striped bass (Figure 3). Spiny dogfish occurred in 71.1 % of tows that contained striped bass before management, and striped bass occurred in 78.9% of tows containing dogfish. In the tows after management for spiny dogfish was established, dogfish occurred in 89.8 % of tows containing striped bass, while striped bass occurred in 46.1 % of tows containing dogfish (Table 1).

Overall, striped bass CPUE showed weak but significant positive correlations with depth (R = 0.07) and salinity (R = 0.09), while a stronger significant negative relationship was found between spiny dogfish CPUE and salinity (R = -0.32) (Table 2). Striped bass CPUE correlated negatively with salinity in the 1996-1998 sampling period (R = -0.25), but showed significant positive correlations with all environmental factors during the 2006-2010 period (Table 2). Spiny dogfish CPUE did not correlate significantly with any environmental factors when all years were combined, but showed a significant positive correlation with depth in 1996-1998 samples (R = 0.18) and significant negative correlations with depth (R = -0.08) and salinity (R = -0.36) during the 2006-2010 period (Table 2). Spiny dogfish and striped bass CPUE did not correlate significantly with each other overall or over either of the sampling periods.

Depth, salinity, and temperature were significantly correlated overall and in both sampling periods. All three environmental factors were positively correlated when all years were combined and during the 2006-2010 sampling period. During the 1996-1998 sampling period depth showed significant negative correlations with temperature (R = -0.15) and salinity (R = -0.21), while temperature and salinity were positively correlated (R = 0.23) (Table 2).

As might be expected from the high degree of spatial overlap between the two species, spiny dogfish and striped bass tended to occur in high abundance near the same geographic features. Within the time series of this study, the densest aggregations of both spiny dogfish and striped bass were found on the northern side of Platt Shoals, as well as in the area of Oregon Inlet and Wimble Shoals. Large numbers of spiny dogfish were also caught on Diamond Shoals, an area where the largest aggregations of striped bass were not present (Figure 4A-B).

There was little sampling around Platt Shoals during the 1996-1998 surveys, but some large catches of striped bass were found there. Large schools of striped bass were also found on Wimble Shoals and lower abundances of striped bass were consistently found on Diamond Shoals (Figure 5A). The largest catches of spiny dogfish from 1996-1998 were all in the Diamond Shoals area and some scattered large aggregations were captured west of Wimble Shoals, but dogfish occurred in relatively low densities elsewhere (Figure 5B).

During the 2006-2010 sampling period most large striped bass catches occurred in the Platt Shoals area, with some sporadic mid-sized catches around Wimble Shoals and Oregon Inlet (Figure 6A). Spiny dogfish occurred in moderate to high numbers around Platt Shoals, but were most abundant on the eastern portion of Wimble Shoals (Figure 6B). Sampling did not extend far south of Wimble Shoals during this period.

Feeding Habits

Stomach contents were analyzed from 73 spiny dogfish and 64 striped bass during the 2006-2007 CWTC surveys. Spiny dogfish showed a greater proportion of empty stomachs than striped bass; 24 (32.88%) spiny dogfish stomachs contained no food while only five (7.81%) striped bass stomachs were empty. An additional 253 spiny dogfish stomachs were sampled during the 2010 CWTC, of which 58 (22.92%) were empty, and 13 (5.14%) were too deteriorated to produce useful data. Net feeding by spiny dogfish was not observed during the 2010 survey, but did occur on weakfish (*Cynoscion regalis*) at one station during the 2007 cruise.

Between the two predators and over the two sampling periods, 49 prey taxa were identified. The Teleost category was the most diverse with 23 identified taxa, followed by the Crustaceans with 12 identified taxa. All prey taxa classified by category are listed in Table 3.

Both predators had diets dominated by teleost prey. The Teleost category was the most important for striped bass in 2006-2007, with the Crustacean and Other Invertebrate categories showing only marginal importance (Table 4). Teleost prey was also most important to spiny dogfish sampled in 2006-2007, and Crustacean prey was secondary

(Table 4). Teleosts were the most important prey category in the diet of spiny dogfish sampled in 2010, and Ctenophores showed the second highest importance (Table 4). The Teleost category showed a greater than 90% IRI in the diet of both predators, and across both spiny dogfish sampling periods. Due to the prevalence of Teleost prey, dietary overlap by prey category was 89.49% between striped bass and spiny dogfish in 2006-2007, 95.09% between striped bass in 2006-2007 and spiny dogfish sampled in 2010, and 91.50% between spiny dogfish from the two sampling periods (Table 5).

Striped bass sampled during the 2006-2007 surveys showed a relatively limited diet, feeding upon only six identified prey taxa (Table 6). The diet of striped bass was dominated by bay anchovy, at 97.13% IRI. Atlantic menhaden were the second most important (2.67% IRI) and spot (*Leiostomus xanthurus*) were of tertiary importance (0.02% IRI). All other prey taxa were less than 0.01% IRI (Table 6).

Atlantic menhaden (50.24% IRI), bay anchovy (19.03% IRI) and weakfish (*Scionoscion regalis*)(12.34% IRI) were the most important of the 48 prey taxa identified in spiny dogfish sampled in 2006-2007 (Table 7). However, evidence of net feeding was observed in the case of weakfish. Striped bass were the fifth most important prey taxa (2.69% IRI), and they made up the third highest percentage of the diet by weight (15.02% W), but relatively low percentage by number (2.44% N), and occurred in 6.12% of the sampled dogfish stomachs (Table 7).

In spiny dogfish sampled in 2010 consumed 47 different prey taxa, of which Atlantic menhaden (57.33% IRI), bay anchovy (31.79% IRI), and unidentified fish (8.88% IRI) were the most important (Table 8). Striped bass were of relatively minor importance (0.07% IRI), making up 2.30% of the diet by weight, 0.14% by number, and occurring in only 1.65% of the sampled stomachs (Table 8).

When all prey taxa are included, dietary overlap varied between the data sets. Striped bass (2006-2007) showed only 24.19% overlap with spiny dogfish from the same period, but 84.49% overlap with spiny dogfish from 2010 (Table 9). This is likely due to the numerical dominance of bay anchovy in the diet of both striped bass and spiny dogfish sampled in 2010. Spiny dogfish from 2006-2007 showed only 34.73% overlap with spiny dogfish from 2010 (Table 9).

When prey taxa accounting for less than 1% IRI were removed, dietary overlap increased between all predators and sample periods. Overlap between striped bass (2006-2007) and spiny dogfish (2006-2007) was 28.39%, while overlap was 87.56% between striped bass (2006-2007) and spiny dogfish (2010) (Table 10). The diet of spiny dogfish from 2006-2007 overlapped 39.57% with spiny dogfish sampled in 2010 (Table 10).

The current estimated spawning stock biomass of spiny dogfish is approximately 163,256,000 kg and total exploitable biomass is estimated to be 361,040,000 kg (Rago and Sosebee 2010). Assuming that all dogfish consume 1.5 times their body weight per year (Brett and Blackburn 1978), the total SSB of dogfish would require approximately 244,884,000 kg of food for routine metabolism, while an annual prey intake of 541,560,000 kg would be required to sustain the TEB. If an annual ration of 2.5 times to dogfish body weight is assumed (Jones and Geen 1977), then 408,140,000 kg of prey would be needed by the SSB and 902,600,000 kg would be needed by the TEB in order to fulfill the spiny dogfish stock's metabolic needs.

According to the 2010 spiny dogfish diet data, striped bass made up 2.30% of the diet by weight (Table 8). If spiny dogfish require 1.5 times their body weight in prey, then the amount of striped bass consumed by 100-25% of the SSB would equal 2.60-0.65% of the coast-wide 2009 landings of striped bass or 0.40-0.10% of the estimated striped bass biomass, while the TEB would consume 5.75-1.44% of striped bass landings and 0.88-0.22% of the stock biomass. The estimated SSB present off of North Carolina would have consumed 1.61% of striped bass landings and 0.24% of the stock biomass, and the North Carolina TEB would have accounted for 3.56% of landings and 0.55% of biomass (Table 11). Assuming an annual ration of 2.5 times the dogfish body weight, 100-25% of the dogfish SSB would consume 4.33-1.08% of striped bass landings and 0.66-0.17% of the striped bass stock biomass, while the TEB would consume 9.58-2.40% of landings and 1.47-0.37% of the stock biomass. The population off of North Carolina would have consumed 2.68% of landings and 0.41% of the striped bass stock (SSB) or 3.56% of landings and 0.91% of the stock biomass (Table 12).

Discussion

This study confirms that spiny dogfish and striped bass interact regularly in North Carolina waters during the months of January and February, and that interactions between these species may be ecologically significant. The high percentage of spatial and dietary overlap make these two predators potential competitors, with bay anchovy and Atlantic menhaden the most important shared prey. Striped bass are a relatively unimportant prey species for spiny dogfish, and when the consumption rate is extrapolated to a population level predation by spiny dogfish may potentially account for nearly 1 % of the stock biomass of striped bass in the month of February. However, spiny dogfish feeding habits vary by location (Bowman et al. 2000, Smith and Link 2010), so it is highly unlikely that the same proportion of the spiny dogfish population is consistently consuming the same amount of striped bass.

According to Link et al. (2002) species must show high spatial overlap in order to have strong ecological interactions. In the case of spiny dogfish and striped bass in their overwintering habitat, this requirement is met. Overlap between the two predators was never less than 67%, but this relationship was not symmetrical. The higher spatial overlap was observed in whichever species happened to be present in fewer tows, and lower spatial overlap likely reflects increased abundance as the species becomes ubiquitous in the tows. The general trend in the case of spiny dogfish and striped bass is that dogfish overlapped more often with striped bass in the 1996-1998 surveys (Table 1, Figure 3), which coincided with striped bass occurring in a greater percentage of tows (Table 1, Figure 2). This trend reversed in the 2006-2010 data as spiny dogfish occurred in nearly all tows (Table 1, Figures 2 and 3).

Though spatial overlap was high, there was no definite long-term pattern observed between the catch of spiny dogfish and striped bass. However, the two species showed opposite correlations to the same environmental factors, particularly salinity. Striped bass CPUE showed a significant positive relationship with salinity in all sampling periods, while the correlation between spiny dogfish CPUE and salinity was significantly negative in the 2006-2010 sampling period and when all years were combined (Table 2). This suggests that apparent correlations in abundance between striped bass and spiny dogfish may be indirect, representing variation in habitat preference rather than behavioral response on the part of either species. In addition, the moratorium on the striped bass fishery was lifted at the beginning of the survey period (Richards and Rago 1999), so renewed fishing mortality may account for the apparent drop in striped bass frequency (Figure 1).

Spiny dogfish had a considerably more diverse diet than striped bass, reflecting their tendency to prey on the most available species rather than being selective feeders (Moustahfid et al. 2010). Though striped bass and spiny dogfish from the same sampling period (2006-2007) had less than 30% dietary overlap, striped bass diet from 2006-2007 had over 84% with spiny dogfish sampled in 2010 (Tables 9 and 10). Atlantic menhaden and bay anchovy were the most important prey species for both predators (Tables 6-8). The low overlap between dogfish and striped bass in 2006-2007 was largely due to the relative amount of menhaden and anchovies in the diet; for spiny dogfish menhaden were more important, while anchovies dominated the striped bass diet from that period. Other studies support the importance of Atlantic menhaden and bay anchovy to the diet of striped bass off of North Carolina (Walter et al. 2003, Overton et al. 2008). Long-term data also show that spiny dogfish consistently prey on menhaden and other clupeids in the southern end of their range (Bowman et al. 2000, Smith and Link 2010). Atlantic menhaden and bay anchovy may represent an important shared prey resource between spiny dogfish and striped bass. If these two species are consistently the most important prey for both predators, then there is the potential for competitive interactions.

Measuring diet by weight tends to overestimate the importance of striped bass in the diet of spiny dogfish. In both the 2006-2007 and 2010 data sets the percent by weight of striped bass was relatively high while the number and frequency of striped bass were among the lowest of the identified prey taxa. Though striped bass were of low importance as a prey item, they were present in the diet in both the 2006-2007 and 2010 sampling periods. The amount estimated biomass of striped bass consumed by dogfish during the month of February represents over 3% of the most current estimate of the spawning stock biomass of striped bass (NEFSC 2008), but this estimate assumes that the entire stock of spiny dogfish is feeding on the same prey species in the same proportions. Spiny dogfish shift feeding habits seasonally and by size, with only mature dogfish classifying as part of the piscivore guild (Garrison and Link 2000). Though both predators are highly migratory, they likely do not interact constantly over the course of the year, especially since striped bass spend a large amount of time in fresh water (Klein-MacPhee 2002). In addition, the majority of dogfish in shallow continental shelf waters are mature females, with the males occupying deep waters along the shelf break and continental slope (Shepherd et al. 2002), meaning that mature females are the segment of the spiny dogfish population most likely to interact with striped bass. The estimated proportion of the U.S. Atlantic dogfish stock overwintering off of North Carolina (Register 2006) may vary between years. For this reason, the estimates of striped bass consumption by 75-50% of the dogfish SSB (Tables 11 and 12) may be closest to the true predation impact of spiny dogfish.

Two estimates of annual ration were used in the calculation of striped bass consumption. The estimate of 1.5 times the dogfish weight was found in the laboratory by calculating the oxygen consumed during normal swimming motion and may underestimate the true metabolic needs of spiny dogfish (Brett and Blackburn 1978). Jones and Geen (1977) used a variety of methods including some field studies to estimate that spiny dogfish require 2.5 times their body weight in order to provide enough energy for daily survival and growth, so their estimate may be more accurate in depicting the dietary requirements for this species. However, both Jones and Geen (1977) and Brett and Blackburn (1978) derived their estimates using spiny dogfish from the North Pacific population, which have different life history characteristics from those in the Atlantic and have recently been recognized as a separate species, *Squalus suckleyi* (Ebert et al. 2010). Though the species are very closely related, differences in growth and habitat may result in significant differences in dietary needs. Additionally, both estimates of annual ration are derived from metabolic rates recorded at a constant temperature of 10°C (Jones and Geen 1977, Brett and Blackburn 1978), so the consumption estimates in this study are calculated assuming that dogfish metabolism at the temperatures observed during field sampling is not significantly different from that at 10°C. Currently there is no published estimate of feeding ration for spiny dogfish in the Northeast Atlantic, and the reliance on ration estimates from a separate species cannot be discounted as a potential confounding factor.

The diet data used in this study are snapshots of the feeding habits of spiny dogfish and striped bass from the sampling periods, and the 2006-2007 data are taken from relatively low sample sizes (73 for spiny dogfish, 64 for striped bass). With a sample size of 254, the data from spiny dogfish sampled in 2010 may represent a more complete view of the diet from that year. Data from the Northeast Area Monitoring and Assessment Program (NEAMAP) from 2007-2009 confirm a comparable presence of striped bass in the diet of spiny dogfish on a coast-wide scale (2.2% by number, 6.7% by weight, 5.1% frequency)

(Bonzek et al. 2010). The presence of striped bass in the dogfish diet may be partially explained by scavenging the fish from commercial and recreational fishing gear, and there is currently no estimate of the amount of food from scavenging in the dogfish diet. However, the consistent appearance of striped bass in spiny dogfish stomach contents suggests that relatively low amounts of striped bass predation by large female spiny dogfish may be a regular occurrence in inshore waters.

Spiny dogfish are a potential competitor of striped bass based on dietary overlap, and striped bass are present in the dogfish diet. This combination of competition and predation may make spiny dogfish intraguild predators of striped bass, as defined by Polis et al. (1989). Though striped bass are of relatively low importance in the diet of spiny dogfish, in other cases intraguild predation can be an ecologically significant interaction despite low predation rates. In Shark Bay, Australia, the threat of predation by tiger sharks (*Galeocerdo cuvieri*) effectively excludes bottlenose dolphins (*Tursiops truncatus*) from seagrass beds where fish prey is abundant, despite the relatively low rate of predation on dolphins by the sharks (Heithaus and Dill 2002). Frid et al. (2008) found that in the Pacific northwest harbor seals (*Phoca vitulina*) will avoid feeding in deep waters where more nutritious prey is present in order to avoid interacting with Pacific sleeper sharks (*Somniosus pacificus*), which only rarely prey on seals. The threat of predation also allows white sharks (*Carcharodon carcharias*) to competitively exclude other shark species from scavenging on whale carcasses (Pratt et al. 1982).

Asymmetrical intraguild predation occurs when one intraguild (IG) predator preys upon the other without the threat of predation in return (Polis et al. 1989). The data in our study suggest that intraguild predation between spiny dogfish and striped bass is asymmetrical, with dogfish functioning as the IG predator and striped bass functioning as the IG prey. However, both predators show high spatial and geographical overlap, suggesting that predation by dogfish does not exclude striped bass from shared foraging habitat.

Co-occurrence of spiny dogfish and striped bass may be explained by models of intraguild predation (Holt and Polis 1997, Heithaus 2001b). Holt and Polis (1997) found that intraguild predation is a stable ecological interaction if the IG predator gains more by consuming the IG prey than by consuming the shared prey resource, but can also be stable if the IG prey is relatively unimportant as a prey resource for the IG predator. Heithaus (2001b) modeled habitat use by species involved in asymmetrical intraguild predation and found that co-occurrence depends on the competitive ability of both predators and the importance of the shared prey to each predator. Generally, if the IG predator is also a better competitor and the shared prey is an important resource to it, the IG prey will be excluded from more productive habitats (Heithaus 2001b). Access to alternative prey by the IG predator or an increase in production of the shared prey can offset intraguild predation, allowing IG predators and IG prey to co-occur (Heithaus 2001b).

Atlantic menhaden and bay anchovy were the most important shared prey species for spiny dogfish and striped bass in this study, but the diet of spiny dogfish was considerably more diverse than that of striped bass, which may alleviate competition between the two predators. Also, menhaden and anchovy may be abundant enough in North Carolina waters to satisfy the needs of both predators, though the non-standardized experimental design and large-meshed sampling gear used by the CWTC do not provide sufficient data on the relative abundance of these forage species. The CWTC data do show that spiny dogfish may be intraguild predators of striped bass but that co-occurrence between the two species is still high. This may be due to the relatively low importance of striped bass as spiny dogfish prey, a greater variety of prey in the spiny dogfish diet, or a sufficiently high abundance of the shared prey species. These conditions may allow for a stable intraguild predation interaction between striped bass and spiny dogfish that still allows both species to co-occur (Holt and Polis 1997, Heithaus 2001b). However, the stability of this relationship may be susceptible to changes in the abundance of the shared prey species (Heithaus 2001b).

Striped bass show competitive and predatory relationships with other piscivorous species in the Northwest Atlantic. The importance of bay anchovy and menhaden as prey species causes high dietary overlap and potential competition between striped bass, bluefish (*Pomatomus saltatrix*), and weakfish in the Chesapeake Bay ecosystem (Hartman and Brandt 1995). Bluefish in particular interact regularly with striped bass. There may be symmetric intraguild predation between the two species as both predators consume juveniles of the other species (Klein-MacPhee 2002). Adult and sub-adult striped bass are also capable of competitively excluding adult bluefish (Buckel et al. 2009).

Competitive and predatory interactions between high trophic level piscivores can be important influences on the abundance, distribution, and resource use of those species. Understanding these interactions will help to better manage these species at an ecosystem level, and to predict how these interactions can affect recruitment and harvest levels of economically-important species. This study represents a preliminary attempt at describing the ecological interactions between spiny dogfish and striped bass, but these relationships are likely more complex than simple consumption models. Long-term systematic data on the diet of both species, the abundance of shared prey, and the environmental conditions of areas where they co-occur will be needed to better understand the importance of intraguild predation in managing these important predators.

References

ASMFC. 2009. 2009 stock assessment report for Atlantic striped bass. Atlantic States Marine Fisheries Commission.

Bearden, C.M. 1965. Occurrence of spiny dogfish, *Squalus acanthias*, and other elasmobranchs in South Carolina coastal waters. Copeia 1965: 378-378.

Bloom, S.A. 1981. Similarity indices in community studies: potential pitfalls. Marine Ecology Progress Series 5: 125-128.

Bonzek, C.F., J. Gartland, J.D. Lange, Jr., and R.J. Latour. 2010. Data collection and analysis in support of single and multispecies stock assessments in the Mid-Atlantic: Northeast Area Monitoring and Assessment Program Near Shore Trawl Survey (NEAMAP). Award Number: NA10NMF450018. Annual data report to the National Oceanographic and Atmospheric Administration, National Marine Fisheries Service – Northeast Fisheries Science Center and the Mid-Atlantic Fishery Management Council. Virginia Institute of Marine Science, Gloucester Point, VA.

Bowman, R.E., C.E. Stillwell, W.L. Micheals, and M.D. Grosslein. 2000. Food of Atlantic fishes and two common species of squid. NOAA Technical Memorandum NMFS-NE-155. NOAA, Woods Hole, Massachusetts.

Bray, J.R. and J.T. Curtis. 1957. An ordination of the upland forest communities of southern Wisconsin. Ecological Monographs 27: 325-349.

Brett, J.R. and J.M. Blackburn. 1978. Metabolic rate and energy expenditure of the spiny dogfish, *Squalus acanthias*. Journal of the Fisheries Research Board of Canada 35: 816-821.

Buckel, J.A., J.P. Pessutti, J.E. Rosendale, and J.S. Link. 2009. Interactions between bluefish and striped bass: behavior of bluefish under size- and number-impaired conditions and overlap in resource use. Journal of Experimental Marine Biology and Ecology 368: 129-

137.

Burgess, G.H. 2002. Spiny dogfish/*Squalus acanthias* (Linneaus 1785). Pages 54-57 *in* B.B. Collette and G. Klein-MacPhee, editors. Bigelow and Schroeder's fishes of the Gulf of Maine, 3rd edition. Smithsonian Institution Press, Washington, D.C.

Chapoten, R.B., and J.E. Sykes. 1961. Atlantic coast migration of striped bass as evidenced by fisheries and tagging. Transactions of the American Fisheries Society 90: 13-20.

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

Dill, L.M., M.R. Heithaus, and C.J. Walters. 2003. Behaviorally mediated indirect interactions in marine communities and their conservation implications. Ecology 84: 1151-1157.

Ebert, D.A., W.T. White, K.J. Goldman, L.J.V. Compagno, T.S. Daly-Engel, and R.D. Ward. 2010. Resurrection and redescription of *Squalus suckleyi* (Girard, 1854) from the North Pacific, with comments on the *Squalus acanthias* subgroup (Squaliformes: Squalidae). Zootaxa 2612: 22-40.

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

Fogarty, M.J. and S.A. Murawski. 1998. Large-scale disturbance and the structure of marine systems: fishery impacts on Georges Bank. Ecological Applications 8: S6-S22.

Frid, A., G.G. Baker, and L.M. Dill. 2008. Do shark declines create fear-released systems? Oikos 117: 191-201.

Gallucci, V.F., and B.J. Langseth. 2009. Interactions between two sharks: spiny dogfish and sixgill sharks in the Puget Sound/Georgia Basin ecosystem, north Pacific Ocean. Pages 277-284 *in* V.F. Gallucci, G.A. McFarlane, and G.G. Bargmann, editors, Biology and management of dogfish sharks. American Fisheries Society, Bethesda, Maryland.

Garrison, L.P., and J.S. Link. 2000. Dietary guild structure of the fish community in the Northeast United States continental shelf ecosystem. Marine Ecology Progress Series 202: 231-240.

Hartman, K.J. 2003. Population-level consumption by Atlantic coastal striped bass and the influence of population recovery upon prey communities. Fisheries Management and Ecology 10: 281-288.

Hartman, K.J. and S.B. Brandt. 1995. Trophic resource partitioning, diets, and growth of sympatric estuarine predators. Transactions of the American Fisheries Society 124: 520-537.

Heithaus, M.R. 2001a. Predator-prey and competitive interactions between sharks (order Selachii) and dolphins (suborder Odontoceti): a review. Journal of the Zoological Society of London 253: 53-68.

Heithaus, M.R. 2001b. Habitat selection by predators and prey in communities with asymmetrical intraguild predation. Oikos 92: 542-554.

Heithaus, M.R. and L.M. Dill. 2002. Food availability and tiger shark predation risk influence bottlenose dolphin habitat use. Ecology 83: 480-491.

Heithaus, M.R., A. Frid, A.J. Wirsing, and B. Worm. 2008. Predicting ecological consequences of marine top predator declines. Trends in Ecology and Evolution 23: 202-210.

Heithaus, M.R., A. Frid, J.J. Vaudo, B. Worm, and A.J. Wirsing. 2010. Unraveling the ecological importance of elasmobranchs. Pages 612-636 *in* J.C. Carrier, J.A. Musick, and M.R. Heithaus, editors. Sharks and their relatives II: biodiversity, adaptive physiology, and conservation. CRC Press, Boca Raton, Florida.

Holt, R.D. and G.A. Polis. 1997. A theoretical perspective for intraguild predation. The American Naturalist 149: 745-764.

Huber, D.R., and P.J. Motta. 2004. Comparing analysis of methods for determining bite force in the spiny dogfish *Squalus acanthias*. Journal of Experimental Zoology 301A: 26-37.

Jones, B.C. and G.H. Geen. 1977. Food and feeding of spiny dogfish (*Squalus acanthias*) in British Columbia waters. Journal of the Fisheries Research Board of Canada 34: 2067-2078.

Kitchell, J.F., T.E. Essington, C.H. Boggs, D.E. Schindler, and C.J. Waters. 2002. The role of sharks and longline fisheries in a pelagic ecosystem of the central Pacific. Ecosystems 5: 2002-2016.

Klein-MacPhee, G. 2002. Striped bass/*Morone saxatilis* (Walbaum 1792). Pages 377-389 *in* B.B. Collette and G. Klein-MacPhee, editors. Bigelow and Schroeder's fishes of the Gulf of Maine, 3rd edition. Smithsonian Institution Press, Washington, D.C.

Link, J.S. and L.P. Garrison. 2002. Changes in piscivory associated with fishing induced changes in the finfish community on Georges Bank. Fisheries Research 55: 71-86.

Link, J.S., L.P. Garrison, and F.P. Almeida. 2002. Ecological interactions between elasmobranchs and groundfish species on the Northeastern U.S. contintental shelf. I. Evaluating predation. North American Journal of Fisheries Managament 22: 550-562.

Moustahfid, H., M.C. Tyrrell, J.S. Link, J.A. Nye, B.E. Smith, and R.J. Gamble. 2010. Functional feeding responses of piscivorous fishes from the northeast U.S. continental shelf. Oceologia

163: 1059-1067.

Myers, R.A., J.K. Baum, T.D. Shepherd, S.P. Powers, and C.H. Peterson. 2007. Cascading effects and the loss of apex predatory sharks from a coastal ocean. Science 315: 1846-1850.

NMFS Fisheries Statistics Division, personal communication. Silver Spring, MD. http://www.st.nmfs.noaa.gov/st1/index.html.

Overholtz, W.J., and J.S. Link. 2007. Consumption impacts by marine mammals, fish, and seabirds on the Gulf of Maine-Georges Bank Atlantic herring (*Clupea harengus*) complex during the years 1977-2002. ICES Journal of Marine Science 64: 83-96.

Overholtz, W.J., J.S. Link, and L.E. Suslowicz. 2000. Consumption of important pelagic and squid by predatory fish in the northeastern USA shelf ecosystem with some fishery comparisons. ICES Journal of Marine Science 57: 1147-1159.

Overton, A.S., C.S. Manooch, III, J.W. Smith, and K. Brennan. 2008. Interactions between adult migratory striped bass (*Morone saxatilis*) and their prey during winter off the Virginia and North Carolina Atlantic coast from 1994 through 2007. Fishery Bulletin 106: 174-182.

Papastamatiou, Y.P., B.M. Wetherbee, C.G. Lowe, and G.L. Crow. 2006. Distribution and diet of four Carcharhinid sharks in the Hawaiian islands: evidence for resource partitioning and competitive exclusion. Marine Ecology Progress Series 320: 239-251.

Polis, G.A., C.A. Myers, and R.D. Holt. 1989. The ecology and evolution of intraguild predation: potential competitors that eat each other. Annual Review of Ecological Systems 20: 297-330.

Pratt, H.L, Jr., J.G. Casy, and R.B. Conklin. 1982. Observations on large white sharks, *Carcharodon carcharias*, off Long Island, New York. Fishery Bulletin 80: 153-156.

Rago, P.J., K.A. Sosebee, J.K.T. Brodziak, S.A. Murawski, and E.D. Anderson. 1998. Implications of recent increases in catches on the dynamics of Northwest Atlantic spiny dogfish (*Squalus acanthias*). Fisheries Research 39: 165-181.

Rago, P.J. and K.A. Sosebee. 2009. The agony of recovery: scientific challenges of spiny dogfish recovery programs. Pages 343-372 *in* V.F. Gallucci, G.A. McFarlane, and G.G. Bargmann, editors. Biology and management of dogfish sharks. American Fisheries Society, Bethesda, Maryland.

Rago, P.J. and K.A. Sosebee. 2010. Biological reference points for spiny dogfish. Northeast Fisheries Science Center Document 10-06. NOAA, Woods Hole, Massachusetts.

Register, K. E. 2006. Population estimation and female reproductive state of spiny dogfish (*Squalus acanthias*) overwintering in North Carolina coastal waters. Master's thesis. East Carolina University, Greenville, North Carolina.

Richards, R.A., and P.J. Rago. 1999. A case history of effective fishery management: Chesapeake Bay striped bass. North American Journal of Fisheries Management 19: 356-375.

Ruderhausen, P.J., J.E. Tuomikoski, J.A. Buckel, and J.E. Hightower. 2005. Prey selectivity and diet of striped bass in western Albemarle Sound, North Carolina. Transactions of the American Fisheries Society 134: 1059-1074.

Rulifson, R.A. and T.M. Moore. 2009. Population estimates of spiny dogfish aggregations overwintering south of Cape Hatteras, North Carolina, using an area density method. Pages 133-138 *in* V.F. Gallucci, G.A. McFarlane, and G.G. Bargmann, editors. Biology and management of dogfish sharks. American Fisheries Society, Bethesda, Maryland.

Shepherd, T., F. Page, and B. MacDonald. 2002. Length and sex-specific associations between spiny dogfish (*Squalus acanthias*) and hydrographic variables in the Bay of Fundy and Scotian Shelf. Fisheries Oceanography 11: 78-89.

Smith, B.E. and J.S. Link. 2010. The trophic dynamics of 50 finfish and 2 squid species on the Northeast U.S. continental shelf. NOAA Technical Memorandum NMFS-NE-216. NOAA, Woods Hole, Massachusetts.

Stehlik, L.L. 2007. Essential fish habitat source document: spiny dogfish, *Squalus acanthias*, life history and habitat characteristics. NOAA Technical Memorandum NMFS-NE-203, NOAA, Woods Hole, Massachusetts.

Uphoff, J.H., Jr. 2003. Predator-prey analysis of striped bass and Atlantic menhaden in upper Chesapeake Bay. Fisheries Management and Ecology 10: 313-322.

Walter, J.F., III, A.S. Overton, K.H. Ferry, and M.E. Mather. 2003. Atlantic coast feeding habits of striped bass: a synthesis supporting a coast-wide understanding of trophic biology. Fisheries Management and Ecology 10: 349-360.

Wilga, C.D. and P.J. Motta. 1998. Conservation and variation in the feeding mechanism of the spiny dogfish *Squalus acanthias*. Journal of Experimental Biology 201: 1345-1358.

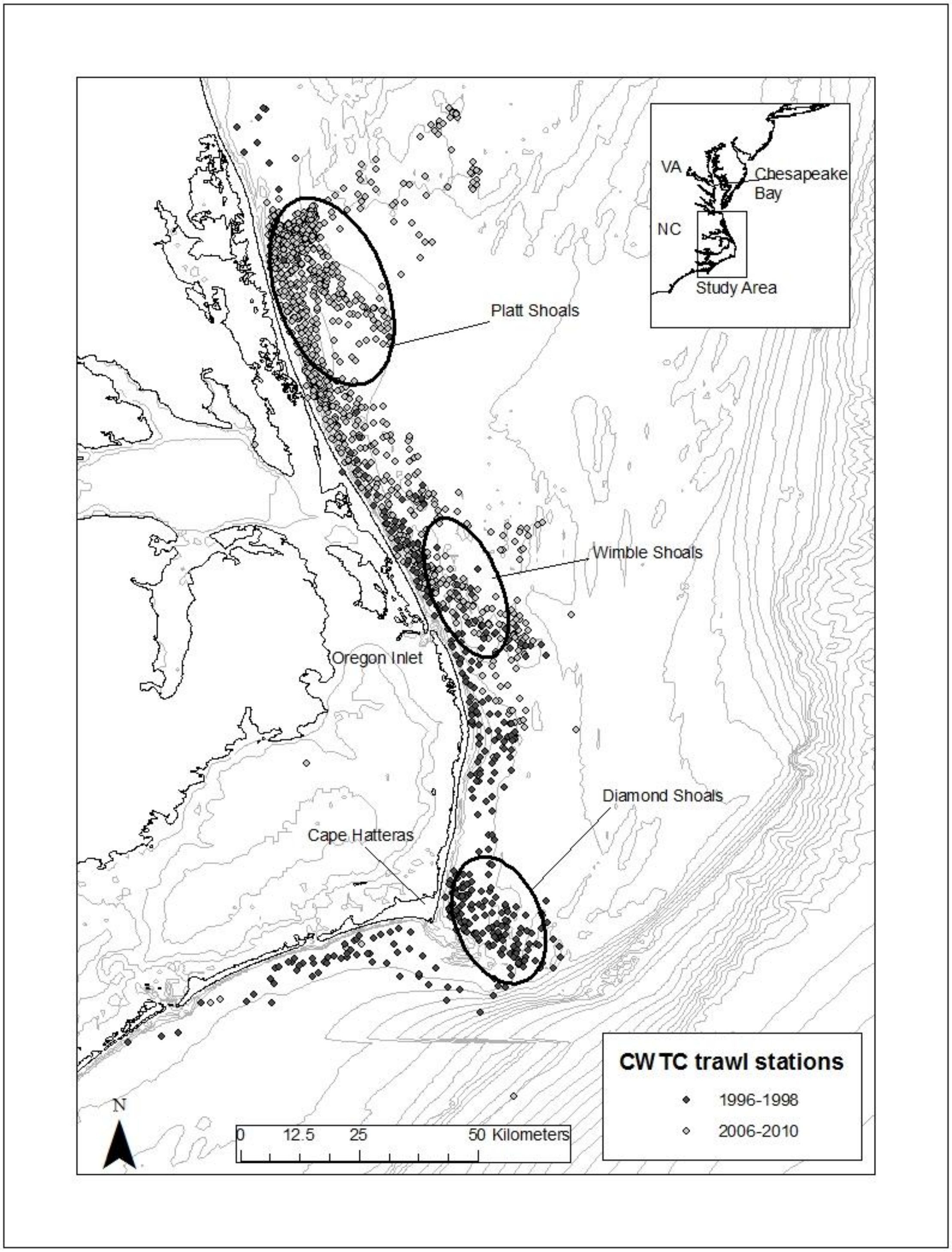


Figure 4-1. Sampling stations from the 1996-1998 and 2006-2010 CWTC surveys.

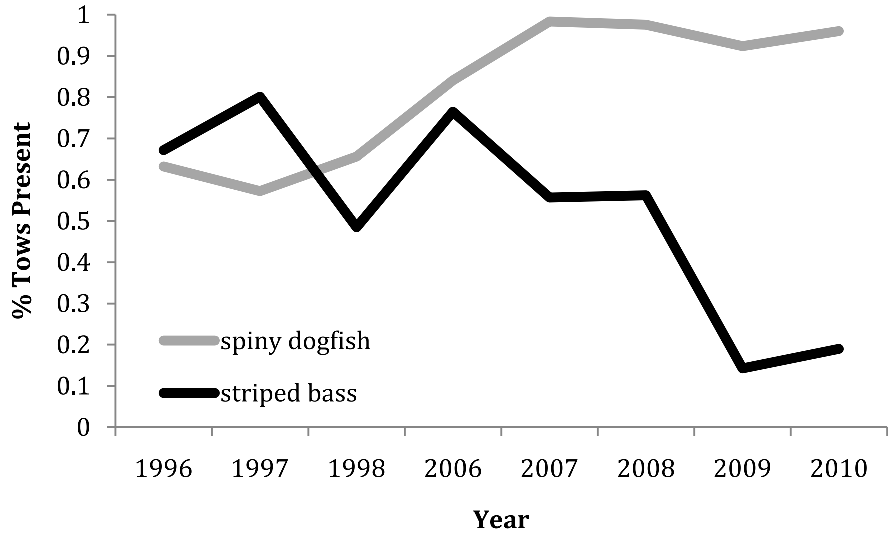


Figure 4-2. Percentage of CWTC tows that contained spiny dogfish and striped bass during the years 1996-1998 and 2006-2010.

Table 4-1. Total tows, frequency of spiny dogfish and striped bass, and percent spatial overlap between spiny dogfish and striped bass for each CWTC year and sampling period.

Year	Total tows	Spiny dogfish frequency (%)	Striped bass frequency (%)	Overlap dogfish with bass (%)	Overlap bass with dogfish (%)
Overall	1625	85.48	51.63	51.91	85.94
1996	204	63.24	67.16	78.29	67.16
1997	131	57.25	80.15	88.00	80.15
1998	64	65.63	48.44	64.29	48.44
1996-1998	399	61.65	68.42	78.86	71.06
2006	302	84.11	76.49	79.13	87.01
2007	185	98.38	55.68	43.96	77.67
2008	329	97.57	56.23	56.07	97.30
2009	210	92.38	14.29	14.95	96.67
2010	200	96.00	19.00	19.27	97.37
2006-2010	1226	93.23	47.88	46.11	89.78

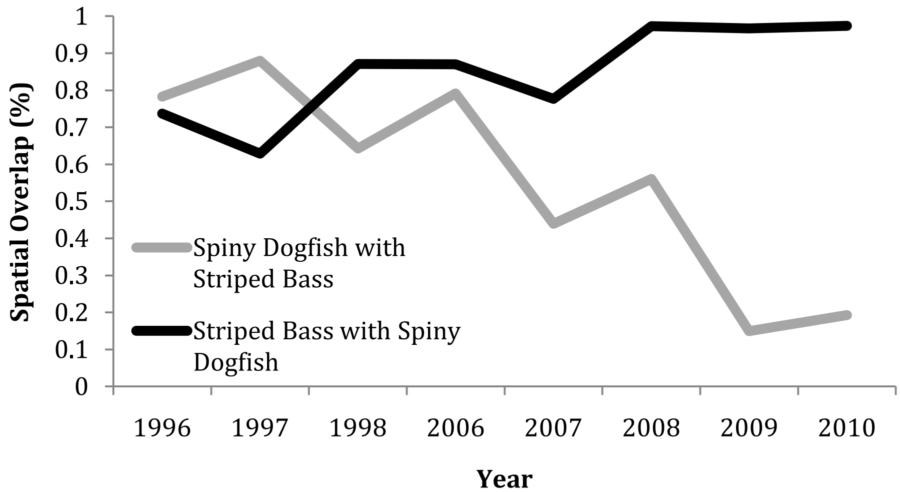


Figure 4-3. Spatial overlap (%) between spiny dogfish and striped bass during CWTC sampling from 1996-1998 and 2006-2010.

Table 4-2. Pearson correlations (R) between spiny dogfish and striped bass CPUE (fish/km^2), trawl depth (m), surface temperature (°C), and salinity (ppm) for the overall survey and the 1996-1998 and 2006-2010 sampling periods.

	R	Depth (m)	Temp (°C)	Salinity (ppm)	Bass (fish/km^2)	Dogfish (fish/km^2)
Overall	Depth	1				
	Temp	0.52*	1			
	Salinity	0.34*	0.33*	1		
	Bass	0.07*	0.05	0.09*	1	
	Dogfish	-0.05	-0.02	-0.33*	0.02	1
1996-1998	Depth	1				
	Temp	-0.15*	1			
	Salinity	-0.21*	0.23*	1		
	Bass	-0.03	0.02	-0.25*	1	
	Dogfish	0.18*	-0.02	0.09	0.09	1
2006-2010	Depth	1				
	Temp	0.73*	1			
	Salinity	0.34*	0.35*	1		
	Bass	0.09*	0.06*	0.12*	1	
	Dogfish	-0.08*	-0.02	-0.36*	-0.01	1

* significant at $\alpha = 0.05$

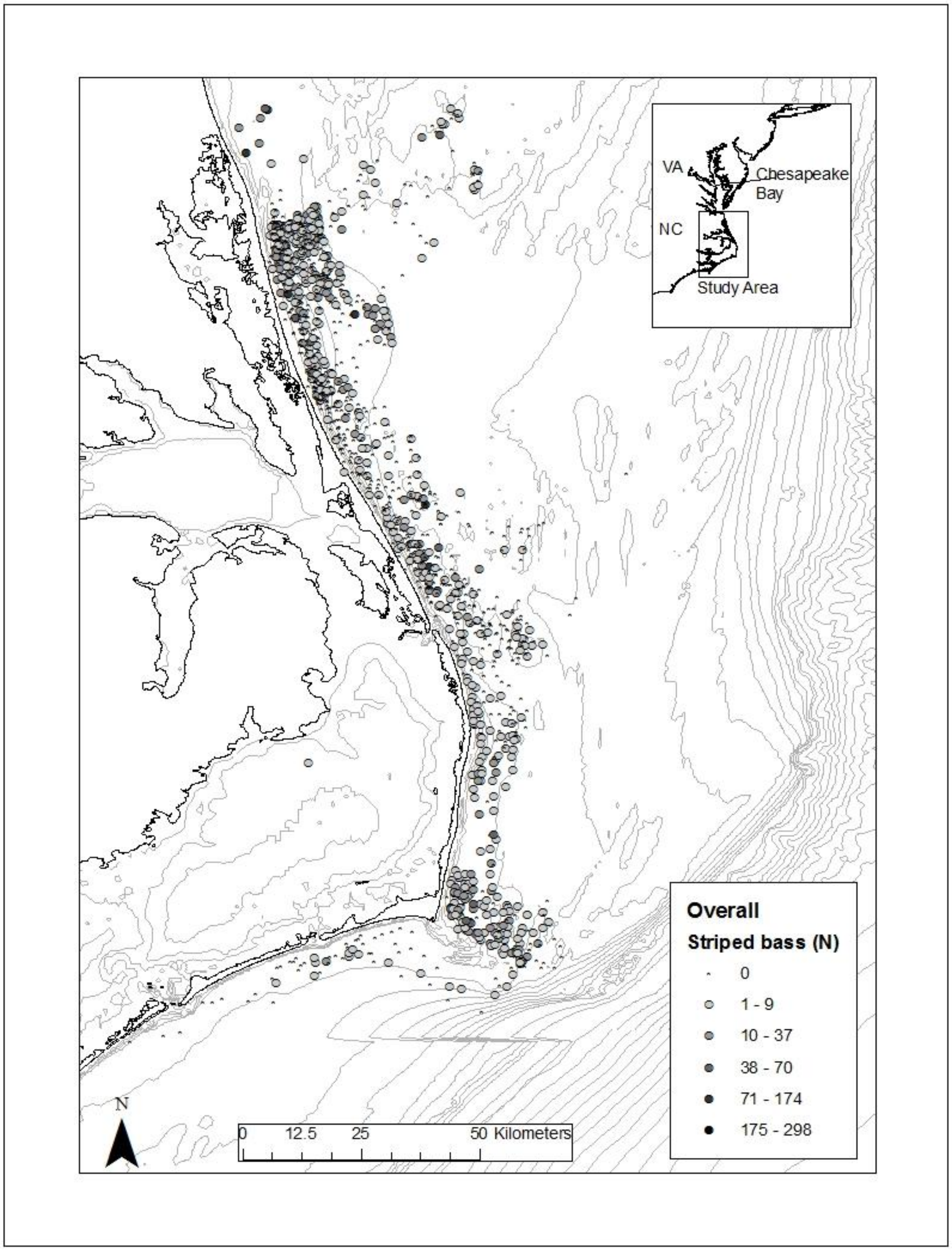


Figure 4-4A. Striped bass abundance at CWTC stations sampled from 1996-1998 and 2006-2007.

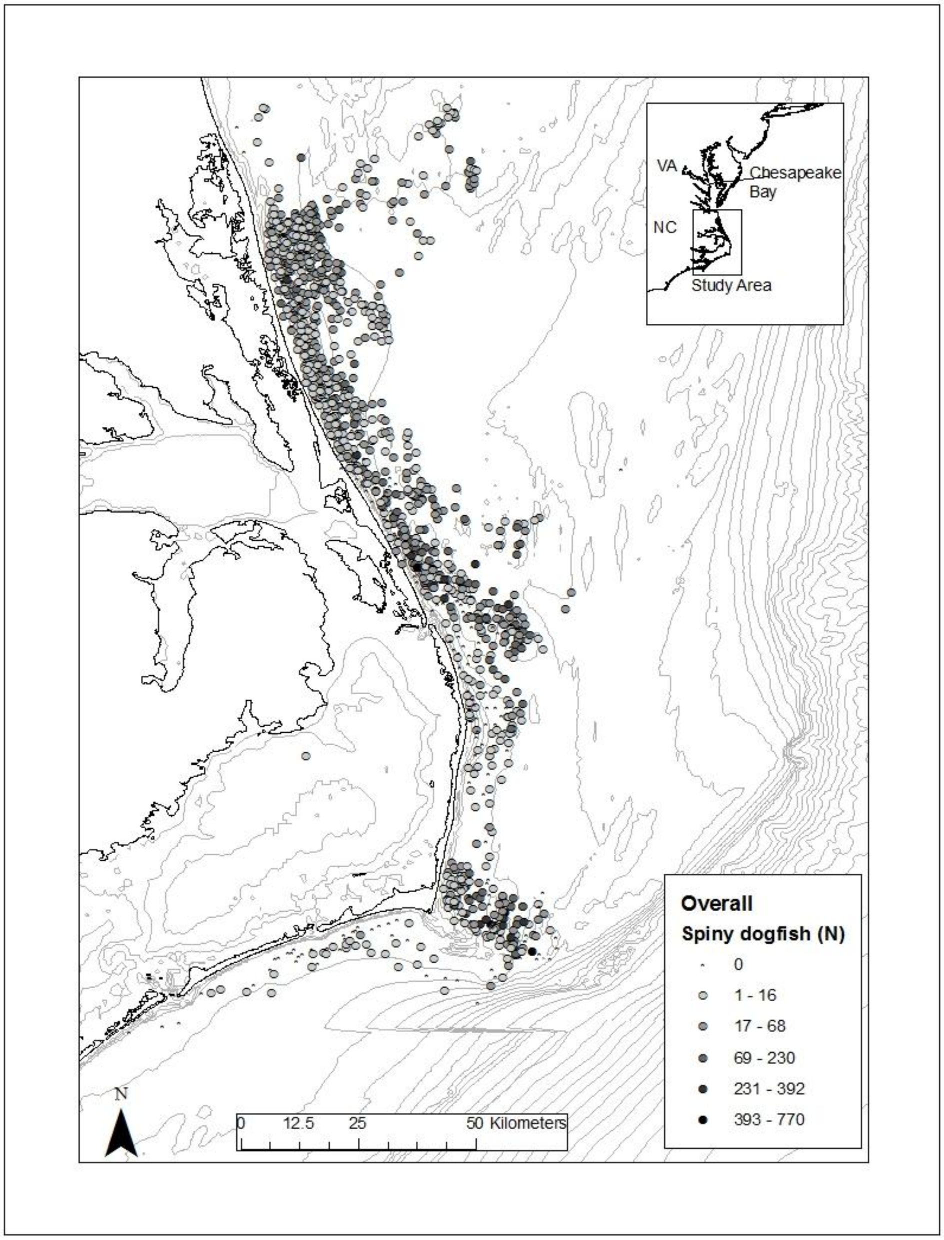


Figure 4-4B. Spiny dogfish abundance at CWTC stations sampled from 1996-1998 and 2006-2010.

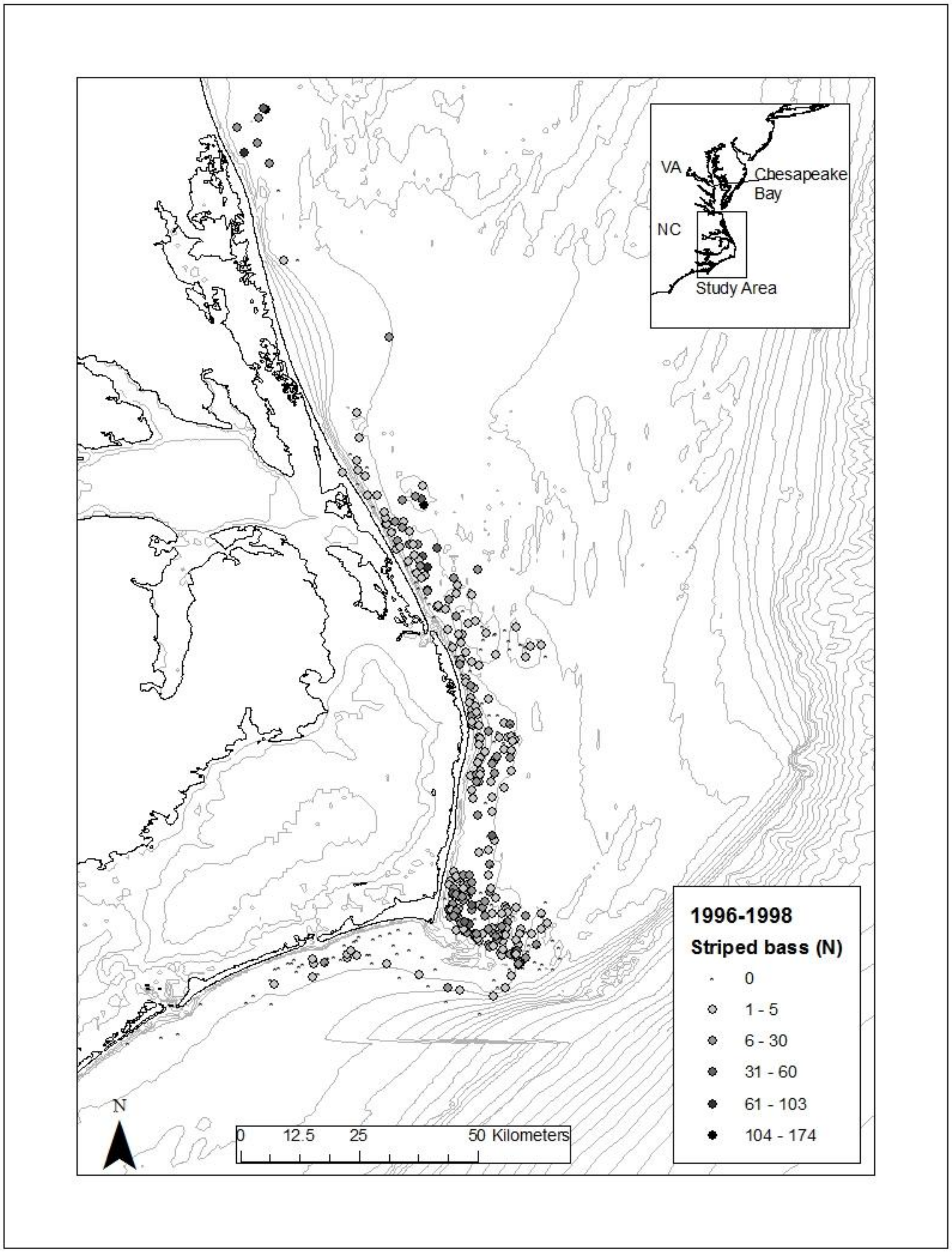


Figure 4-5A. Striped bass abundance at CWTC stations sampled from 1996-1998.

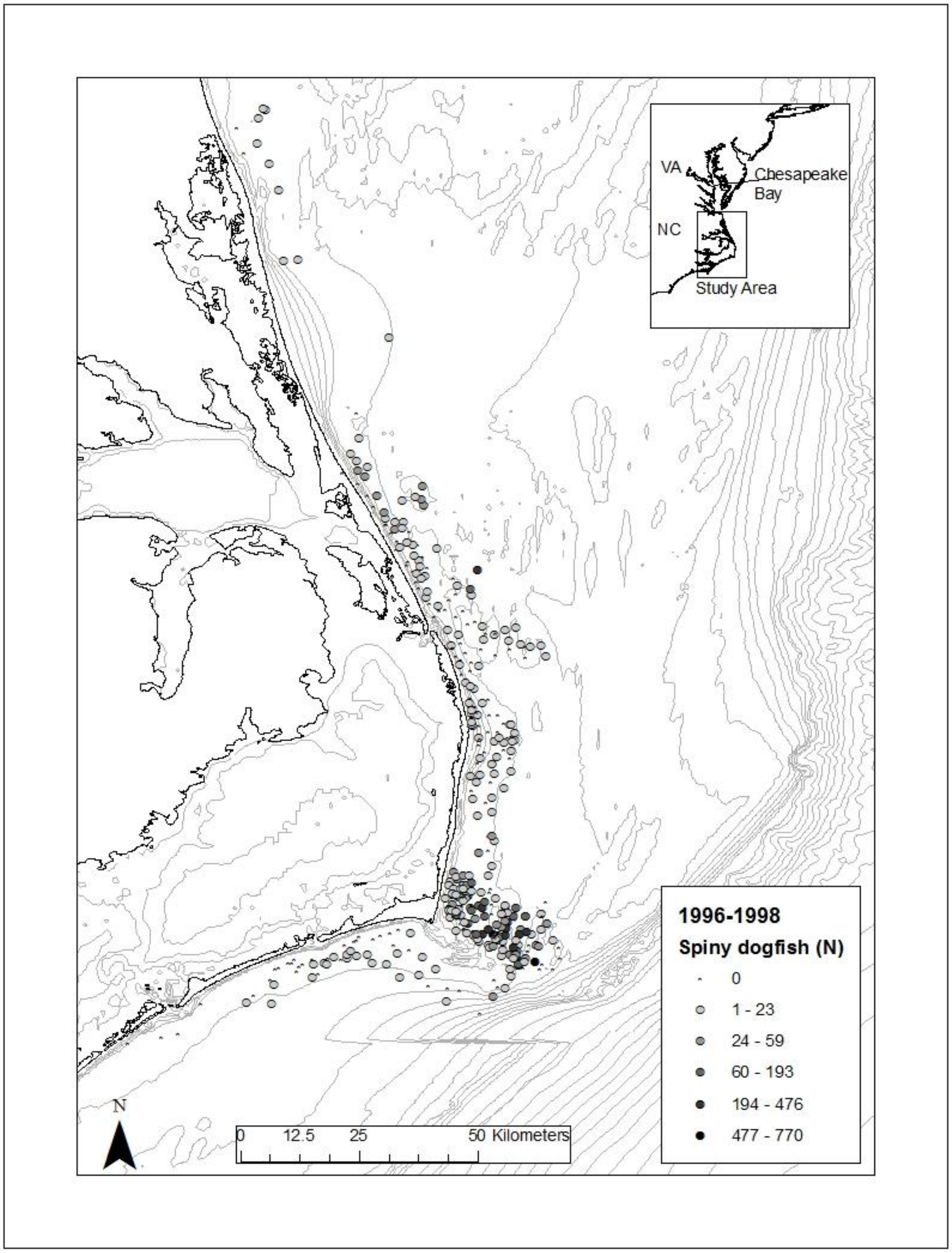


Figure 4-5B. Spiny dogfish abundance at CWTC stations sampled from 1996-1998.

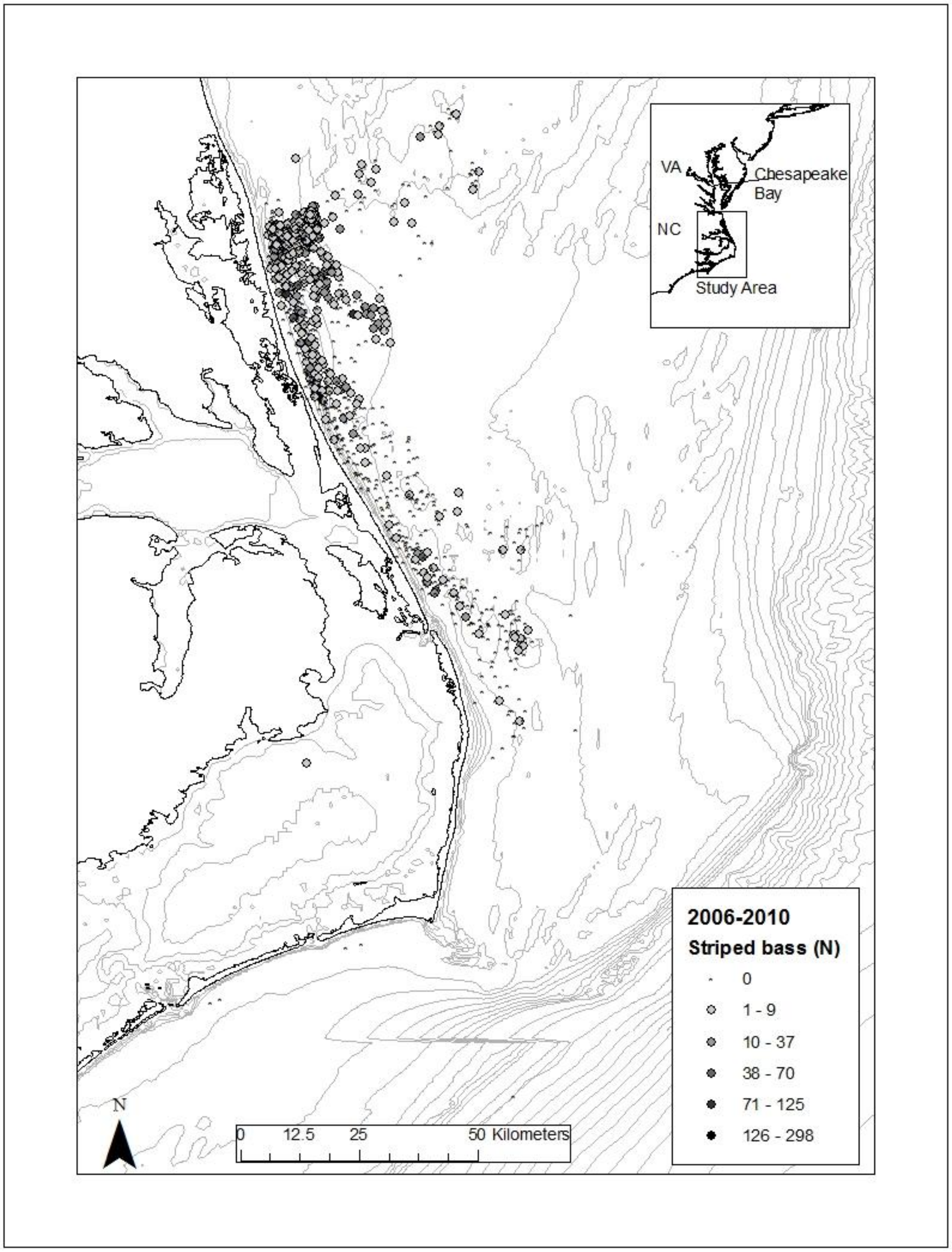


Figure 4-6A. Striped bass abundance at CWTC stations sampled from 2006-2010.

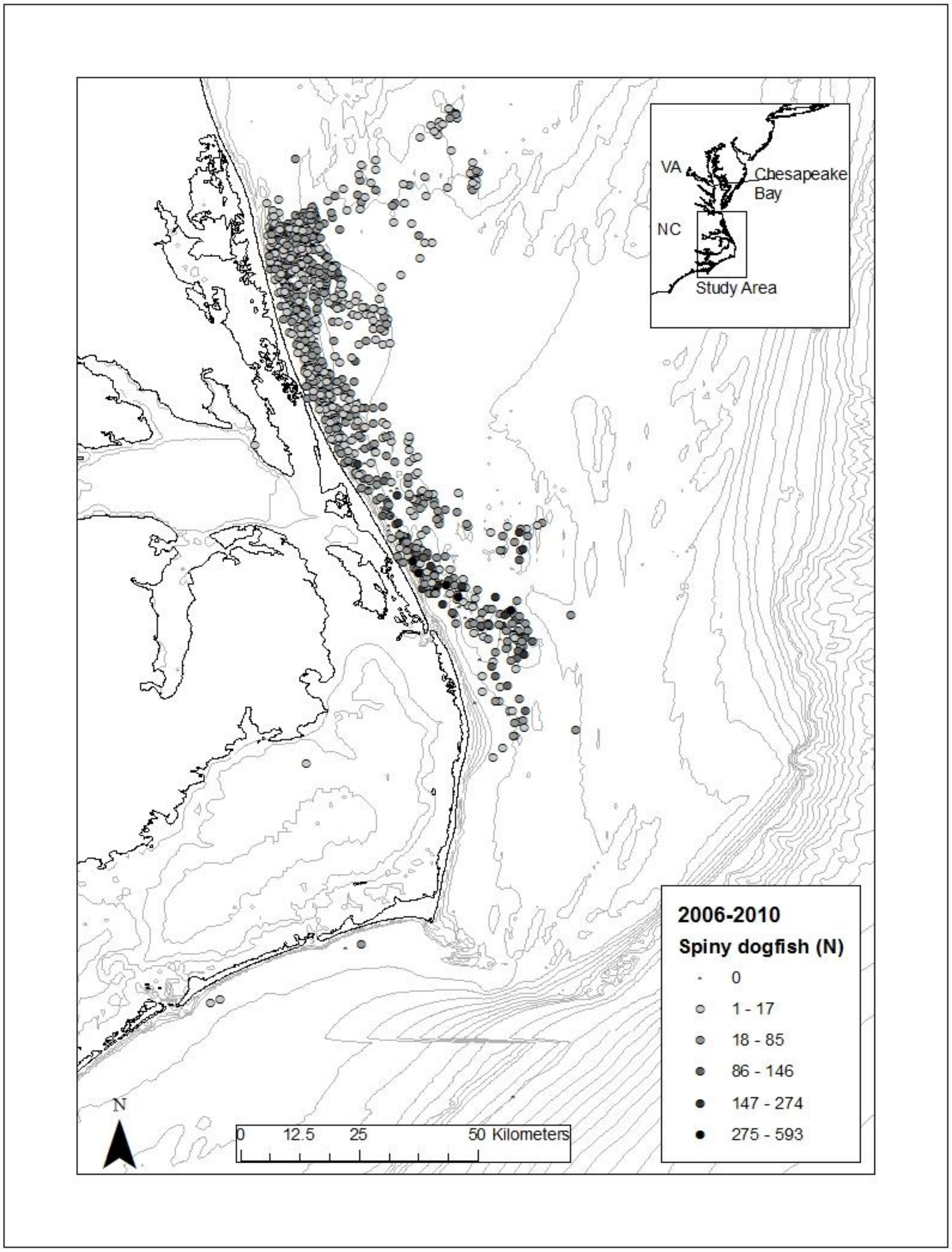


Figure 4-6B. Spiny dogfish abundance at CWTC stations sampled from 2006-2010.

Table 4-3. Common and scientific names of all prey taxa collected from spiny dogfish and striped bass stomach contents during the 2006, 2007, and 2010 CWTC surveys, grouped by category.

Prey Taxa/Category	Scientific Name
Teleost	
American eel	*Anquilla rostrata*
Anchovy sp.	*Anchoa* sp.
Atlantic croaker	*Micropogonius undulatus*
Atlantic menhaden	*Brevoortia tyrannus*
Bay anchovy	*Anchoa mitchilli*
Blueback herring	*Alosa aestevalis*
Butterfish	*Peprilus triacanthus*
Eel sp.	Anguilliformes
Goby sp.	Gobiidae
Hake sp.	*Urophycis* sp.
Paralichthyid flounder	*Paralichthys* sp.
Seahorse	*Hippocampus* sp.
Smallmouth flounder	*Etropus microstomus*
Southern kingfish	*Menticirrhus americanus*
Spot	*Leiostomus xanthurus*
Striped bass	*Morone saxatilis*
Summer flounder	*Paralicthys dentatus*
Tonguefish sp.	Cynoglossidae
Unidentified fish	Teleostii
Unidentified flatfish	Pleuronectiformes
Unidentified herring	Cupleidae
Weakfish	*Cynoscion regalis*
Windowpane flounder	*Scopthalamus aquosus*
Elasmobranch	
Skate sp.	Rajidae
Unidentified elasmobranch	Elasmobrancii
Crustacean	
Decapod	Decopoda
Four-eyed amphipod	Amphipoda
Hermit Crab	Paguroidea
Isopod	Isopoda
Lady crab	*Ovalipes ocellatus*
Mantis shrimp	Stomatopoda
Mole crab	Hippoidea
Mysid shrimp	Mysidae
Peneaid shrimp	*Penaeus* sp.
Rock crab	*Cancer irrorata*
Sand shrimp	*Crangon septemspinosa*
Unidentified crab	Brachyura

Unidentified shrimp	Malacostraca
Mollusc	
Bivalve	Bivalva
Loligo squid	*Loligo* sp.
Squid sp.	Teuthoidea
Stout razor clam	*Tagelus plebius*
Unidentified mollusc	Mollusca
Ctenophore	
Comb jelly	Ctenophora
Other Invertebrate	
Blood worm	*Glycera* sp.
Brittle star	Ophiuroidea
Nematode	Nematoda
Polychaete	Polychaeta
Unidentified worms	-

Table 4-4. Percent weight, number, frequency of occurrence, and Index of Relative Importance for prey categories making up the diet of striped bass sampled in 2006 and 2007 (n = 59), spiny dogfish sampled in 2006-2007 (n = 49) and spiny dogfish sampled in 2010 (n = 182).

	Prey Category	% W	% N	% O	% IRI
Striped Bass 2006-2007	Teleost	99.78	99.76	120.34	100.00
	Elasmobranch	0.00	0.00	0.00	0.00
	Crustacean	0.19	0.16	1.69	>0.01
	Mollusk	0.00	0.00	0.00	0.00
	Other Invert	0.03	0.08	1.69	>0.01
	Unidentified	0.00	0.00	0.00	0.00
	Detritus	0.00	0.00	0.00	0.00
Spiny Dogfish 2006-2007	Teleost	89.24	65.85	134.69	93.94
	Elasmobranch	3.09	0.81	2.04	0.04
	Crustacean	6.13	21.14	42.86	5.25
	Mollusk	1.31	6.50	14.29	0.50
	Other Invert	0.23	5.69	10.20	0.27
	Unidentified	0.00	0.00	0.00	0.00
	Detritus	0.00	0.00	0.00	0.00
Spiny Dogfish 2010	Teleost	94.85	94.16	122.53	99.52
	Elasmobranch	0.05	0.35	0.55	>0.01
	Mollusk	0.68	1.29	6.59	0.06
	Crustacean	1.31	0.40	15.38	0.11
	Ctenophore	1.45	2.73	9.34	0.17
	Other Invert	1.27	0.43	17.58	0.13
	Unidentified	0.36	0.65	4.40	0.02
	Detritus	0.05	0.00	0.55	>0.01

Table 4-5. Dietary overlap by prey category expressed as Bray-Curtis Index of Similarity (BCIS) values between striped bass (2006-2007), spiny dogfish (2006-2007), and spiny dogfish (2010).

	Prey Category		
BCIS	Striped Bass 2006-2007	Spiny Dogfish 2006-2007	Spiny Dogfish 2010
Striped Bass 2006-2007	100		
Spiny Dogfish 2006-2007	89.49	100	
Spiny Dogfish 2010	95.09	91.50	100

Table 4-6. Percent weight, number, frequency of occurrence, and Index of Relative Importance for prey categories making up the diet of striped bass sampled in 2006 and 2007 (n = 59). Scientific names found in Table 3.

Striped bass 2006-2007				
Common Name	% W	% N	% O	% IRI
Bay anchovy	77.45	97.60	96.61	97.31
Atlantic menhaden	21.11	1.68	20.34	2.67
Spot	1.22	0.40	1.69	0.02
Lady crab	0.19	0.16	1.69	>0.01
Bloodworm	0.03	0.08	1.69	>0.01
Unidentified fish	0.01	0.08	1.69	>0.01

Table 4-7. Percent weight, number, frequency of occurrence, and Index of Relative Importance for prey categories making up the diet of spiny dogfish sampled in 2006 and 2007 (n = 49). Scientific names found in Table 3.

Spiny dogfish 2006-2007				
Common Name	% W	% N	% O	%IRI
Atlantic menhaden	31.05	17.89	40.82	50.24
Bay anchovy	1.22	21.95	32.65	19.03
Weakfish	23.54	6.50	16.33	12.34
Rock crab	5.78	10.57	20.41	8.39
Striped bass	15.02	2.44	6.12	2.69
Unidentified fish	1.80	4.88	10.20	1.71
Squid sp.	1.07	4.07	8.16	1.05
Polychaete	0.17	4.88	8.16	1.04
Penaeid shrimp	0.23	4.07	8.16	0.88
American eel	5.40	0.81	2.04	0.32
Windowpane flounder	4.83	0.81	2.04	0.29
Spotted hake	0.11	2.44	4.08	0.26
Smallmouth flounder	0.59	1.63	4.08	0.23
Summer flounder	3.60	0.81	2.04	0.23
Skate spp	3.09	0.81	2.04	0.20
Unidentified mollusc	0.16	1.63	4.08	0.18
Mantis shrimp	0.07	1.63	4.08	0.17
Spot	0.85	0.81	2.04	0.09
Sand shrimp	0.01	1.63	2.04	0.08
Blackcheek tonguefish	0.43	0.81	2.04	0.06
Unidentified flatfish	0.35	0.81	2.04	0.06
Southern kingfish	0.32	0.81	2.04	0.06
Unidentified herring	0.08	0.81	2.04	0.05
Stout razor clam	0.08	0.81	2.04	0.05
Bloodworm	0.05	0.81	2.04	0.04
Anchovy spp	0.04	0.81	2.04	0.04
Unidentified crab	0.02	0.81	2.04	0.04
Unidentified shrimp	0.01	0.81	2.04	0.04
Goby spp	0.01	0.81	2.04	0.04
Four-eyed amphipod	0.00	0.81	2.04	0.04
Mysid shrimp	0.00	0.81	2.04	0.04

Table 4-8. Percent weight, number, frequency of occurrence, and Index of Relative Importance for prey categories making up the diet of spiny dogfish sampled in 2010 (n = 182). Scientific names found in Table 3.

Spiny dogfish 2010				
Common Name	% N	% W	% O	% IRI
Atlantic menhaden	6.96	59.82	49.45	57.33
Bay anchovy	82.51	18.49	18.13	31.79
Unidentified fish	3.48	10.01	37.91	8.88
Ctenophore	1.45	2.73	17.58	1.27
Croaker Atlantic	0.95	0.47	6.59	0.16
Polycheate	0.68	0.27	5.49	0.09
Bivalve	0.41	1.09	3.30	0.09
Animal Remains	0.36	0.65	4.40	0.08
Striped bass	0.14	2.30	1.65	0.07
Unidentified shrimp	0.50	0.09	6.04	0.06
Tonguefish Uncl	0.18	0.91	2.20	0.04
Decapod	0.32	0.16	3.85	0.03
Worms Uncl	0.41	0.15	2.75	0.03
Unidentified Herring	0.18	0.64	1.10	0.02
Paralicthyid flounder	0.09	0.57	1.10	0.01
Eel Uncl	0.14	0.16	1.65	0.01
Mantis Shrimp Uncl	0.14	0.06	1.65	0.01
Isopod	0.18	0.01	1.65	0.01
Squid sp.	0.14	0.05	1.65	0.01
Butterfish	0.05	0.43	0.55	>0.01
Elasmobranch	0.05	0.35	0.55	>0.01
Unidentified mollusc	0.09	0.06	1.10	>0.01
Mole Crab	0.09	0.05	1.10	>0.01
Seahorse	0.05	0.16	0.55	>0.01
Hake sp.	0.05	0.14	0.55	>0.01
Loligo squid	0.05	0.09	0.55	>0.01
Nematode	0.14	0.00	0.55	>0.01
Blueback herring	0.05	0.03	0.55	>0.01
Unidentified flatfish	0.05	0.03	0.55	>0.01
Hermit Crab	0.05	0.03	0.55	>0.01
Brittle star	0.05	0.01	0.55	>0.01
Lady crab	0.05	0.00	0.55	>0.01
Algae/Detritus	0.05	0.00	0.55	>0.01

Table 4-9. Dietary overlap expressed as Bray-Curtis Index of Similarity (BCIS) values between striped bass (2006-2007), spiny dogfish (2006-2007), and spiny dogfish (2010), with all prey taxa included.

All prey taxa			
BCIS	Striped Bass 2006-2007	Spiny Dogfish 2006-2007	Spiny Dogfish 2010
Striped Bass 2006-2007	100		
Spiny Dogfish 2006-2007	24.19	100	
Spiny Dogfish 2010	84.49	34.73	100

Table 4-10. Dietary overlap expressed as Bray-Curtis Index of Similarity (BCIS) values between striped bass (2006-2007), spiny dogfish (2006-2007), and spiny dogfish (2010), with only prey taxa greater than 1% IRI included.

Prey taxa > 1% IRI			
BCIS	Striped Bass 2006-2007	Spiny Dogfish 2006-2007	Spiny Dogfish 2010
Striped Bass 2006-2007	100		
Spiny Dogfish 2006-2007	28.39	100	
Spiny Dogfish 2010	87.56	39.57	100.00

Table 4-11. Estimated biomass (kg) of striped bass consumed in February 2010 by proportions of the total spiny dogfish spawning stock biomass (SSB) and total exploitable biomass (TEB), compared to total recreational and commercial landings from 2009 (NMFS Fisheries Statistics Division, personal communication) and estimated striped bass spawning stock biomass from 2008 (ASMFC 2008), assuming annual ration of 1.5 times spiny dogfish body weight.

	Percent dogfish biomass	February consumption (kg)	Total landings 2009 (kg)	Percent landings consumed	Striped bass biomass (kg)	Percent biomass consumed
SSB	100	432069.30	16620137	2.60	108300000	0.40
	75	324051.98	16620137	1.95	108300000	0.30
	50	216034.65	16620137	1.30	108300000	0.20
	25	108017.33	16620137	0.65	108300000	0.10
	61.92	*267537.31*	*16620137*	*1.61*	*108300000*	*0.24*
TEB	100	955519.56	16620137	5.75	108300000	0.88
	75	716639.67	16620137	4.31	108300000	0.66
	50	477759.78	16620137	2.87	108300000	0.44
	25	238879.89	16620137	1.44	108300000	0.22
	61.92	*591657.71*	*16620137*	*3.56*	*108300000*	*0.55*

Table 4-12. Estimated biomass (kg) of striped bass consumed in February 2010 by proportions of the total spiny dogfish spawning stock biomass (SSB) and total exploitable biomass (TEB), compared to total recreational and commercial landings from 2009 (NMFS Fisheries Statistics Division, personal communication) and estimated striped bass spawning stock biomass from 2008 (ASMFC 2009), assuming annual ration of 2.5 times spiny dogfish body weight.

	Percent dogfish biomass	February consumption (kg)	Total landings 2009 (kg)	Percent landings consumed	Striped bass biomass (kg)	Percent biomass consumed
SSB	100	720115.51	16620137	4.33	108300000	0.66
	75	540086.63	16620137	3.25	108300000	0.50
	50	360057.75	16620137	2.17	108300000	0.33
	25	180028.88	16620137	1.08	108300000	0.17
	61.92	*445895.52*	*16620137*	*2.68*	*108300000*	*0.41*
TEB	100	1592532.60	16620137	9.58	108300000	1.47
	75	1194399.45	16620137	7.19	108300000	1.10
	50	796266.30	16620137	4.79	108300000	0.74
	25	398133.15	16620137	2.40	108300000	0.37
	61.92	*986096.19*	*16620137*	*5.93*	*108300000*	*0.91*

Appendix A

East Carolina University
Animal Use Protocol (AUP) Form
Latest Revision, May 29, 2008

Project Title:

Food and Feeding Habits of Spiny Dogfish Overwintering off of North Carolina and Potential Effects on Commercially-Important Species.

Funding Source:

Internal:
External (Sponsor, Grant #):

1. Personnel

1.1. Principal investigator and email: Roger A. Rulifson, rulifsonr@ecu.edu

1.2. Department, **office phone:** Biology, Flanagan 388, 252.328.9400

1.3. Emergency numbers:

	Principal Investigator	Other (Co-I, technician, student)
Name:	Roger A. Rulifson	Charles W. Bangley
Cell:	252.916.1599	401.829.0782
Pager:		
Home:	252.355.7632	Lab. 252.328.9407

1.4. Co-Investigators if any:

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AUP #
New/renewal:
Date received:
Full Review and date: Designated Reviewer and date:
Approval date:
Study type:
Pain/Distress category:
Surgery: Survival: Multiple:
Prolonged restraint:
Food/fluid restriction:
Hazard approval/dates: Rad: IBC: EH&S:
OHP enrollment/mandatory animal training completed :
Amendments approved:

1.5.

List all personnel (PI, Co-I, technicians, students) that will be performing procedures on live animals and describe their qualifications and experience with these specific procedures. If people are to be trained, indicate by whom:

Name	Relevant Animal Experience
PI: Roger A. Rulifson	Senior Scientist – Institute for Coastal and Marine Resources Professor – Department of Biology Director – Field Station for Coastal Studies at Mattamuskeet
Others:	
Charles Bangley	Masters Student in Biology 1 year of fisheries field experience, encompassing a wide variety of procedures and gill types including otter trawling and beach seining (assisted with counting and measuring aboard a research trawling vessel, learned how to handle fishes in a trawl situation to reduce stress and mortality) B.S. Marine Biology - University of Rhode Island

2. Regulatory Compliance

2.1 Non-Technical Summary

Using language a non-scientist would understand, please provide a 6 to 8 sentence summary explaining the overall study objectives and benefits of proposed research or teaching activity, and a brief overview of procedures involving live animals (more detailed procedures are requested later in the AUP). Do **not** cut and paste the grant abstract.

Spiny dogfish have long been considered a pest species by commercial and recreational fishermen, and have been increasing in abundance. There is some controversy as to what effects this increase has had on species that are valuable to fishing interests, and one theory is that dogfish function as population-limiting predators on some of these species (Link *et al.* 2002). The objective of this research is to quantify the food and feeding habits of spiny dogfish overwintering off the coast of North Carolina and establish whether predation by these sharks is a significant source of mortality for commercially-important species. Dogfish will be collected during research trawls that will also sample the general marine community in the area. The dogfish will be inverted to induce narcosis. An acrylic tube of appropriate size will be inserted down the shark's esophagus into the stomach, encompassing any food items within, and suction will be created by cupping a hand over the exposed end of the tube. The shark will then be lifted tail-first to allow gravity and suction to remove stomach contents, which will be preserved in 70% EtOH, returned

Date Search was performed: *09/20/09*
Database searched: *Google Scholar*
Period of years covered in the search: *1966 to 2009*
Keywords used and strategy (must include the word alternatives): food and feeding, nonlethal methods, gastric lavage, spiny dogfish, sharks, elasmobranchs, diet, stomach contents, alternatives
Other sources consulted: Chapter on the anatomy of the shark digestive tract in *Biology of Sharks and their Relatives*, conversations with researchers familiar with spiny dogfish and food habit studies, observations made during dissection of dead spiny dogfish.

Narrative indicating the results of the search (2-3 sentences) and why there are no alternatives to your proposed use of the animals in this protocol. If alternatives exist, describe why they are not adequate. Please use the concept of the 3 R's when considering alternatives (reducing the number of animals to what is necessary to obtain scientifically sound results; refining techniques to minimize pain and discomfort to animals; and replacing animal models with non-animal models whenever possible):

Nonlethal techniques for sampling stomach contents have been proven effective in several species of sharks, including spiny dogfish (Hannan 2009, Bush and Holland 2002). Various forms of gastric lavage have been proven to be just as effective at extracting stomach contents as sacrifice and dissection, and in most cases are actually quicker than sacrificing and dissecting the fish (Fowler and Morris 2008). Stomach tube lavage was chosen as the method for this study due to its low cost and ease of operation aboard a research vessel (Kamler and Pope 2001). Stomach tube sampling is most effective with large predatory species of fish with relatively large mouths (Kamler and Pope 2001, Waters *et al.* 2004). Shark stomachs are j-shaped, with the cardiac stomach directly attached to the esophagus and the narrower pyloric stomach leading up to the intestine (Holmgren and Nilsson 1999). Stomach tube lavage will target the contents of the cardiac stomach, which are more desirable due to having been in the stomach for less than 24 hours and therefore less damaged by digestion. This type of research cannot be completed with non-animal models.

to the lab, and analyzed for prey species identification and composition. Dogfish will be released upon evidence of recovery.

2.2. Duplication

Does this study duplicate existing research? Yes ☒ No ☐

If yes, why is it necessary? (note: teaching by definition is duplicative)

Food and feeding studies have been performed on spiny dogfish in the past, however these studies have encompassed the entire Atlantic coast over the course of the entire calender year. The authors of these studies even admit that such a broad scale may have missed smaller-scale and seasonal feeding events. This research is intended to find food and feeding data specific to dogfish overwintering in North Carolina waters.

2.3 Literature Search to ensure that there are no alternatives to the use of animals

List the following information for each search (please do not submit search results but retain them for your records):

2.4 Hazardous agents

2.4a. Protocol related hazards

Will any of the following be used in live animals and therefore pose a potential risk for animal care and research personnel:

	Oversight committee/ approval date	Safety procedures attached (Yes/No)
Radioisotopes	Radiation	
Ionizing radiation	Radiation	
Infectious agents	IBC	
Toxins of biological origins (venoms, etc)	IBC	
Oncogenic/toxic/mutagenic chemical agents	EH&S	
Human tissues, cells, body fluids	IBC	
Cell lines injected or implanted (MAP test)	DCM	
Recombinant DNA in animals	IBC	
Nanoparticles	EH&S	
Other agents		

If any hazardous agents are used, please fill out the attached Hazardous Agents Form (Appendix 1).

2.4b. Incidental hazards

Will personnel be exposed to any incidental zoonotic diseases or hazards during the study (field studies, primate work, etc)? If so, please identify each and explain steps taken to mitigate risk:

Dr. Rulifson and Charles are experienced in boating safety and hazards. Dr. Rulifson has co-taught a class on boating safety in conjunction with the NC Coast Guard Auxiliary. Charles has had CPR/First Aid and Lifeguard training. Both have experience working aboard research vessels in all types of weather, and are familiar with the hazards associated with working aboard boats in inclement conditions. Suitable personal equipment (life jackets, rain gear, float coats, insulated work boots, mustang survival suits) is available for protection against wintertime marine hazards. The potential exists to encounter hazardous marine life, and this is mitigated by the use of protective equipment such as gloves and foul-weather gear. Both Dr. Rulifson and Charles are experienced in identifying potentially hazardous marine organisms. Spiny dogfish possess venomous spines, but this risk is mitigated through protective equipment (gloves) and proper handling. The sharks will be anesthetized and inverted to induce tonic immobility, reducing panic response in the animals. Exposure to parasitic, viral, or bacterial diseases from contact with dogfish will be minimized by wearing gloves when handling sharks and washing hands after contact.

Total number of animals in treatment and control groups	Additional animals (Breeders, substitute animals)	Total number of animals used for this project
240 60 mature females + 60 immature females + 60 mature males + 60 immature females = 240 sharks	+Additional contingency sharks = 240, 60 each immature and mature females, immature and mature males	=60 + 60 + 60 + 60 + 240 = 480 **480 sharks total**

3. Animals and Housing

3.1. Species and strains:

Squalus acanthias

3.2. Weight, sex and/or age:

Mature females (> 80 cm), immature females (<80 cm), mature males (>60 cm), immature males (<60cm).

3.3. Justify the species and number (use statistical justification when applicable) of animals requested:

This is the target species and cannot be replaced by another. A representative sample of mature and immature males and females will need to be sampled to determine any ontogenetic and sex-specific trends related to feeding habits. At least 30 sharks of each demographic will be required to collect enough stomach content data to make the results statistically significant. In addition, spiny dogfish are intermittent feeders and 47% of dogfish stomachs will be empty (Link *et al* 2002), effectively doubling the number of sharks that will need to be sampled in order to collect an adequate number of stomach contents.

3.4. Justify the number and use of any additional animals needed for this study (i.e. breeder animals, inappropriate genotype/phenotype, extra animals due to problems that may arise, etc.):

Additional animals will only be used if greater than 50% of the stomachs sampled are empty in any of the demographic groups. In such a case only additional sharks of that particular demographic group will be sampled. Spiny dogfish exhibit a 100% survival rate from capture by bottom trawl (Rulifson 2007), so significant mortality from sampling is not expected. 10% of the sharks from each of the four demographic groups will be randomly chosen and sacrificed after collection of stomach contents and dissected to detect any remaining stomach contents. This will be used to validate the efficiency of the lavage method.

3.5. Will the phenotype of mutant, transgenic or knockout animals predispose them to any health behavioral, or physical abnormalities? Yes ☐ No ☒ (if yes, describe)

3.6. Are there any unusual husbandry and environmental conditions required? Yes ☐ No ☒
If yes, then describe conditions and justify the exceptions to standard housing (temperature, light cycles, sterile cages, special feed, feed on cage floor, prolonged weaning times, wire-bottom cages, no enrichment, social isolation, etc.):

3.7. If wild animals will be captured or used, provide permissions (collection permit # or other required information):

NC DMF permit # 706671 ("Scientific or educational collection permit")

3.8. List all laboratories or locations outside the animal facility where animals will be used. Note that animals may not stay in areas outside the animal facilities for more than 12 hours without prior IACUC approval. For field studies, list location of work/study site.

Trawl sampling and stomach tube lavage will be performed aboard research vessels off the coast of North Carolina. Sharks will be released back into the wild as close as possible to their original capture location.

4. Animal Procedures

4.1. Will procedures other than euthanasia and tissue collection be performed? Yes ☒ No ☐

If animals will be used exclusively for tissue collection following euthanasia (answer "no" above), then skip to Question 5 (Euthanasia).

4.2. Outline the Experimental Design including all treatment and control groups and the number of animals in each. If this is a breeding protocol, please describe the breeding strategy (pairs, trios, etc.) and

60 mature and immature female and male spiny dogfish will be opportunistically collected by bottom trawl aboard research trawlers sampling off the coast of North Carolina. All trawls will be performed North of Cape Hatteras.

Stomach contents will be collected using the stomach tube method. Sharks will be measured, weighed, and inverted to induce narcosis before lavage is performed. Gastric lavage will be performed by inserting an acrylic tube down the esophagus to the stomach, partially filling the tube with water, clasping a hand over the outer end of the tube and lifting the shark by the tail. After removing the hand a combination of suction and gravity will remove the stomach contents. The stomach tube will have beveled edges to prevent and damage to the esophagus by insertion. A range of tube sizes will be on hand so that an appropriately sized tube is available for any given shark.

Any shark not showing immediate signs of recovery upon being righted will be kept in a live well with flowing seawater until recovery is observed. Some sharks will be sacrificed to test the validity of the stomach tube method (see below). All others will be released alive as close as possible to their original capture location.

10% of the sharks from each of the four demographic groups will be chosen at random and sacrificed post-lavage by being anesthetized with MS-222 and having their spinal cords severed. These sharks will be dissected to determine if any stomach contents remain. This will be used to validate the efficiency of the tube lavage method.

method and age of genotyping (if applicable). Tables or flow charts are particularly useful to communicate your design.

In sections 4.3-4.19 below, please respond to all items relating to your proposed animal procedures. If a section does not apply to

your experimental plans, please leave it blank.

Note: Procedures covered by DCM and IACUC guidelines and policies are indicated by asterisk (*). Please refer to these and justify any departures.

4.3. Anesthesia/Analgesia/Tranquilization/Pain/Distress Management (for procedures other than surgery)

Adequate records describing anesthetic monitoring and recovery must be maintained for all species.

If anesthesia/analgesia must be withheld for scientific reasons, please provide compelling scientific justification as to why this is necessary.

Describe the pre-procedural preparation of the animals:

1a. Food restricted for hours

1b. Food restriction is not recommended for rodents and rabbits and must be justified:

2a. Water restricted for hours

2b. Water restriction is not recommended in any species for routine pre-op prep and must be justified:

	Agent	Concentration	Dose (mg/kg)	Volume	Route	Frequency	Duration
Pre-emptive analgesic							
Pre-anesthetic							
Anesthetic							
Analgesic Post procedure							
Other							

a. Reason for administering agent(s):

b. For which procedure(s):

c. Method of monitoring anesthetic depth:

d. Methods of physiologic support during anesthesia and recovery:

e. Duration of recovery:

f. Frequency of recovery monitoring:

g. Specifically what will be monitored?

h. When will animals be returned to their home environment?

i. Describe any behavioral or husbandry manipulations that will be used to alleviate pain, distress, and/or discomfort:

4.4 Use of Paralytics

Will paralyzing drugs be used?

For what purpose:

Please provide scientific justification for paralytic use:

Paralytic drug:

Dose:

Method of ensuring appropriate analgesia during paralysis:

4.5. Blood or Body Fluid Withdrawal/Tissue Collection/Injections/Tail Snip*/Gavage

Please fill out appropriate sections of the chart below:

	Location on animal	Needle/ catheter/ gavage tube size	Route of administration	Biopsy size	Volume collected	Compound and volume administered (include concentration and/or dose)	Frequency of procedure
Body Fluid Withdrawal	Stomach, esophagus	Varies with size of shark, 20mm to 35mm diameter	N/A	N/A	Full volume of stomach contents (0-0.5L)	N/A	Once for each shark
Tissue Collection		N/A	N/A		N/A	N/A	
Injection/Infusion				N/A	N/A		
Tail snip*		N/A	N/A		N/A	N/A	
Gavage	Stomach, esophagus	Varies with size of shark, 20mm to 35mm diameter	Mouth, esophagus	N/A	N/A	Full volume of stomach contents removed (0-0.5L), nothing added	Once for each shark
Other							

4.6. Prolonged restraint with mechanical devices

Restraint in this context means beyond routine care and use procedures, and includes rodent and rabbit restrainers, primate chairs, stocks, slings, tethers, metabolic crates, inhalation chambers, and radiation exposure restraint devices).

a. For what procedure(s):

b. Restraint device(s):

c. Duration of restraint:

d. Frequency of observations during restraint/person responsible

e. Frequency and total number of restraints:

f. Conditioning procedures:

g. Steps to assure comfort and well-being:

h. Adverse effects/humane endpoints:

4.7 Tumor* and Disease Models/Toxicity Testing

a. Describe methodology:

b. Expected model and/or clinical/pathological manifestations:

c. Signs of pain/discomfort:

d. Frequency of observations:

e. Adverse effects/humane endpoints*:

4.8 Treadmills/Swimming/Forced Exercise

a. Describe aversive stimulus (if used):

b. Conditioning:

c. Safeguards to protect animal:

d. Duration:

e. Frequency:

f. Total number of sessions:

g. Adverse signs/humane endpoints:

4.9 Projects Involving Food and Water Deprivation or Dietary Manipulation

(Routine pre-surgical fasting not relevant for this section)

a. Food Restriction

i. Amount restricted and rationale:

ii. DDuration (hours for short term/weeks or months for long term):

iii. Frequency of observation/parameters documented (weight, etc):

iv. Adverse effects/humane endpoints:

b. Fluid Restriction
   i. Amount restricted and rationale:

   ii. Duration (hours for short term/weeks or months for long term):

   iii. Frequency of observation/parameters documented:

   iv. Adverse effects/humane endpoints:

c. Dietary Manipulations
   i. Compound supplemented/deleted and amount:

   ii. Duration (hours for short term/weeks or months for long term):

   iii. Frequency of observation/parameters documented:

   iv. Adverse effects/humane endpoints:

4.10 Endoscopy/Fluroscopy/X-Ray/Ultrasound/MRI/CT/PET/Other Imaging

a. Describe animal methodology:

b. Duration of procedure:

c. Frequency of observations during procedure:

d. Frequency/total number of procedures:

e. Method of transport to/from procedure area:

f. Please provide or attach appropriate permissions/procedures for animal use on human equipment:

4.11 Polyclonal Antibody Production*

a. Antigen/adjuvant used:

b. Needle size:

c. Route of injection:

d. Site of injection:

e. Volume of injection:

f. Total number of injection sites:

g. Frequency and total number of boosts:

h. What will be done to minimize pain/distress:

i. Adverse effects/humane endpoints:

4.12 Monoclonal Antibody Production

a. Describe methodology:

b. Is pristane used: [ ] Yes [ ] No

- Volume of pristane:

c. Will ascites be generated: [ ] Yes [ ] No

d. Criteria/signs that will dictate ascites harvest:

e. Size of needle for taps:

f. Total number of taps:

g. How will animals be monitored/cared for following taps:

h. What will be done to minimize pain/distress:

j. Adverse effects/humane endpoints:

4.13 Temperature/Light/Environmental Manipulations

a. Describe manipulation(s):

b. Duration:

c. Intensity:

d. Frequency:

e. Frequency of observations/parameters documented:

f. Adverse signs/humane endpoints:

4.14 Behavioral Studies

a. Describe methodology/test(s) used:

b. If aversive stimulus used, frequency, intensity and duration:

c. Frequency of tests:

d. Length of time in test apparatus/test situation:

e. Frequency of observation/monitoring during test:

Adverse effects/endpoints:

4.15 Capture with Mechanical Devices/Traps/Nets

a. Description of capture device/method:

Dogfish will be captured by bottom trawl opportunistically aboard research vessels. 19.81 m bottom trawls will be towed from the vessel for 10 minutes along the 30 and 40 ft depth contours. Tow speed will be between 2.8 and 3.1 knots. This is standard for most research trawls but may vary by vessel since multiple vessels may be used for sampling.

b. Maximum time animal will be in capture device:

10 minutes.

c. Frequency of checking capture device:

The net will be checked after every trawl.

d. Methods to ensure well-being of animals in capture device:

Gear will be pulled at the same speed for each deployment. Sharks will be processed quickly to facilitate rapid release.

e. Methods to avoid non-target species capture:

This research will be conducted aboard research vessels that will use data from the bycatch in the trawl. All bycatch animals will be returned as quickly as possible to the water. Procedures for treatment of bycatch will follow approved NOAA/NMFS procedures as outlined by Grosslein (1969) and reviewed by SWP (1988) and NEFSC (1995).

Method of transport to laboratory/field station/processing site and duration of transport:

Sharks will be lavaged and released at the sampling site. Sharks may be placed in holding tanks to recover if recovery is not immediate.

g. Methods to ensure animal well-being during transport:

Circulating seawater tanks will be available for sharks that do not recover immediately.

h. Expected mortality rates:

Aside from dogfish sacrificed to validate the method, no mortality is expected.

i. Endpoints (criteria for either humanely euthanizing or otherwise removing from study) for injured/ill animals:

Tonic immobility will be induced, sharks will be anesthetized with 100 mg/L MS-222 buffered in seawater, and euthanized by severing the spinal cord.

4.16 Manipulation of Wild-Caught Animals in the Field or Laboratory

a. Parameters to be measured/collected:

The animals will be measured, weighed, sexed, and subjected to stomach tube gastric lavage.

b. Approximate time required for data collection per animal:

2 minutes for recording the length, weight, and sex, and an additional 3 minutes for collection of stomach contents.

c. Method of restraint for data collection:

The animal will be held down while being measured and sexed, and will be weighed in a basket. The shark will be inverted during lavage to induce narcosis, and will be lifted tail-first to allow gravity to aid in stomach content collection.

d. Methods to ensure animal well-being during processing:

All sharks will be kept wet and handled gently. Processing will be accomplished quickly to ensure rapid release.

e. Disposition of animals post-processing:

Sharks showing immediate recovery after being righted will be released. Any shark that does not immediately recover will be allowed to recover in a live well.

f. Endpoints (criteria for either humanely euthanizing or otherwise removing from study) for injured/ill animals:

Sharks that do not recover after half an hour in the live well or are critically injured during lavage will have tonic immobility induced, anesthetized with 100 mg/L of MS-222 buffered in seawater and euthanized by severing the spinal cord.

4.17 Wildlife Telemetry/Other Marking Methods

a. Describe methodology (including description of device):

b. Will telemetry device /tags/etc be removed? If so, describe:

c. Adverse signs/humane endpoints:

4.18 Other Animal Manipulations

a. Describe methodology:

b. Steps to ensure animal comfort and well-being:

c. Adverse effects/humane endpoints for ill/injured animals:

4.19 Surgical Procedures

All survival surgical procedures must be done aseptically, regardless of species or location of surgery. Adequate records describing surgical procedures, anesthetic monitoring and postoperative care must be maintained for all species.

A. Location of Surgery:

B. Type of Surgery:

[ ] Nonsurvival surgery (animals euthanized without regaining consciousness)
[ ] Major survival surgery (major surgery penetrates and exposes a body cavity or produces substantial impairment of physical or physiologic function
[ ] Minor survival surgery

[ ] Multiple survival surgery*
If yes, provide scientific justification for multiple survival surgical procedures:

C. Describe the pre-op preparation of the animals:

1a. Food restricted for hours

1b. Food restriction is not recommended for rodents and rabbits and must be justified:

2a. Water restricted for hours

2b. Water restriction is not recommended in any species for routine pre-op prep and must be justified:

D. Minimal sterile techniques will include (check all that apply):

**Please refer to DCM Guidelines for Aseptic Surgery for specific information on what is required for each species.*

[ ] Sterile instruments

- How will instruments be sterilized:
- If serial surgeries are done, how will instruments be sterilized between surgeries:

[ ] Sterile gloves
[ ] Cap and mask
[ ] Sterile gown
[ ] Sterile operating area
[ ] Clipping or plucking of hair or feathers
[ ] Skin preparation with a sterilant such as betadine
[ ] Practices to maintain sterility of instruments during surgery

E. Describe the following surgical procedures:

1. Skin incision size and site on the animal:

2. Describe surgery in detail (include size of implant if applicable):

3. Method of wound closure:
   a. Number of layers
   b.

   Type of wound closure and suture pattern:

   c. Suture type/size / wound clips/tissue glue:

   d. Plan for removal of skin sutures/wound clips/etc:

F. Anesthetic Protocol:

If anesthesia/analgesia must be withheld for scientific reasons, please provide compelling scientific justification as to why this is necessary.

	Agent	Concentration	Dose (mg/kg)	Route	Frequency	Duration
Pre-emptive analgesic						
Pre-anesthetic						
Anesthetic						
Analgesic Post Op						
Other						

1. Criteria to monitor anesthetic depth, including paralyzing drugs:

2. Methods of physiologic support during anesthesia and recovery:

3. Duration of recovery from anesthesia:

4. Frequency/parameters monitored during recovery:

5. When will animals be returned to their home environment:

6. Describe any behavioral or husbandry manipulations that will be used to alleviate pain, distress, and/or discomfort:

G. Recovery from Surgical Manipulations (after animal regains consciousness)

1. Following recovery, what parameters will be monitored:

2. How frequently will animals be monitored:

3. How long post-operatively will animals be monitored:

5. Euthanasia

**Please refer to the 2007 AVMA Guidelines on Euthanasia and DCM Guidelines to determine appropriate euthanasia methods.*

5.1 Euthanasia Procedure. If a physical method is used, the animal should be first sedated/anesthetized with CO_2 or other anesthetic agent. If prior sedation is not possible, a **scientific justification** must be provided. All investigators, even those doing survival or field studies, must complete this section in case euthanasia is required for humane reasons.

Sharks will be induced into tonic immobility, anesthetized by immersion in at least 100 mg/L of MS-222 buffered in seawater and euthanized by severing the spinal cord. Amount of MS-222 will be adjusted based on the size of the shark.

5.2. Method of ensuring death:

Freezing following euthanasia will be used to confirm death.

5.3. For field studies, describe disposition of carcass following euthanasia (If carcass will be kept for genetic/morphological/phylogenetic analysis, please include preservation, transportation, and storage technique):

Carcasses will be returned to the university for examination, dissection, and disposal. Carcasses will be placed in red biohazard bags and frozen until pick-up. Contents of biohazard bags are incinerated.

I acknowledge that humane care and use of animals in research, teaching and testing is of paramount importance, and agree to conduct animal studies with professionalism, using ethical principles of sound animal stewardship. I further acknowledge that I will perform only those procedures that are described in this AUP and that my use of animals must conform to the standards described in the Animal Welfare Act, the Public Health Service Policy, The Guide For the Care and Use of Laboratory Animals, the Association for the Assessment and Accreditation of Laboratory Animal Care, and East Carolina University.

Please submit the completed animal use protocol form via e-mail attachment to iacuc@ecu.edu. You must also carbon copy your Department Chair.

PI Signature: Roger A. Rulifson Date: 11-6-09

Veterinarian: ______________________ Date: __________

IACUC Chair: ______________________ Date: __________

Appendix 1 - Hazardous Agents					
Principal Investigator:	Campus Phone:		Home Phone:		
IACUC Protocol Number:	Department:		E-Mail:		
Secondary Contact: Department:	Campus Phone:	Home Phone:		E-Mail:	
Chemical Agents Used:		Radioisotopes Used:			
Biohazardous Agents Used:		Animal Biosafety Level:		Infectious to humans?	
Personal Protective Equipment Required:					
Route of Excretion:					
Precautions for Handling Live or Dead Animals:					
Animal Disposal:					
Bedding / Waste Disposal:					
Cage Decontamination:					
Additional Precautions to Protect Personnel, Adjacent Research Projects including Animals and the Environment:					
Initial Approval Safety/Subject Matter Expert Signature & Date ____ _____________					

Additional Literature Cited or Referred to in the Development of this SOP:

Bush, A., Holland, K. 2002. Food limitation in a nursery area: estimates of daily ration in juvenile scalloped hammerheads *Sphyrna lewini* in Kaneohe Bay, Oahu, Hawaii. Journal of Experimental Marine Biology and Ecology 278:157-178.

Grosslein, M.D. 1969. Groundfish survey program of BCF Woods Hole. Comm. Fish. Rev. 31(8-9):22-35.

Hannan, K. 2009. Determination of gastric evacuation rate for immature spiny dogfish. Pages 253-258 *in* V.F. Gallucci, G.A. McFarlane, and G.G. Bargmann, editors. Biology and management of dogfish sharks. American Fisheries Society, Bethesda, Maryland.

Holmgren, S., Nilsson, S. 1999. Chapter 6. Digestive System. From: Sharks, Skates, and Rays: the Biology of Elasmobranch Fishes. Ed. Hamlett, W. Johns Hopkins University Press. Baltimore, MD. 144-168.

Kamler, J.F., Pope, K.L. 2001. Nonlethal methods of examining fish stomach contents. Reviews in Fisheries Science 9:1-11.

Link, J.S., Garrison, L.P., Almeida, F.P. 2002. Ecological interactions between elasmobranchs and groundfish on the Northeastern U.S. continental shelf 1. evaluating predation. North American Journal of Fisheries Management 22:550-562.

Northeast Fisheries Science Center (NEFSC). 1995. Status of fishery resources off the northeastern United States for 1994. NOAA Tech. Memo. NMFS-NE-108, 140 pp.

Rulifson, R. 2007. Spiny dogfish mortality induced by gill-net and trawl capture and tag and release. North American Journal of Fisheries Management 27:279-285

Survey Working Group (SWG). 1988. An evaluation of the bottom trawl survey program of the Northeast Fisheries Center. U.S. Department of Commerce, National Oceanic and Atmospheric Administration, NOAA Technical Memorandum NMFS-F/NEC-52