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Diet Analysis of Loggerhead Sea Turtles in New York Waters

A Thesis Presented

by

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Abstract of the Thesis

Diet Analysis of Loggerhead Sea Turtles in New York Waters

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This thesis examines the diet of loggerhead sea turtles (*Caretta caretta*) in New York between 1995 – 2014 using stomach contents analysis. Loggerheads are one of four sea turtle species that occur in the temperate waters of New York during summer months. Estuaries of Long Island provide foraging habitat for juvenile loggerheads from June to November. In order to quantify loggerhead diet, I examined individual and inter-annual variation in the stomach contents of 123 individual turtles that stranded along Long Island. Prey items were identified to the lowest possible taxonomic level, and the minimum number of prey items was assessed for each sample. Principal Component Analysis (PCA), Redundancy Analysis (RDA), and Non-Metric Multidimensional Scaling (NMDS) were used to characterize variability in loggerhead diet. Results of these ordination analyses indicated a temporal shift in prey composition before and after 2000, from large prey species such as rock crab (*Cancer irroratus*) to smaller species such as hermit crabs (*Pagurus* spp.) and moonsnails (Naticidae). Redundancy analyses suggest

that observed diet shifts were likely temperature-driven due to the importance of the Gulf Stream North Wall index. Similar temporal trends were observed in benthic communities in this region, suggesting that loggerhead diet can provide an indicator of the relative abundance of benthic organisms. Additionally, a spatial assessment of loggerhead sea turtle strandings suggested that juvenile loggerheads are predominantly foraging in Long Island Sound, Peconic Bay, and Gardiners Bays, while mature loggerheads appear to exclusively forage in offshore waters, indicating that Long Island estuaries provide important stage-specific foraging habitats for loggerhead sea turtles.

To my parents,

*Who have supported me through several career changes
and have always encouraged me in all my endeavors.*

Thank you.

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List of Abbreviations

AMO: Atlantic Multidecadal Oscillation

ANOSIM: Analysis of Similarities

DPS: Distinct Population Segment

ESA: Endangered Species Act

GI: Gastrointestinal

GSNW: Gulf Stream North Wall

IRI: Index of Relative Importance

IUCN: International Union for Conservation of Nature

NAO: North Atlantic Oscillation

NMDS: Non-Metric Multidimensional Scaling

NOAA: National Oceanic and Atmospheric Administration

NYSDOS: New York State Department of State

PCA: Principal Component Analysis

PERMANOVA: Permutational Analysis of Variance

RDA: Redundancy Analysis

SCL: Straight Carapace Length

USFWS: United States Fish and Wildlife Service

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INTRODUCTION

The loggerhead sea turtle (*Caretta caretta*) is one of seven species of sea turtle found worldwide, inhabiting the Atlantic, Pacific and Indian Oceans. Nine distinct population segments (DPS) have been defined for loggerheads under the US Endangered Species Act (ESA), four of which are threatened while the remaining five are endangered (Conant et al. 2009). Current threats to loggerhead sea turtle populations include bycatch, particularly in longline and gillnet fisheries (Lewison et al. 2004, Murray 2006, Lutz & Musick 1996, NMFS & USFWS 2008, Bolten et al. 2011), light pollution (Witherington & Martin 2000), ingestion of marine debris (Tomas et al. 2002, Lazar & Garcan 2011), oil pollution (Witherington 1999), and ecosystem alterations such as beach armoring, erosion and nourishment (Crain et al. 1995, Mosier & Witherington 2002). Loggerhead population models show that the survival of large juveniles has the greatest positive impact on population growth, making it particularly important to understand the habitat use of this life stage (Crouse et al. 1987, Crowder et al. 1994, Heppell et al. 2003).

Loggerhead sea turtles have a complex life history: they are long lived, slow growing, late to mature, highly migratory (Bolten 2003), and their lifespan is characterized by distinct ontogenetic shifts that are reflected in their habitat usage (Musick & Limpus 1997, McClellan & Read 2007, Lazar et al. 2011). After emerging from their terrestrial nests, loggerhead hatchlings disperse into the ocean, where they associate with floating *Sargassum* spp. in order to avoid predators (Musick & Limpus 1997). Once they have reached a size large enough to minimize predation, juvenile sea turtles return to neritic waters (waters on the continental shelf that are less than 200 m in depth) to forage on benthic invertebrates (Bjorndal 1997). After reaching neritic habitats, loggerheads are generally believed to remain in coastal waters, migrating latitudinally between foraging and breeding sites (Musick & Limpus 1997). However, there is uncertainty as

to the mechanistic drivers of this niche shift, and how pervasive this model of behavior is. Increased foraging on benthic invertebrates in neritic habitats has been proposed as a means of allowing loggerheads to maximize their growth rate and more quickly reach reproductive size (Werner & Gilliam 1984, McClellan & Read 2007, Wallace et al. 2009). However, Ramirez et al. (2017) only observed increased growth rates in loggerheads for the first year of benthic foraging after the ontogenetic niche shift, indicating that other factors may be influencing this shift. Recent findings have shown that niche shifts might be optional (Hawkes et al. 2007, Casale et al. 2008b, Mansfield et al. 2009, Ramirez et al. 2017), and that up to one third of the northwest Atlantic loggerhead population may not exhibit a permanent ontogenetic shift (McClellan & Read 2007), and may continue to forage on pelagic prey in the open ocean.

Loggerhead sea turtles are primarily opportunistic carnivores, taking advantage of abundant prey items in their foraging habitat (Plotkin et al. 1993, Casale et al. 2008b, Frick et al. 2009) and foraging primarily on benthic invertebrates and freshly deceased fish (Plotkin et al. 1993, Tomas et al. 2001, Casale et al. 2008b). Consequently, there is considerable regional variability in loggerhead diet. For example, diet varies with foraging habitat along the east coast of the United States; blue crabs (*Callinectes sapidus*) and whelks (Buccinidae) are the predominant prey species for loggerheads in Core Sound in North Carolina (Wallace et al. 2009), while spider (*Libinia* spp.), stone (*Menippe mercenaria*), and hermit crabs are important prey species in Georgia (Frick et al. 2001, Younkin & Wyneken 2007), and sea pens (*Virgularia presbytes*) are predominantly taken by loggerheads in the Gulf of Mexico (Plotkin et al. 1993). Within the Mediterranean Sea, the predominant prey species for loggerheads varies from Mediterranean jellyfish (*Cotylorhiza tuberculata*) off the Balearic archipelago (Revelles et al. 2007b), to hermit crabs in the central Mediterranean (Casale et al. 2008b), to Mediterranean

mussel (*Mytilus galloprovincialis*) and sea grass (*Posidonia oceanica*) off the Greek coast (Houghton et al. 2000), and European clams (*Corbula gibba*) in the Adriatic Sea (Lazar et al. 2011). As a result of this regional variability in diet, there are still many regions where a detailed knowledge of loggerhead diet is lacking (Burke et al. 1993), such as in New York waters.

The New York Bight is a highly productive ecosystem, comprised of estuaries, bays, and coastal and offshore waters, which sustains a diverse range of marine wildlife (Stone et al. 1994) and supports a billion-dollar commercial fishery (NYSDEC 2017). Several species, some of which are endangered (e.g., North Atlantic right whale (*Eubalaena glacialis*), Atlantic sturgeon (*Acipenser oxyrinchus oxyrinchus*), and Kemp's ridley sea turtle (*Lepidochelys kempii*)), use this area for breeding and spawning (Wuenschel et al. 2009, Gahagan et al. 2015), as nursery habitats (Rountee & Able 1996), as migratory corridors (Whitt et al. 2013) and as seasonal foraging grounds (Burke et al. 1994, Curtis et al. 2014). Increased urbanization and human activity along the New York coast can have negative effects on species abundance and survival (Sandove & Morreale 1989, Hartig et al. 2002). Therefore, it is necessary to understand how marine animals use the New York Bight in order to understand how future urbanization might impact species in this region.

Waters off the coast of Long Island provide important seasonal foraging habitat for large juvenile loggerhead sea turtles, but information on the distribution, diet, and habitat use of loggerheads in this area is lacking. Loggerheads occur in New York waters from late spring to fall (Burk et al. 1993, Klinger and Musick 1995, Morreale & Standora 1998, Coles 1999). Since New York is located in the northernmost portion of the foraging range of juvenile loggerheads (Shoop & Kenney 1992, McClellan & Read 2007, Mansfield et al. 2009), studying loggerheads in this region provides the opportunity to study how climate-driven environmental variability

influences their distribution and foraging habits. Waters of the Northwest Atlantic are warming rapidly (Belkin 2009, Pershing et al. 2015), and the number of loggerhead strandings in New York is thought to be increasing (Riverhead Foundation, unpublished data), possibly due to warmer water temperatures in this region. Loggerheads occurring in this region belong to the Northwest Atlantic Ocean DPS, which continues to experience population declines as a result of fisheries interactions (Murray 2006), changes in prey availability (Seney & Musick 2007), and habitat alterations (NMFS & USFWS 2008). Burke et al. (1993) examined diet for a small number of loggerheads in 1989 using fecal samples and found that they predominantly fed on spider crabs (*Libinia emarginata*). However, more recent information is needed to better understand the foraging behavior and requirements of loggerhead sea turtles in this region, and to understand how continuing environmental change might impact this species.

Shifts in loggerhead sea turtle diet have been linked with long-term changes in prey availability (Youngkin & Wyneken 2005, Seney & Musick 2007). In Virginia, Seney and Musick (2007) observed a shift in loggerhead diet from horseshoe crabs (*Limulus polyphemus*) in the 1980's, to blue crabs in the early 1990's, to finfish (*Brevoortia tyrannus* and *Micropogonias undulatus*) in the late 1990's and early 2000's. These shifts in diet reflected changes in the abundance of prey items; increased fishing pressure on horseshoe crabs in the late 1980's likely depleted the horseshoe crab population and led to the first diet shift to blue crab (Seney & Musick 2007). Similarly, higher fishing pressure, low larval recruitment and natural mortality in blue crabs led to the second diet shift to predominantly finfish. Youngkin & Wyneken (2007) also documented a cyclical change in loggerhead diet prey composition with prey items shifting between crabs or mollusks every three to four years.

Declines in prey abundance as a result of fishing pressure is not the only possible source of shifts in the benthic community. Effects of long-term climate events such as the North Atlantic Oscillation (NAO), the Atlantic Multidecadal Oscillation (AMO), and the movement of the Gulf Stream North Wall (GSNW) have been well studied for pelagic organisms in the Northwest Atlantic Ocean (Dawe et al. 2000, Condrón et al. 2005, Hare and Able 2007, Collie et al. 2008, Nye et al. 2011, Friedland et al. 2014, Nye et al. 2014, Pershing et al. 2015), and likely have important effects on the benthic community as well (Sanchez-Rubio et al. 2011, Colton et al. 2014). For example, Friedland et al. (2014) found that increasing temperatures related to AMO negatively affected North American and Southern European Atlantic salmon (*Salmo salar*) stocks through two different mechanisms: increased predation due to distributional shift of predators, and decreased growth rate of post-smolt salmon in summer months, respectively. In Narragansett Bay, Rhode Island, Collie et al. (2008) documented a slow shift from demersal fish to invertebrates, which was correlated with AMO, and a more rapid shift from benthic to pelagic species, which they attributed to NAO. In Long Island Sound, increasing bottom temperatures from 1984 – 2008 resulted in an increase of warm-adapted finfish species (Howell & Auster 2012) and the authors documented that the species composition before and after 1999 were significantly different. Also on Long Island, analyses of trawl surveys in the Peconic Bay estuary from 1987 – 2012 showed that there was a significant and rapid change in the benthic community in the early 2000's, including a decline in horseshoe and lady crabs (*Ovalipes ocellatus*) and an increase in blue and spider crabs. This change was linked to a shift in AMO phases (Abruzzo 2015).

Howell and Auster (2012) and Abruzzos's (2015) documentation of the effects of climatic indices on benthic community structure in New York waters suggests that changes in

loggerhead diet could also be influenced by basin-scale climate variability. Assessing the effects of trophic changes on loggerhead sea turtles is a goal highlighted in the recovery plan for the Northwest Atlantic loggerhead population (NMFS & USFWS 2008). An improved understanding of loggerhead sea turtle diet and foraging habitat will allow for the implementation and improvement of effective management plans and conservation efforts in New York waters. My thesis addresses this gap in knowledge, using a long-term data set of loggerhead sea turtle stomachs collected from stranded loggerhead sea turtles on Long Island to evaluate variability in diet over a 20-year time period, and to examine how climate variables influenced observed changes in diet.

METHODS

Study Area

Loggerhead sea turtles forage in the bays and coastal waters of Long Island, New York from late May through early November (Burke et al. 1993, Morreale & Standora 1998, Lopez et al. 2014; Figure 1). Loggerhead foraging habitat in New York includes the offshore waters of the New York Bight up to the edge of the continental shelf, inshore estuaries and bays (i.e., Peconic Estuary, Great South Bay, Moriches Bay, Shinnecock Bay), as well as Long Island Sound. These regions are highly diverse, and support a wide array of benthic organisms (Morreale & Standora 1998). The continental shelf in the New York Bight gently slopes from the shore to the shelf edge (200 m depth) over a distance of approximately 160 km, with sediments ranging from coarse and medium sands close to shore to finer sediments such as silts and clays closer to the shelf edge (Williams et al. 2006, NYS DOS 2013). The Long Island Sound ranges in depth from 20-70 meters with coarse sediments in the eastern Sound and finer sediments in the western and

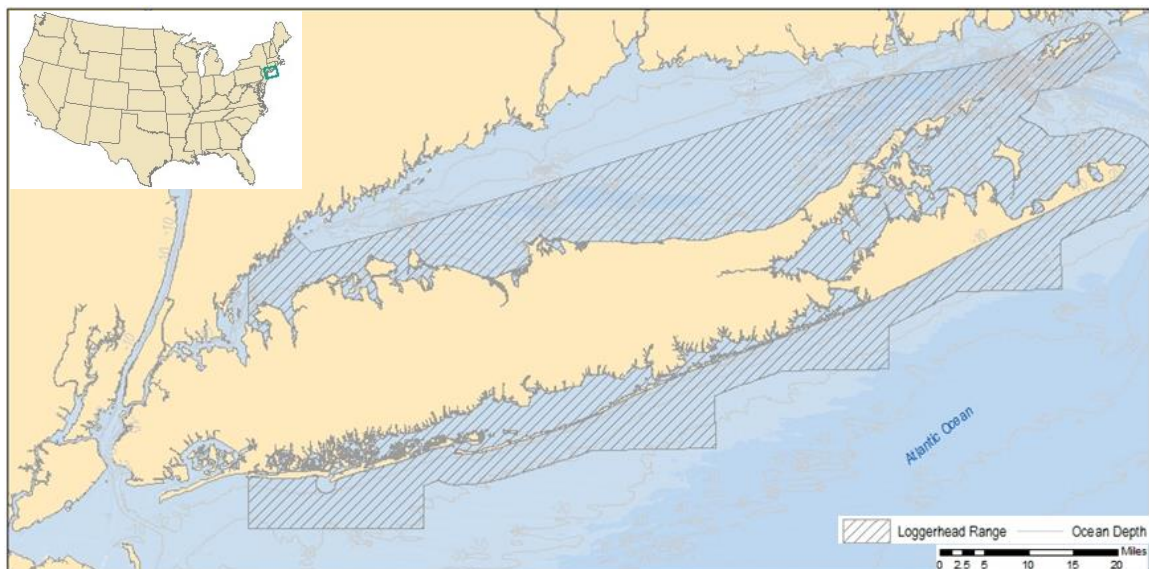


FIGURE 1. Loggerhead sea turtle range around Long Island. (Map recreated with data from NOAA 2009.)

central basins (Zajac et al. 2000). The bays along the south shore of Long Island are shallow coastal lagoons, which are connected to the Atlantic Ocean through a number of inlets. They are predominantly made up of sandy and muddy sediments and have an average depth of 1.5 m (Shubel 1991, Sagarese et al. 2011). Similarly, the Peconic Estuary system comprises a series of shallow bays composed of sandy muds, with an average depth of 4.7 m (Hardy 1976). These bays and estuaries are highly productive areas, and when water temperatures are sufficiently warm, they provide important foraging grounds for loggerhead sea turtles (Morreale & Standora 1998, NYSDEC 2017).

Eelgrass provides important habitat for loggerhead sea turtles, serving as a nursery, as refuge from predators, and as foraging grounds (NYS Seagrass Taskforce 2009). Eelgrass coverage in New York waters has greatly decreased in the past 87 years from nearly 200,000 acres in 1930, to just over 21,000 acres today (Lopez et al. 2014). The majority of eelgrass found in New York waters today occurs in the South Shore Estuary Reserve (i.e., Great South Bay, Moriches Bay, and Shinnecock Bay), with some patches occurring in the eastern part of the Peconic Estuary, and patches in the Sound limited to Fishers Island and the southern coast of Connecticut (Lopez et al. 2014).

Temperatures in the bays can range from 2°C in the winter to 26°C in the summer. Loggerheads typically arrive in these areas beginning in the late spring when temperatures rise over 18°C (Lutz & Musick 1995), and leave by the beginning of fall, when water temperatures decrease below 13°C (Coles & Musick 2000). Whereas juvenile loggerheads tend to occur in the enclosed shallow waters of the estuaries (NMFS & USFWS 2008), adult loggerheads are more frequently observed on the continental shelf (NYSDOS 2013).

Sample Collection

The New York State Stranding Program, now known as the Riverhead Foundation for Marine Research and Preservation (described henceforth as the Riverhead Foundation) has been responding to dead stranded sea turtles and sea turtles incidentally caught in fishing gear in New York waters since its founding in 1980. The foundation responded to 809 stranded turtles between 1980 – 1996, of which loggerheads comprised 36.2%, Kemp’s ridleys 33.6%, greens (*Chelonia mydas*) 3.8% and leatherbacks (*Dermochelys coriacea*) 26.3% (Gerle et al. 2000). While reports on more recent numbers of sea turtle strandings in New York have not been published, records indicate that 1179 stranded turtles were observed between 1995 and 2014, 44% of which were loggerheads (Riverhead Foundation, unpublished data). The body condition of these turtles typically ranged from freshly dead to severely decomposed, with the majority falling between moderately and severely decomposed.

This study examined 123 stomach samples collected from July 1995 to November 2014. The majority of samples from this study came from loggerhead sea turtles that stranded in July and August and in most cases, they are believed to be a result of fisheries interactions. Sea turtles can become “cold stunned” when waters cool suddenly (Morreale et al. 1992, Epperly et al. 1995, Gerle et al. 2000, Milton & Lutz 2003), entering hypothermic shock and becoming buoyant and unresponsive (Burke et al. 1991). In Long Island, cold stunning seasons usually begins at the end of October/start of November when water temperatures fall below 10°C and cold-stunned sea turtles tend to strand on north-facing beaches (Burke et al. 1991, Gerle et al. 2000). Samples used in the present study were not thought to be from cold-stunned turtles; when necropsied, animals were robust and had adequate levels of adipose tissue, and the vast majority of samples used in this study were taken from south-facing beaches. Thus, samples used in this

analysis were likely from healthy animals who suffered acute deaths and I feel confident assuming that the stomach samples studied here serve as an accurate long-term representation of loggerhead diet in New York waters over the past 20 years.

Samples were stored dry before 1999 and frozen from 2003 onward. Up until 2012, the Riverhead Foundation only collected stomach samples, but starting in 2013, the entire digestive tract was collected. In order to compare samples over time, only prey items found in the stomach of these samples were used in the analyses. Similarly, samples that were severely decomposed or experienced trauma to the abdominal cavity resulting in stomach contents occurring outside of the GI tract were not included in the analyses. The stranding date, stranding location, sex, size (SCL, curved carapace length, and both straight and curved carapace width), and body condition (based on amount of adipose tissue present) were recorded both upon collection of the carcass and during the necropsy, along with any evidence of human interactions (e.g., propeller scars, presence of fishing line and/or hooks, etc.).

Diet Analysis

There are three methods that are typically used to evaluate the diet of sea turtles: stable isotope analysis, DNA analysis, and gut content analysis. These approaches each have advantages and disadvantages, and it is important to understand what each can reveal about sea turtle diet. Stable isotope analysis is minimally invasive, requiring only small tissue samples from live animals (Revelles et al. 2007a). The use of stable isotope analysis allows for the study of pelagic diets, which tend to consist of soft bodied or gelatinous prey items that are digested quickly (Revelles et al. 2007a, Wallace et al. 2009). Additionally, certain tissues can retain the isotopic signature of the prey for weeks or months, and thus stable isotope analysis can provide a

more accurate representation of an animal's diet integrated over longer time scales (Wallace et al. 2009). However, stable isotope analysis cannot typically be used to examine prey at the species level. DNA analysis is also minimally invasive, and is typically used to identify species present in animal feces (Deagle et al. 2005 and 2009, Dunshea 2009). DNA analysis can also detect prey items that are easily digested (Deagle et al. 2005, Dunshea 2009), or that are consumed in small quantities (Deagle et al. 2005). However, DNA analysis cannot be used to examine quantities of prey ingested and represents a snapshot of an animal's diet over a short time frame; prey in fecal samples represent items ingested within 48 hours (Deagle et al. 2009). In addition, DNA analysis requires previous diet knowledge in order to select species specific primers for prey items, making it better suited as a supplement to gut content analysis, rather than a standalone method of diet analysis (Deagle et al. 2005, Parsons et al. 2005). Gut content analysis takes advantage of deceased animals in order to study diet and often allows prey to be identified to species level. However, animals might not have been foraging under normal conditions immediately before death, and thus gut contents may not reflect the animal's typical diet (Revelles et al. 2007a). Gut content analysis tends to be biased towards benthic prey items in nearshore environments and their hard, indigestible parts (Plotkin et al. 1993, Revelles et al. 2007a, Casale et al. 2008b). Lastly, gut content analysis provides information on diet over short time scales (days) (Revelles et al. 2007a); loggerhead sea turtles take approximately 2.5-3 days to fully digest prey items (Casale et al. 2008a).

Traditionally, diet studies of sea turtles relied on gut content analysis (Plotkin et al. 1993, Burke et al. 1993, Godley et al. 1997, Houghton et al. 2000, Seney and Musick 2007, Lazar et al. 2011), although more recent studies have used stable isotope analysis to describe loggerhead diet (Revelles et al. 2007a and 2007b, Wallace et al. 2009, McClellan et al. 2010). I am not aware of

published studies using DNA analysis to study sea turtle diet, though it has frequently been used to examine marine mammal diet (Deagle et al. 2005, Parsons et al. 2005, Deagle et al. 2009, Dunshea 2009). This study used gut content analysis to examine long-term trends in loggerhead sea turtle diet relative to environmental variability using loggerhead sea turtle stomach samples collected over a 20-year time period. I aimed to examine changes in the occurrence and relative abundance of loggerhead prey items at the species level, and using gut content analysis allowed me to investigate both of these factors for a relatively large sample size (123 samples).

Sample Processing

Stomach contents were rinsed in a 1.4 mm fine mesh strainer to retain smaller items present. Each sample was then sorted and ‘hard parts’, such as crab legs and gastropod shells, were identified to the lowest possible taxonomic level. Soft tissues were not quantified because they are more susceptible to degradation and are therefore difficult or impossible to identify (Plotkin et al. 1992, Burke et al. 1993, Godley et al. 1997, Houghton et al. 2000, Seney and Musick 2007, Lazar et al. 2011). Prey in the stomach samples analyzed were typically partially digested and broken into pieces and only certain body parts, such as legs or opercula, could be identified to the species level (Figure 2). Thus, analyses focused on assessing the proportion of identified prey items of a given species and on the presence or absence of individual prey items in each stomach sample.

For crabs, the number of claws, leg tips, and paddles identifiable to the species level were recorded to determine the minimum number of possible prey items per sample. To determine the minimum number of crabs in each sample, the minimum possible number of individuals was calculated based on the number of identified body parts (e.g., the number of right and left claws,



FIGURE 2. Example of identifiable prey items in sample NY2205-98. Prey items included leg tips and claw pieces for Acadian and flat-clawed hermit crabs, moonsnail shells and opercula, eastern white slippersnails, ocean quahog shell fragments, and fish vertebrae.

leg tips and paddles) for each species. For example, sample NY3557-06 had 16 left dactyls, 18 left propodi, 17 right dactyls and 14 right propodi identified as rock crab, meaning that based on claws alone there were a minimum of 18 rock crabs in this sample. That same sample also had 95 rock crab leg tips; this number is divided by the total number of walking legs (eight) and rounded up to the nearest integer, giving a minimum of 12 individual rock crabs based on leg tips. Together, the claws and the leg tips indicate that this sample had a minimum number of 18 rock crabs. Portunid, or swimming, crabs, such as blue and lady crabs, have paddles instead of the last pair of walking legs. For these species, the total number of leg tips was divided by six and the number of paddles was divided by two to estimate the minimum number of individuals. For gastropods, shell pieces and opercula were identified to determine presence of a prey species; however, only full opercula and spires containing the apex were used to quantify the

minimum number of gastropods in the sample. Similarly, estimates of species abundance for bivalves were based on full shell pieces; fragments were omitted from these estimates since it was not possible to determine how many individuals were represented by shell fragments. Body parts identifiable to the species level that could not be used to estimate species abundance in stomach samples, such as carapace and abdomen fragments of crabs, were used to confirm the presence of individual prey species in each sample. Other species identified in loggerhead stomachs included fish and echinoderms. Seahorse and sand dollar prey items were found intact, allowing the relative abundance of these species to be calculated, whereas the percent frequency of occurrence could be calculated when fish vertebrae or sea urchin spines were present in samples, but no minimum number of prey items could be determined. It was not possible to calculate the Index of Relative Importance (IRI), which serves as a proxy of important prey items by adjusting the presence of many small prey items against fewer larger prey items (Seney & Musick 2007, Frick et al. 2009), in this study. Calculating this index requires that the weight or volume of each individual prey species be assessed for each sample. Since this analysis focused on examining prey at the species level whenever possible, and it was not possible to identify many parts of prey items to the species level, I was unable to calculate the weight or volume of each species present in the samples.

I used species accumulation curves to confirm that a sufficient number of samples was analyzed in order to accurately represent loggerhead diet in New York waters. Species accumulation curves plot the cumulative number of species found in each stomach sample against the number of samples analyzed. Once the curve reaches its asymptote, one can infer that the minimum number of samples needed for the study has been reached.

Analysis of stomach samples: general observations

Two diet metrics were used in the analysis of the data: percent frequency of occurrence (defined as the proportion of samples in which the prey species was observed) and relative abundance (defined as the proportion of identifiable prey items of a prey species in each sample). Both metrics were calculated for individual prey species averaged on an annual time scale, though some gastropod taxa were grouped together because of difficulties in identifying prey items to the species level. Channeled (*Busycotypus canaliculatus*), waved (*Buccinum undatum*) and knobbed (*Busycon carica*) whelks were analyzed together as whelks, while northern (*Euspira heros*), spotted (*Natica gualteriana*) and shark eye moonsnails (*Neverita duplicata*) were also combined for analyses. While not classified as crustaceans, horseshoe crabs were included in the broader crustacean category for the purpose of analyses. Only years containing more than five samples were used in analyses to prevent spurious observations due to small sample sizes.

Diversity was calculated using Simpson's (D) diversity index for each individual sample in which prey were observed using the following equation:

$$D = 1 - \sum_{i=1}^S p_i^2$$

where S is the total number of species, and p_i is the proportion of individuals of the i th species in the sample. I used Wilcoxon tests to examine differences in the diversity and total number of prey items observed in loggerhead stomach samples between sexes (male vs. female) and between large and small turtles (using a cutoff of 80 cm based on the average size of maturity from the literature; Bjorndal et al. 1983, Henwood 1987, Wibbels et al. 1991, Botlen et al. 1994). I examined these differences both for the broad prey categories (crustacean, gastropod, and bivalve) and for individual prey species.

Analysis of stomach samples: long-term trends

I examined annual variability in prey composition for the 20-year period of sample collection relative to annual averages of the following climatic and oceanographic variables: Sea Surface Temperature (SST), North Atlantic Oscillation (NAO), Atlantic Multidecadal Oscillation (AMO), and Gulf Stream North Wall (GSNW; Figure 3) indices. The NAO is a climate phenomenon driven by changes in atmospheric pressure, which can affect the strength of westerly winds, and in turn temperature (Hurrell et al. 2003), while the AMO is a climate index that documents sea surface temperature anomalies and large-scale circulation changes in the North Atlantic (McCarthy et al. 2015). Beginning near the Gulf of Mexico, the Gulf Stream moves north along the continental shelf until Cape Hatteras, where it shifts eastward into the Atlantic Ocean (Taylor & Stephens 1980, Halkin & Rossby 1985). The latitude of the Gulf Stream North Wall (GSNW) varies with movements of the Gulf Stream, and has strong impacts on water temperatures on the northeast continental shelf (Taylor & Stephens 1980). I chose these

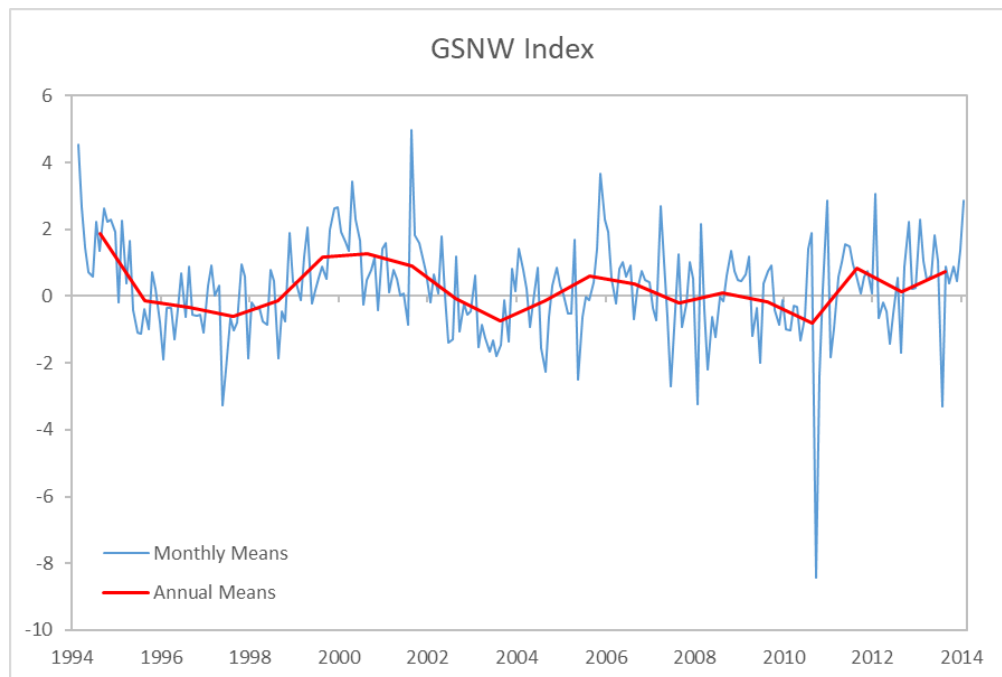


FIGURE 3. Monthly and annual GSNW indices.

climate metrics because they have been associated with ecosystem shifts and their effects on local SST (NAO: Brodziak & O'Brien 2005, Sullivan et al. 2005, Collie et al. 2008; AMO: O'Connor et al 2011, Nye et al. 2014, Auber et al. 2015, Buchheist et al. 2016; GSNW: Schollaerts et al. 2004, Borkman & Smayda 2009, Nye et al. 2011; NAO/AMO: Sanchez-Rubio et al 2011, Pershing et al. 2015; NAO/GSNW: Dawe et al. 2000). NAO and AMO indices were downloaded from NOAA's Physical Sciences Division: (ftp://ftp.cpc.ncep.noaa.gov/wd52dg/data/indices/nao_index.tim and <https://www.esrl.noaa.gov/psd/data/correlation/amon.us.data> respectively; NOAA 2016). GSNW Taylor index data were downloaded from the Plymouth Marine Laboratory (<http://www.pml-gulfstream.org.uk/Data%20Web2014.pdf>; Taylor 2016). I used daily Group for High Resolution SST (GRHSST) images with a 0.25 degree resolution averaged each year from June to October (when 98% of our strandings occurred) at the location of the center mean distribution of the samples analyzed.

I used Principal Component Analysis (PCA), Redundancy Analysis (RDA), and Non-Metric Multidimensional Scaling (NMDS) to characterize variability in loggerhead diet. PCA is an ordination technique that reduces the dimensions of the data into the dominant dimensions that show the greatest variation (Legendre & Legendre 1998). Redundancy Analysis is similar to PCA in that it is an ordination that produces dimensions that show the greatest variation, however, RDA allows for the addition of environmental variables in order to explain the effects of those variables on the community structure (Legendre & Legendre 1998, Griffith & Peres-Neto 2006). NMDS aims to present the distance relationship between samples in a small number of dimensions, with similar samples, being closer together, and dissimilar items farther apart (Legendre & Legendre 1998).

All multivariate analyses were carried out on annual averages of the two diet metrics (percent frequency of occurrence and relative abundance). For RDA, forward selection was used to select linear models of explanatory variables with the lowest Akaike Information Criterion (AIC), which was corrected for the small sample size (AICc) with the following equation:

$$AICc = AIC + \frac{2k(k + 1)}{n - k - 1}$$

where n is the sample size and k is the number of parameters (Burnham & Anderson 1998). I assessed RDA results relative to SST, NAO, AMO and GSNW index, as well as the NAO and AMO indices lagged by one and two years. AMO and NAO were lagged because these are large scale variables whose effects on community structure have been shown to trail shifts between positive and negative phases (Ottersen et al. 2001, O'Connor et al. 2012, Abruzzo 2015). In contrast, SST and GSNW are more proximate variables with more immediate effects, so these variables were not lagged. PCA and RDA were run on dissimilarity matrices of Euclidean distances of the annual averages of the two diet metrics (Legendre & Gallagher 2001), while NMDS was run on a Bray-Curtis dissimilarity matrix (Minchin 1987).

Preliminary analyses, along with the results of Howell and Auster (2012) and Abruzzo (2015) suggested a break in the data around 2000, and thus the NMDS analysis was performed to test whether there were distinct clusters in time. In NMDS analyses, a stress level above 0.2 indicates that possible clustering is arbitrary, whereas a stress levels between 0.1 and 0.2 represents a reasonable fit, and a stress of 0.1 or less is considered a good fit of the clustering to the data (Clarke & Warwick 2001). To test whether clusters produced by the NMDS analyses were significantly different, I used analysis of similarities (ANOSIM), which compares mean ranked dissimilarities within and between groups, as well as permutational analysis of variance (PERMANOVA), which uses squared distances within and between groups (Anderson & Walsh

2013) on the NMDS results. In ANOSIM analyses, an R statistic close to 1 signifies dissimilarities between groups, whereas a value close to zero signifies similarities between groups. In PERMANOVA analyses, a large R^2 value indicates that a greater proportion of the variance is explained by the two groups. All analyses were conducted in the R statistical package using the ‘vegan’ library (Okasen et al. 2017).

Spatial analysis of sea turtle strandings

Using the Riverhead Foundation’s stranding database, I examined spatial patterns in loggerhead sea turtle strandings over the 36-year period (1982 – 2016) for which strandings were recorded.

RESULTS

Loggerhead sea turtle strandings on Long Island

A total of 123 stomachs from loggerhead sea turtles were analyzed. Of these samples, 29 showed definitive signs of human interaction; 23 showed evidence of boat strikes and 6 of fisheries interactions, such as fishing line or hooks. Stranded loggerheads had a mean straight carapace length of 65.9 ± 12.9 cm, ranging from 45.8 – 103.9 cm (n = 120; three stranded turtles could not be measured due to damage to the carapace). The majority of loggerheads for which stomach samples were analyzed in this study stranded on the southern beaches of Long Island (Figure 4). Of the turtle stomachs analyzed, 73% stranded in July and August (Table 1) and were predominantly small females (Table 2).

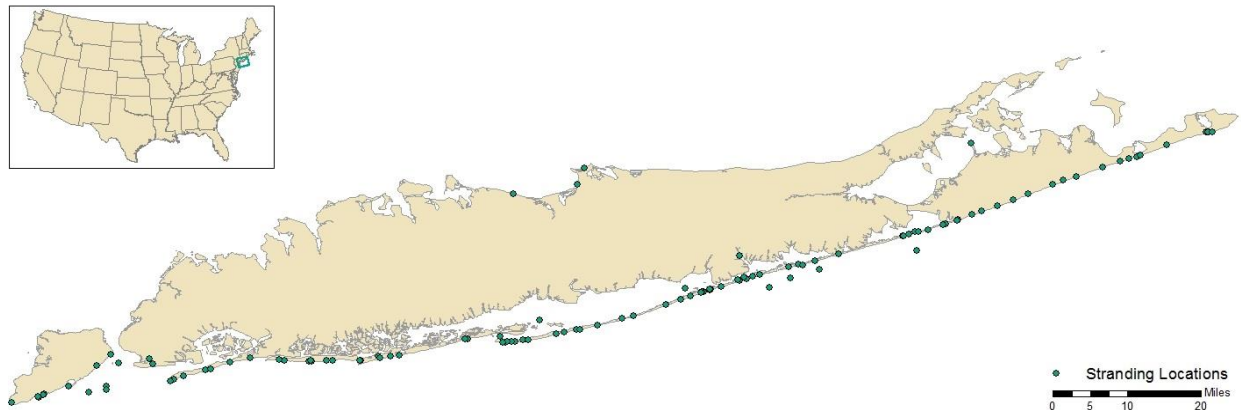


FIGURE 4. Location of loggerhead sea turtle strandings for which stomach samples were analyzed

TABLE 1. Timing of loggerhead strandings by month and time period.

| | June | July | August | September | October | December | <i>Total</i> |
|--------------|------|------|--------|-----------|---------|----------|--------------|
| 1995-1999 | 1 | 12 | 16 | 4 | 0 | 0 | 33 |
| 2000-2004 | 0 | 9 | 5 | 1 | 0 | 0 | 15 |
| 2005-2009 | 0 | 14 | 8 | 3 | 1 | 0 | 26 |
| 2010-2014 | 8 | 17 | 9 | 6 | 7 | 2 | 49 |
| <i>Total</i> | 9 | 52 | 38 | 14 | 8 | 2 | 123 |

TABLE 2. Size and sex of stranded loggerheads by time period. Turtles with a Straight Carapace Length (SCL) of 45-80 cm were categorized as small, while turtles with an SCL of 80-105 cm were considered to be large. Total for 1995 – 1999 includes 3 individuals that could not be measured due to damage to the carapace.

| | Small | Large | Male | Female | Unknown | <i>Total</i> |
|--------------|-------|-------|------|--------|---------|--------------|
| 1995-1999 | 24 | 6 | 6 | 14 | 0 | 33 |
| 2000-2004 | 14 | 1 | 4 | 8 | 3 | 15 |
| 2005-2009 | 22 | 4 | 6 | 14 | 6 | 26 |
| 2010-2014 | 41 | 8 | 11 | 33 | 5 | 49 |
| <i>Total</i> | 101 | 19 | 27 | 69 | 27 | 123 |

The species accumulation curves for all samples analyzed (Figure 5), samples from female sea turtles (Figure 6b) and samples from small sea turtles (Figure 6d) all reached asymptotes, indicating that there were enough samples in these groups to accurately describe the prey items typically taken by these turtles. Species accumulation curves for males (Figure 6a) and for large loggerheads (Figure 6c) did not reach asymptotes, although both curves leveled off enough to suggest that the more commonly occurring prey items were captured by the samples in those two groups, allowing me to include them in my analyses.

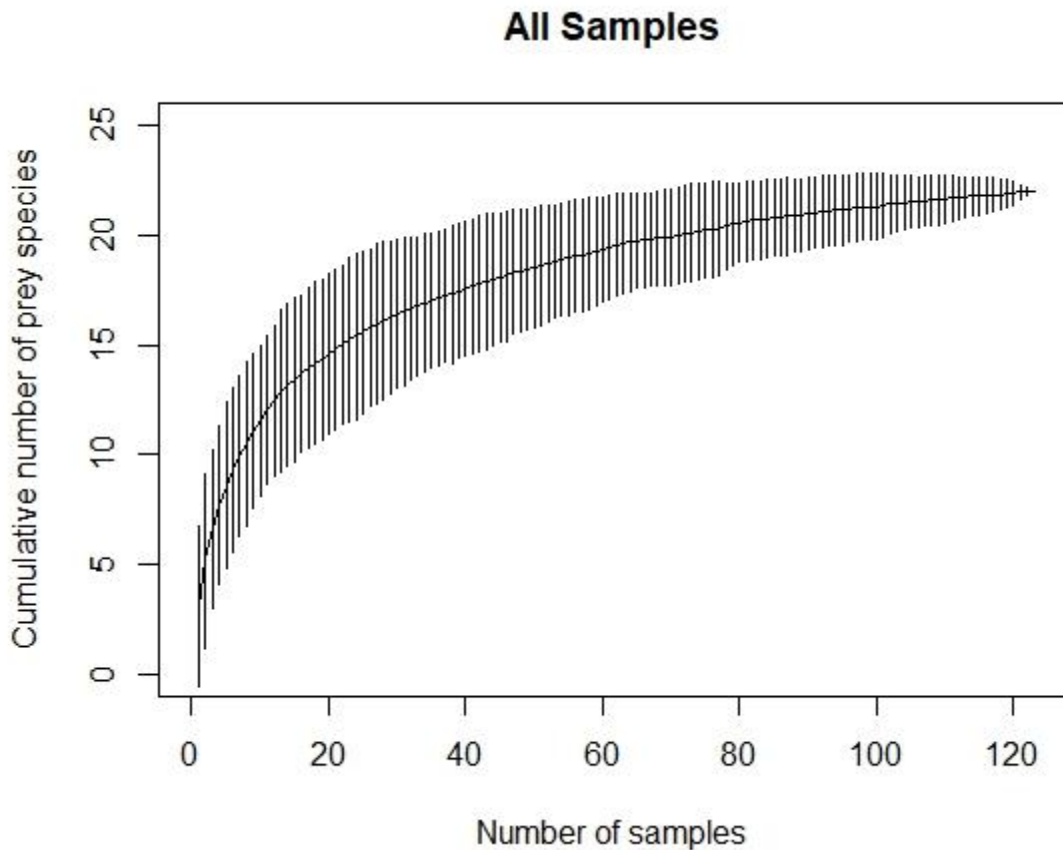


FIGURE 5. Species accumulation curve for all loggerhead samples analyzed (n = 123).

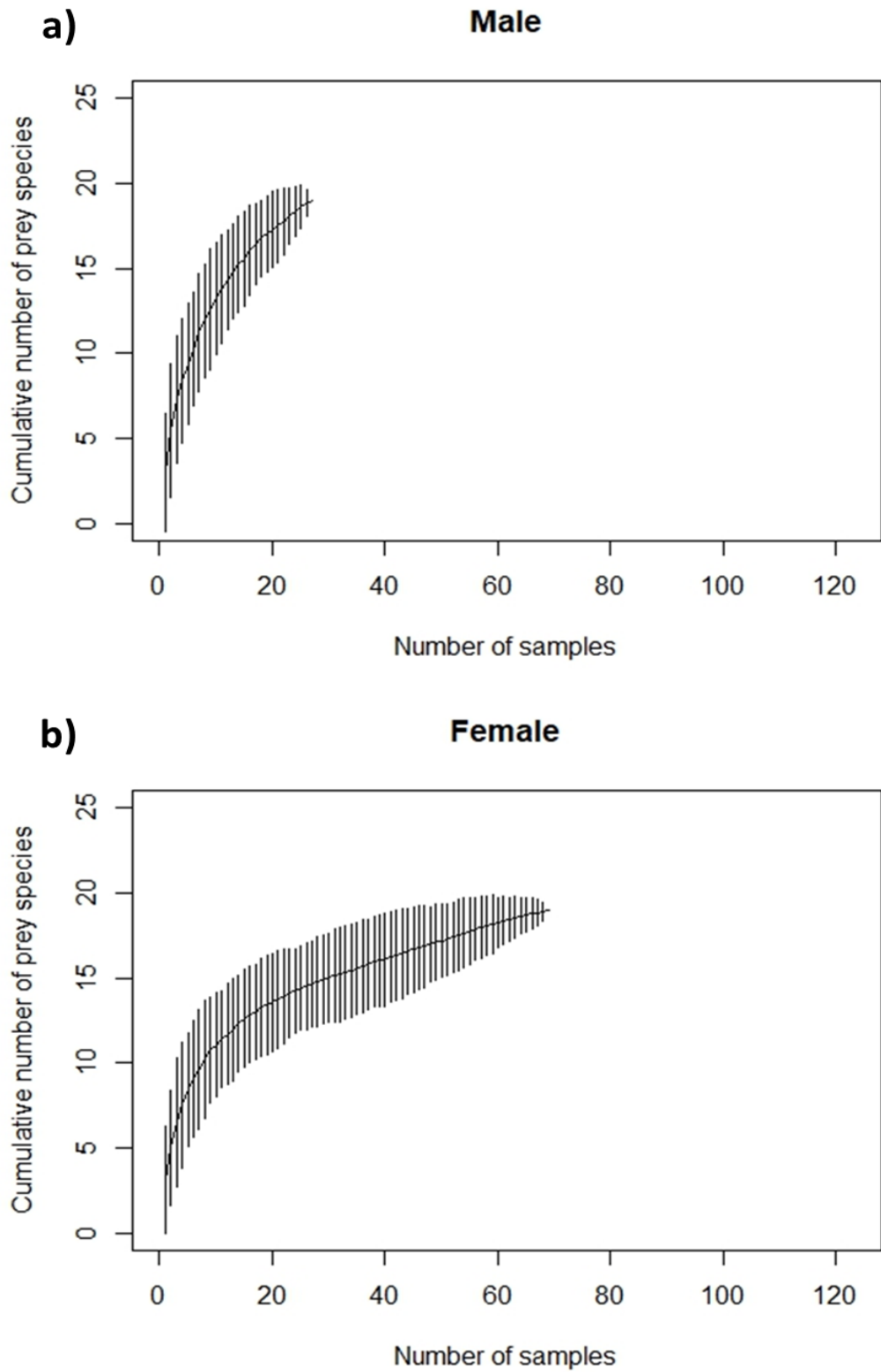


FIGURE 6. Species accumulation curve for a) male ($n = 27$), b) female ($n = 69$), c) small ($n = 101$), and d) large ($n = 19$) loggerhead samples analyzed.

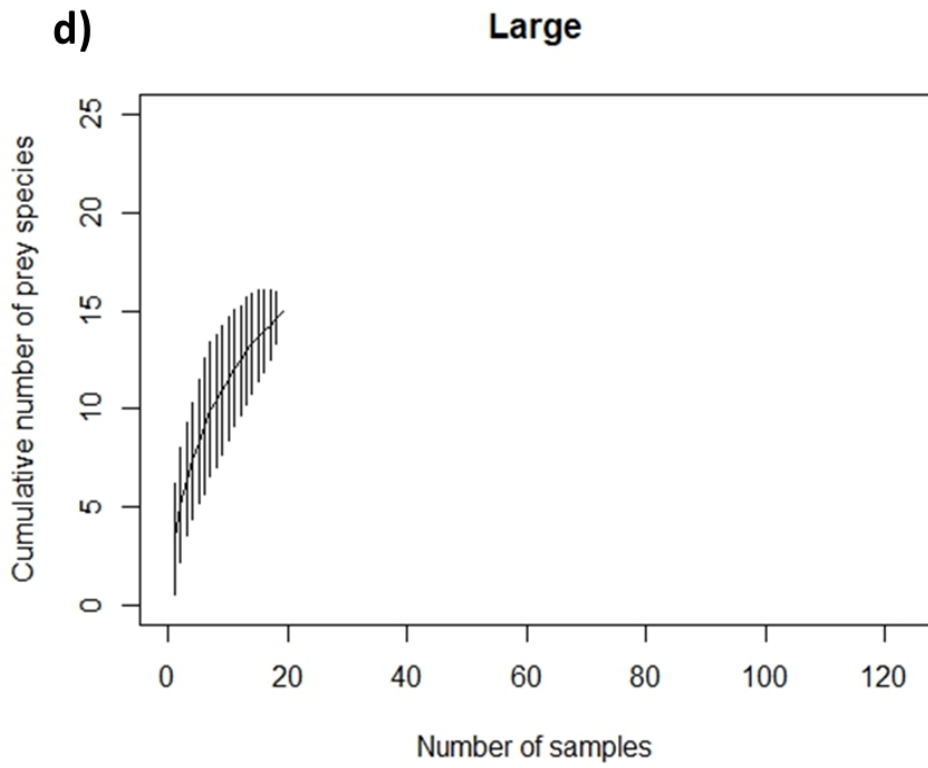
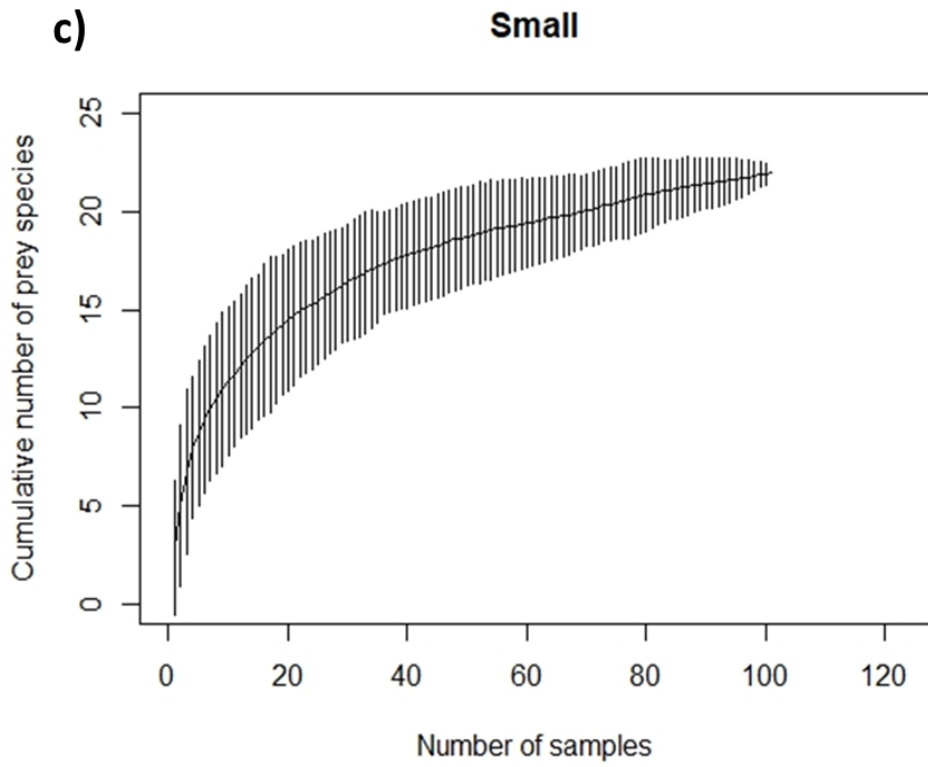


FIGURE 6. Continued

Loggerhead sea turtle diet

The most common prey items observed in the loggerhead stomachs were crustaceans, which were found in 96% of the samples and made up 60% of all prey items consumed, followed by gastropods, found in 65% of samples and making up 34% of all prey items consumed. In terms of the percent frequency of occurrence, Acadian hermit crab (*Pagurus acadianus*), Jonah crab (*Cancer borealis*), moonsnails, flat-clawed hermit crab (*Pagurus pollicaris*), rock crab (*Cancer irroratus*) and spider crab (*Libinia emarginata*) were the most common prey items, while Acadian hermit crab, flat-clawed hermit crab, whelks, moonsnails, rock crab, and blue mussel (*Mytilus edulis*) were the most common prey items in terms of the total number of prey items observed in each sample (Table 3). Based on the high occurrence and abundance of crustaceans, they were also separated into three groups based on the typical size of these species in this area (Weiss 1995, Martinez & Martinez 2003): small crustaceans were those that were less than 5 cm, such as Acadian and Flat-clawed hermit crabs, and Atlantic mud crab. Medium crustaceans were between 5-15 cm, including rock, Jonah and lady crabs. Large crustaceans were species larger than 15 cm, such as blue, spider and horseshoe crabs. Small crustaceans made up 39.4% of the diet, medium crabs 11.3% and large crabs 3.9%. Overall, an average of 45 ± 65 prey items were observed per sample, with the total number of prey items observed ranging between 1 and 473 prey items. For 3 of the 123 stomach samples analyzed, no prey items were observed. Marine debris was observed in 21% of the samples analyzed, predominantly consisting of pieces of plastic, though fishing line and string were also observed in three samples.

On average, samples from larger loggerheads (> 80 cm SCL; range: 80-105 cm) contained 2.6 times more total prey items and 4.6 times more gastropods than those from smaller turtles (< 80 cm SCL; range: 45-80 cm; Wilcoxon test, $W = 475$, $p\text{-value} = 5.0 \times 10^{-4}$ and $W =$

TABLE 3. Summary of prey items identified in the stomachs of stranded loggerhead sea turtles (n = 123)

| | | Percent frequency of occurrence | Relative abundance of prey items |
|--------------------------|----------------------------------|---------------------------------------|--|
| Crustaceans | | 95.93 | 59.67 |
| Decapods | | | |
| Acadian Hermit Crab | <i>Pagurus acadianus</i> | 51.22 | 23.46 |
| Flat-clawed Hermit Crab | <i>Pagurus pollicaris</i> | 35.77 | 15.66 |
| Jonah Crab | <i>Cancer borealis</i> | 42.28 | 4.71 |
| Rock Crab | <i>Cancer irroratus</i> | 34.96 | 6.09 |
| Spider Crab | <i>Libinia emarginata</i> | 25.20 | 2.95 |
| Blue Crab | <i>Callinectes sapidus</i> | 7.32 | 0.67 |
| Lady Crab | <i>Ovalipes ocellatus</i> | 6.50 | 0.51 |
| Atlantic Mud Crab | <i>Panopeus herbstii</i> | 1.63 | 0.24 |
| Unidentified Crustaceans | | 34.15 | 5.38 |
| Chelicerates | | | |
| Horseshoe Crab | <i>Limulus polyphemus</i> | 3.25 | 0.25 |
| Mollusks | | 69.11 | 40.01 |
| Bivalves | | 15.45 | 5.53 |
| Blue Mussel | <i>Mytilus edulis</i> | 10.57 | 5.40 |
| Hard Clam | <i>Mercenaria mercenaria</i> | 0.81 | 0.02 |
| Ocean Quahog | <i>Arctica islandica</i> | 0.81 | 0.02 |
| Atlantic Surf Clam | <i>Spisula solidissima</i> | 1.63 | 0.00 |
| Waved Astarte | <i>Astarte undata</i> | 0.81 | 0.00 |
| Unidentified bivalves | | 3.25 | 0.09 |
| Gastropods | | 65.04 | 34.48 |
| Moonsnails | Naticidae | 37.40 | 11.64 |
| Northern Moonsnail | <i>Euspira heros</i> | 18.70 | 1.61 |
| Shark Eye Moonsnail | <i>Neverita duplicata</i> | 4.88 | 3.26 |
| Spotted Moonsnail | <i>Natica gualteriana</i> | 1.63 | 0.04 |
| Whelks | Buccinidae | 11.38 | 12.78 |
| Channeled Whelk | <i>Busycotypus canaliculatus</i> | 5.69 | 1.34 |
| Knobbed Whelk | <i>Busycon carica</i> | 1.63 | 0.11 |
| Waved Whelk | <i>Buccinum undatum</i> | 3.25 | 2.01 |
| Three-lined Mudsnail | <i>Tritia trivittata</i> | 11.38 | 0.49 |
| Eastern Mudsnail | <i>Tritia obsoleta</i> | 3.25 | 0.20 |

TABLE 3. Continued

| | | Percent frequency of occurrence | Relative abundance of prey items |
|------------------------------|-----------------------------|---------------------------------------|--|
| Atlantic Oyster Drill | <i>Urosalpinx cinera</i> | 3.25 | 0.25 |
| Common Atlantic Slippersnail | <i>Crepidula fornicata</i> | 8.94 | 0.89 |
| Eastern White Slippersnail | <i>Crepidula plana</i> | 1.63 | 0.24 |
| Smooth Periwinkle | <i>Littorina obtusata</i> | 0.81 | 0.02 |
| Unidentified gastropods | | 38.21 | 24.03 |
| Chordata | | | |
| Seahorse | <i>Hippocampus spp.</i> | 1.63 | 0.04 |
| Unidentified fish vertebrae | | 4.88 | - |
| Echinoderms | | | |
| Common Sand Dollar | <i>Echinarachnius parma</i> | 4.07 | 0.04 |
| Unidentified Urchin | | 5.69 | - |
| Marine Debris | | 21.14 | - |

564, $p\text{-value} = 3.7 \times 10^{-3}$, respectively), with larger turtles on average consuming 93 total prey items and 46 gastropods, compared to the average 35 total prey items and 10 gastropods for small turtles. There was a significant positive relationship between size and the total number of prey items consumed (Pearson's correlation, $r = 0.39$, $df = 118$, $p\text{-value} = 1.5 \times 10^{-5}$) and between size and the number of gastropods consumed (Pearson's correlation, $r = 0.31$, $df = 118$, $p\text{-value} = 5.3 \times 10^{-4}$) but there was no significant difference between size and the mean number of crustaceans or bivalves consumed (Wilcoxon test, $p\text{-values} = 0.064$ and 0.075 respectively). When examining prey by species, larger loggerheads ate more horseshoe crabs and moonsnails than smaller loggerheads (mean number of horseshoe crabs was 0.58 for larger loggerheads and 0.03 for smaller loggerheads, Wilcoxon test; $W = 875.5$, $p\text{-value} = 0.054$; and mean number of moonsnails was 19.1 for larger loggerheads and 2.7 for smaller loggerheads, $W = 476.5$, $p\text{-value} = 7.2 \times 10^{-5}$, respectively). There were no significant differences observed based on sex when size was accounted for (i.e., tests of large female vs. large male and small female vs. small male; Wilcoxon test, $p\text{-values} = 0.09$ and 0.61 respectively).

Simpson's diversity index showed a high degree of variability among the samples. The Simpson's diversity index ranged from 0 – 0.83 (1 being the maximum possible diversity index; mean = 0.47, variance = 0.06), however, there were no significant differences in Simpson's diversity indices between large and small turtles, or between male and female turtles (Wilcoxon test, $p\text{-values} = 0.55$ and 0.46 respectively).

Analyses of loggerhead diet in relation to environmental variables

In the PCA for annual percent frequency of occurrence, 56.6% of the variability in loggerhead diet was captured by the first two PC axes (Table 4). All years before 2000 showed

TABLE 4. PCA results showing variance explained for each PC axis for annual percent frequency of occurrence

| | PC1 | PC2 | PC3 | PC4 | PC5 | PC6 | PC7 | PC8 |
|-----------------------|--------|--------|--------|--------|--------|--------|--------|--------|
| Proportion Explained | 0.3629 | 0.1997 | 0.1826 | 0.1037 | 0.0826 | 0.0311 | 0.0207 | 0.0167 |
| Cumulative Proportion | 0.3629 | 0.5626 | 0.7452 | 0.8489 | 0.9315 | 0.9626 | 0.9833 | 1.0000 |

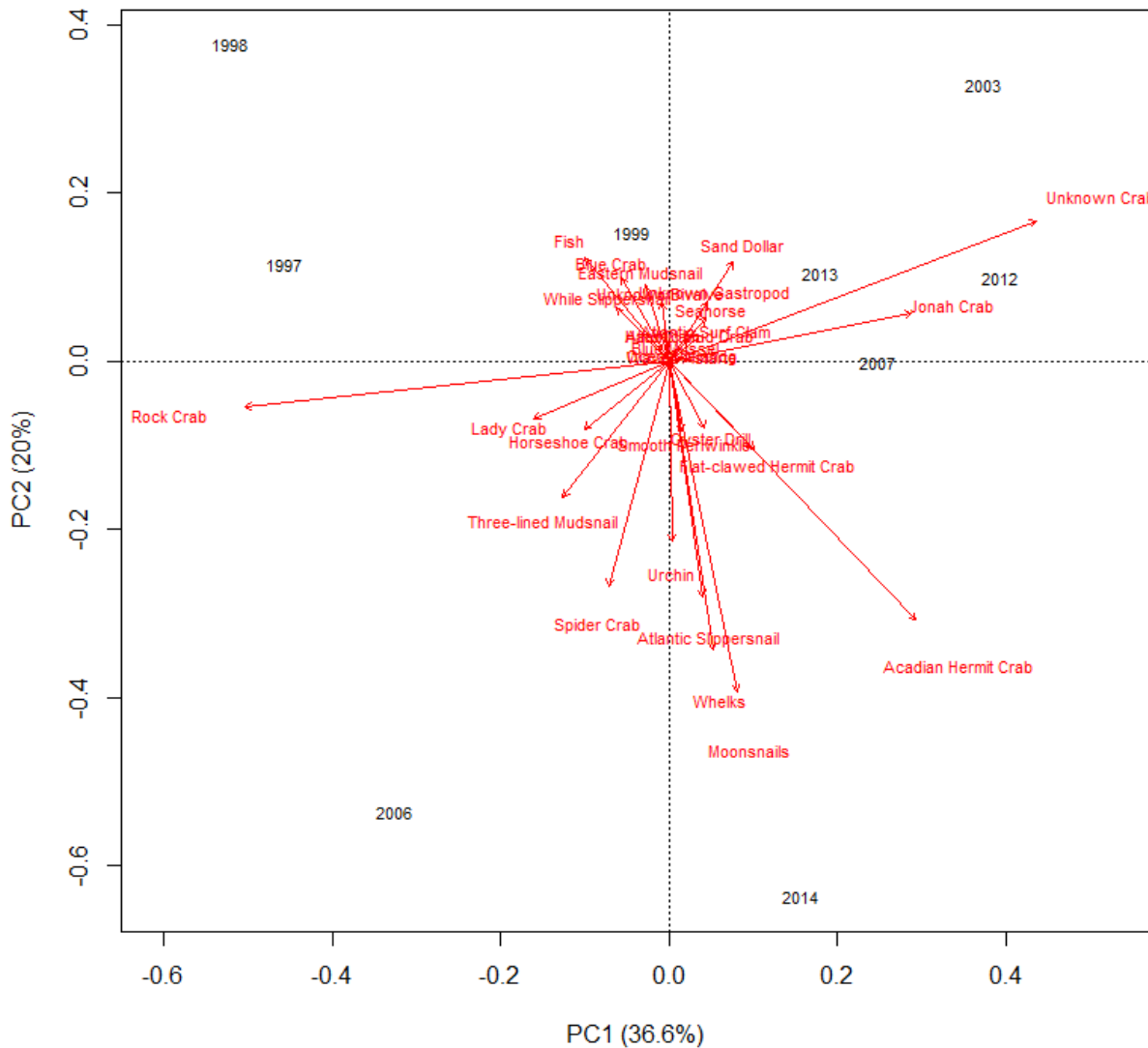


FIGURE 7. Biplot of PCA performed on annual percent frequency of occurrence for loggerhead prey items. Red arrows denote species loadings relative to PCs 1 and 2. Years represent mean PC loadings for samples in that year.

TABLE 5a. Species loading for first two axes of annual percent frequency of occurrence PCA. Species are sorted from highest to lowest loadings on PC1.

| | PC1 | PC2 |
|-------------------------|--------|--------|
| Unknown Crab | 0.513 | 0.196 |
| Acadian Hermit Crab | 0.344 | -0.362 |
| Jonah Crab | 0.338 | 0.068 |
| Flat-clawed Hermit Crab | 0.118 | -0.123 |
| Moonsnails | 0.094 | -0.462 |
| Sand Dollar | 0.088 | 0.138 |
| Whelks | 0.061 | -0.402 |
| Unknown Gastropod | 0.054 | 0.081 |
| Seahorse | 0.051 | 0.061 |
| Oyster Drill | 0.050 | -0.093 |
| Atlantic Slippersnail | 0.047 | -0.330 |
| Atlantic Surf Clam | 0.042 | 0.036 |
| Atlantic Mud Crab | 0.026 | 0.030 |
| Smooth Periwinkle | 0.018 | -0.098 |
| Ocean Quahog | 0.017 | 0.006 |
| Waved Astarte | 0.017 | 0.006 |
| Blue Mussel | 0.008 | 0.016 |
| Urchin | 0.004 | -0.252 |
| Hard Clam | -0.007 | 0.030 |
| Unknown Bivalve | -0.010 | 0.081 |
| Eastern Mudsnaill | -0.034 | 0.106 |
| Blue Crab | -0.068 | 0.117 |
| White Slippersnail | -0.074 | 0.074 |
| Spider Crab | -0.085 | -0.314 |
| Fish | -0.118 | 0.144 |
| Horseshoe Crab | -0.119 | -0.095 |
| Three-lined Mudsnaill | -0.149 | -0.190 |
| Lady Crab | -0.189 | -0.081 |
| Rock Crab | -0.593 | -0.064 |

TABLE 5b. Species loading for first two axes of annual relative abundance PCA. Species are sorted from highest to lowest loadings on PC1.

| | PC1 | PC2 |
|-------------------------|--------|--------|
| Acadian Hermit Crab | 0.462 | 0.030 |
| Spider Crab | 0.230 | 0.304 |
| Unknown Gastropod | 0.129 | 0.170 |
| Flat-clawed Hermit Crab | 0.122 | 0.155 |
| Whelks | 0.110 | 0.002 |
| Unknown Crab | 0.095 | -0.114 |
| Jonah Crab | 0.069 | -0.345 |
| Oyster Drill | 0.022 | 0.007 |
| Lady Crab | 0.018 | 0.112 |
| Eastern Mudsnaill | 0.011 | -0.044 |
| Atlantic Mud Crab | 0.010 | -0.024 |
| Seahorse | 0.006 | -0.016 |
| Smooth Periwinkle | 0.003 | 0.004 |
| Ocean Quahog | 0.000 | 0.000 |
| Sand Dollar | -0.010 | -0.027 |
| Unknown Bivalve | -0.013 | 0.016 |
| Hard Clam | -0.014 | -0.019 |
| Atlantic Slippersnail | -0.016 | -0.037 |
| Horseshoe Crab | -0.033 | 0.059 |
| Blue Mussel | -0.043 | -0.105 |
| Three-lined Mudsnaill | -0.054 | -0.005 |
| White Slippersnail | -0.054 | 0.072 |
| Blue Crab | -0.080 | 0.080 |
| Moonsnails | -0.327 | -0.705 |
| Rock Crab | -0.743 | 0.424 |

negative values of PC1, while with the exception of 2006, years after 2000 showed positive values of PC1 (Figure 7). Correspondingly, species that showed positive loading values along PC1 (Table 5a), such as Acadian and flat-clawed hermit crabs and Jonah crab, occurred more frequently in the diet of loggerheads in the later years, whereas species that showed a negative loading with PC1, such as rock crab, were observed more frequently in earlier samples (Figure 8). Similar trends were observed in the PCA for annual relative abundance (Figure 9), where the first two PC axes captured 66.3% of the variability in loggerhead diet (Table 6). All samples after 2000 showed positive PC1 loadings, while all samples before 2000 showed negative values of PC1. As with the analysis of percent frequency of occurrence, rock crabs showed a negative loading on PC1 (Table 5b), signifying that the presence of rock crabs in loggerhead stomachs decreased with time, and Acadian and flat-clawed hermit crabs had positive loadings on PC1, signifying that these species became more common in loggerhead diet through time (Figure 10).

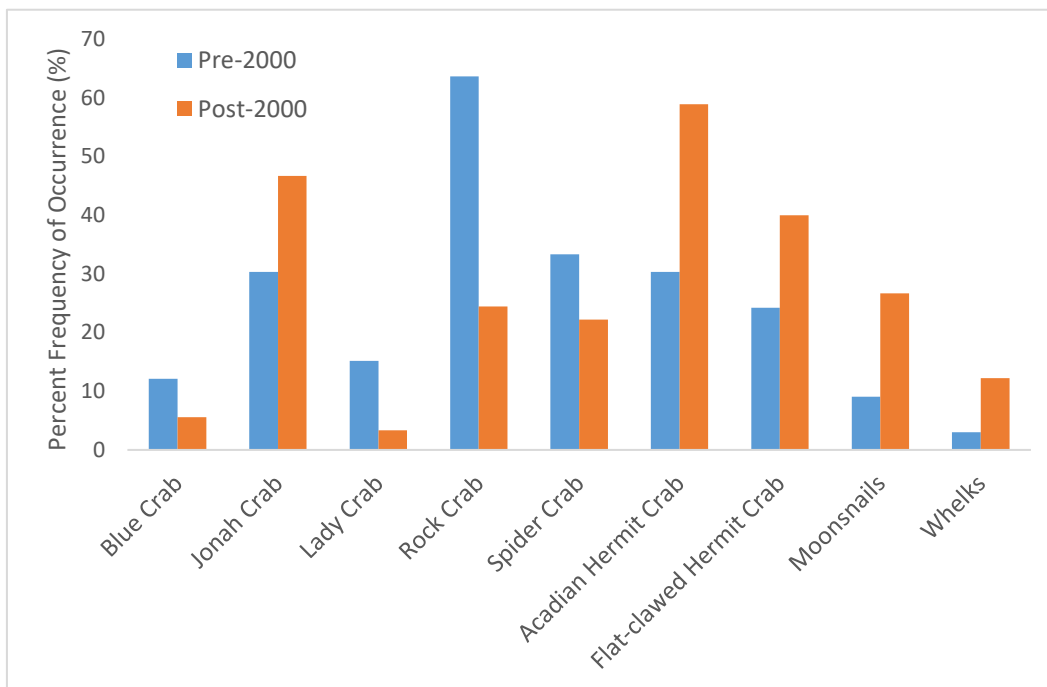


FIGURE 8. Barplot of percent frequency of occurrence for the most frequently occurring prey items in loggerhead diet before and after 2000.

TABLE 6. PCA results showing variance explained for each PC axis for annual relative abundance

| | PC1 | PC2 | PC3 | PC4 | PC5 | PC6 | PC7 | PC8 |
|-----------------------|--------|--------|--------|--------|--------|--------|--------|--------|
| Proportion Explained | 0.4326 | 0.2300 | 0.1239 | 0.1001 | 0.0434 | 0.0381 | 0.0197 | 0.0123 |
| Cumulative Proportion | 0.4326 | 0.6626 | 0.7865 | 0.8866 | 0.9300 | 0.9680 | 0.9877 | 1.0000 |

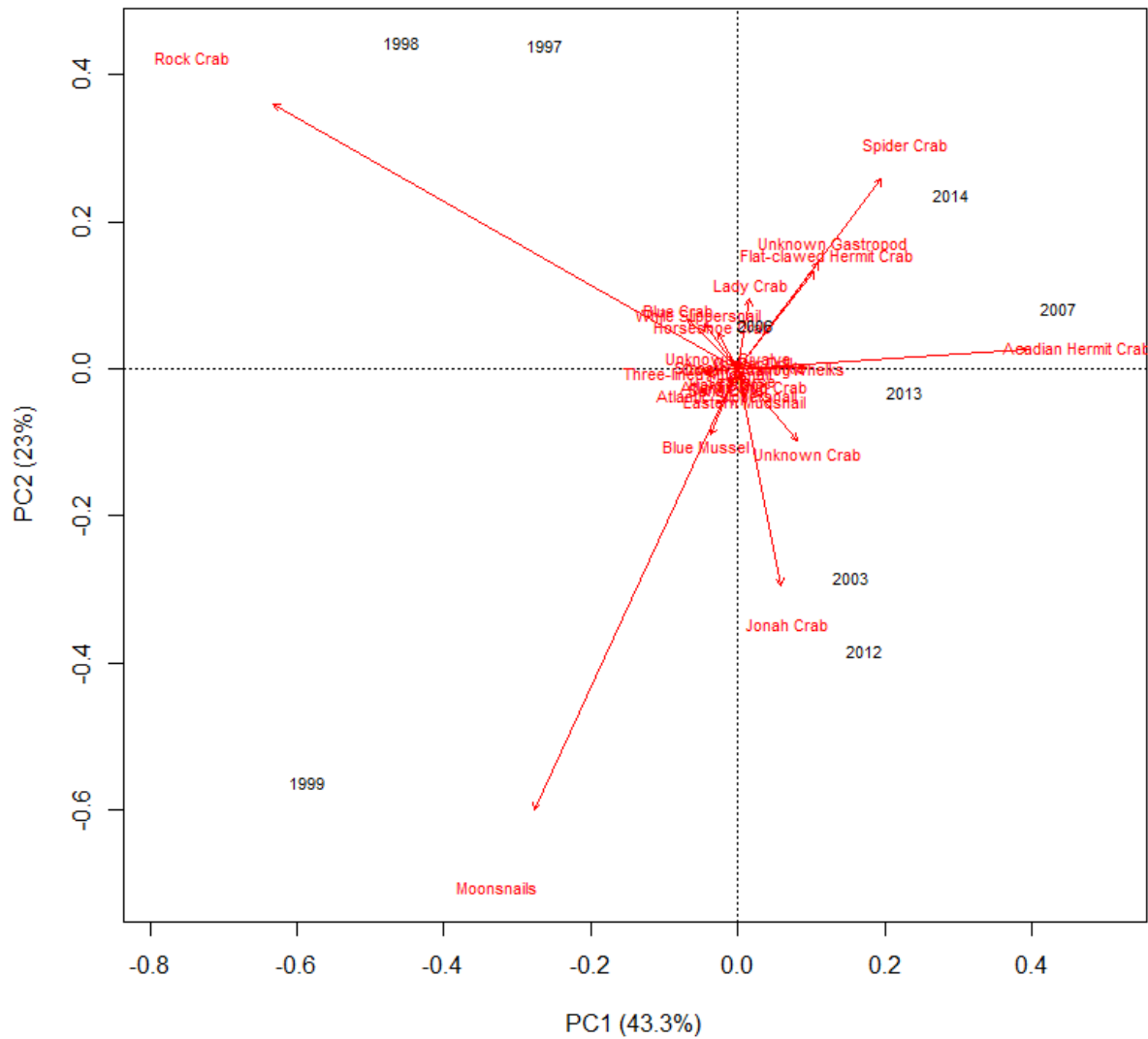


FIGURE 9. Biplot of PCA performed on annual relative abundance for loggerhead prey items. Red arrows denote species loadings relative to PCs 1 and 2. Years represent mean PC loadings for samples in that year.

NMDS was used to assess the annual variability in the occurrence of prey items in the PCAs. Convergent solutions were found for both percent frequency of occurrence and relative abundance analyses with stress values of 0.115 and 0.0886, respectively, indicating that the percent frequency of occurrence model had a fair fit for the data and the relative abundance model had a good fit with the data. In both models, samples were grouped into two distinct clusters in the NMDS analysis, one representing samples collected in the years before 2000, and one representing the years after 2000 (Figures 11 & 12). ANOSIM results showed a significant difference between the mean ranked dissimilarities of pre-and post-2000 groups for both percent frequency of occurrence (R statistic: 0.5494, p-value = 0.032) and relative abundance (R statistic: 0.7099, p-value = 0.009; Figure 13). The PERMANOVA analysis further supported these findings, showing significant p-values for percent frequency of occurrence ($R^2 = 0.26$, p-value = 0.035) and relative abundance ($R^2 = 0.33$, p-value = 0.009).

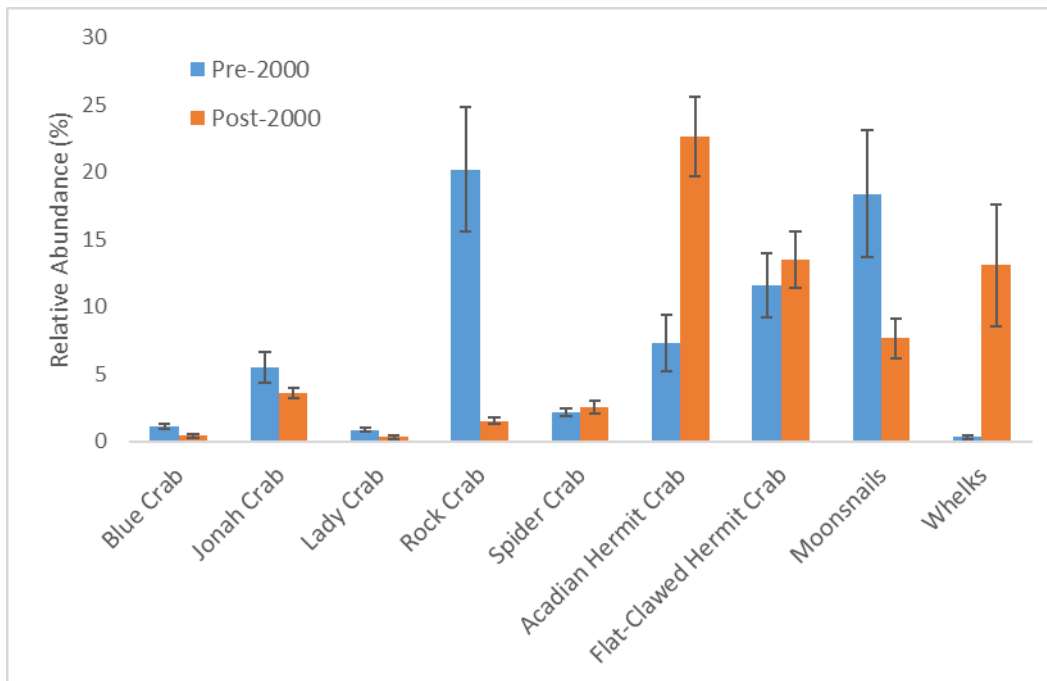


FIGURE 10. Barplot of relative abundance for the most commonly occurring prey items in loggerhead diet before and after 2000. Error bars are standard error of the mean.

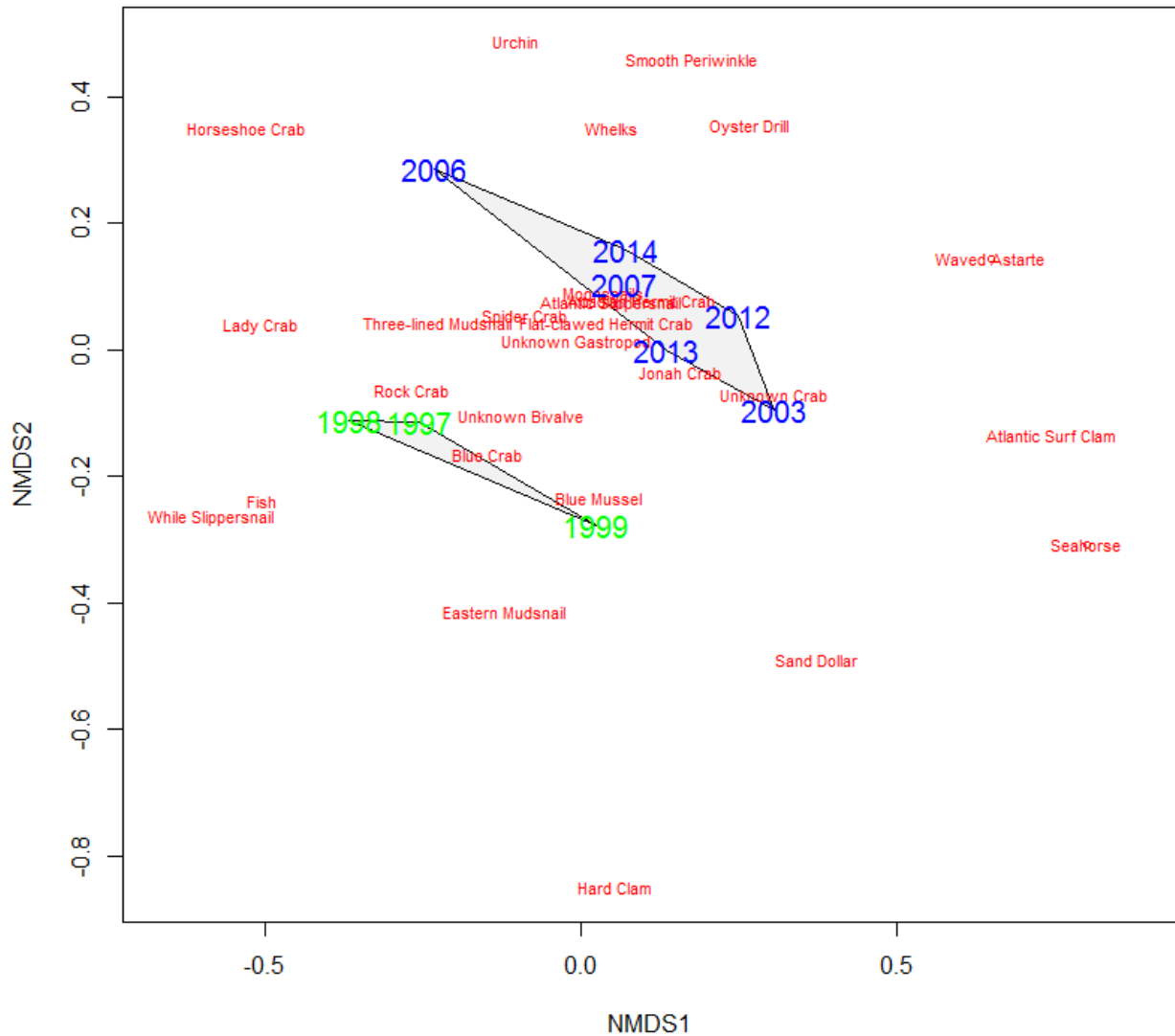


FIGURE 11. Biplot of NMDS model for annual percent frequency of occurrence of loggerhead prey items. There are two distinct clusters based on year, one containing the years before 2000 (green), and one with years after 2000 (blue). Species located near the clusters were more commonly observed during those time periods.

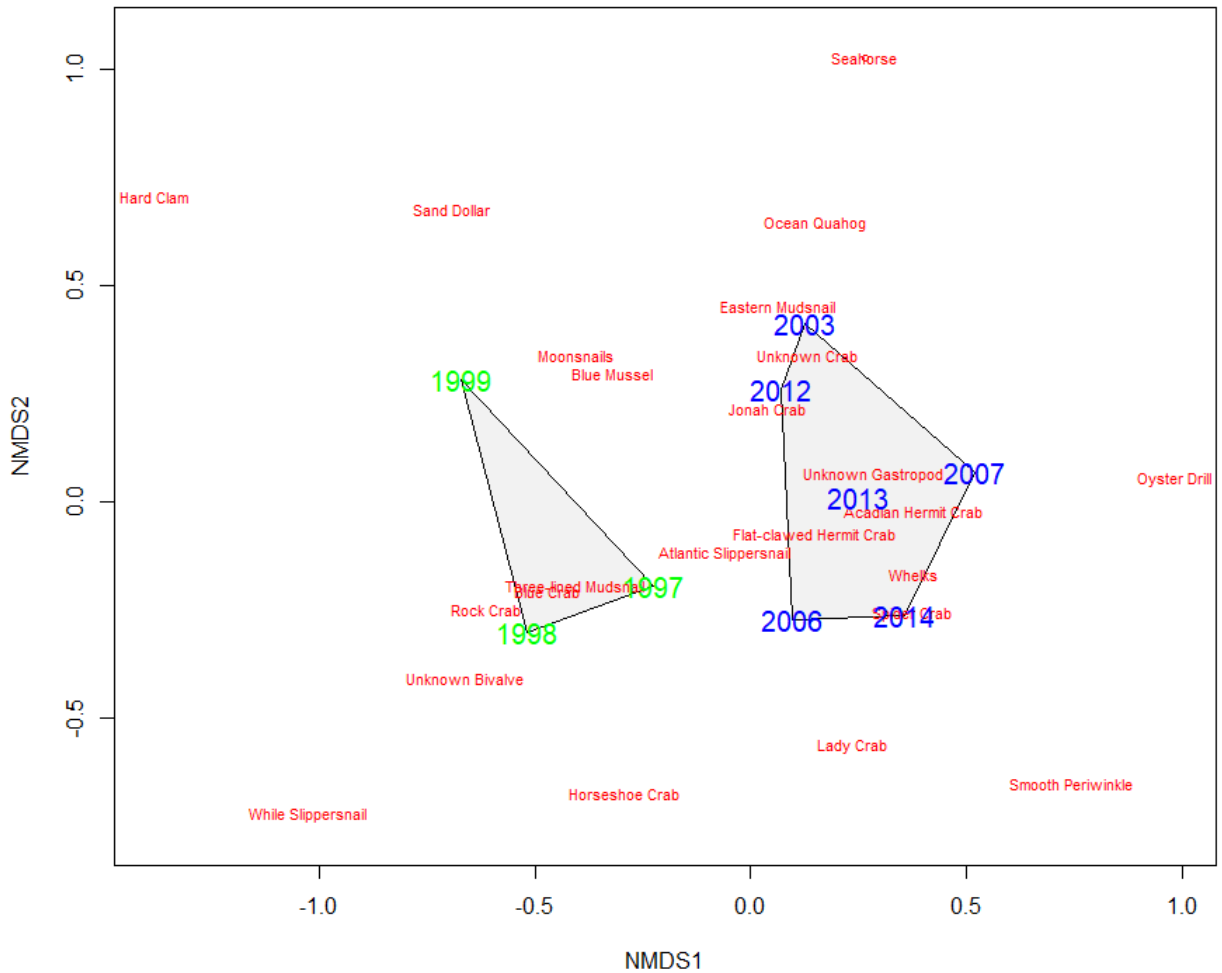


FIGURE 12. Biplot of NMDS model for annual relative abundance of loggerhead prey items. There are two distinct clusters based on year, one containing the years before 2000 (green), and one representing years after 2000 (blue). Species located near the clusters were more commonly observed during those time periods

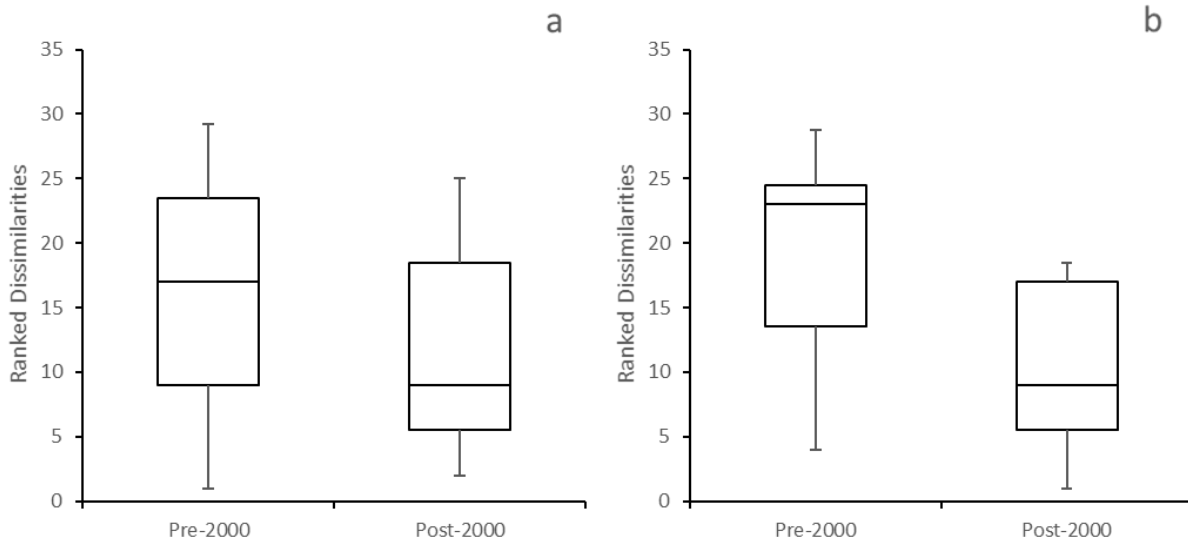


FIGURE 13. Boxplot for ANOSIM results showing the mean of the ranked dissimilarities between the two groups and within the pre-2000 and post-2000 groups for percent frequency of occurrence (a) and relative abundance (b) of loggerhead sea turtle prey items. There was a significant difference in the mean ranked dissimilarities of pre-and post-2000 groups for both percent frequency of occurrence (R statistic: 0.5494, p-value = 0.032) and relative abundance (R statistic: 0.7099, p-value = 0.009).

The best RDA model for both percent frequency of occurrence and relative abundance of prey items contained only the GSNW index. The GSNW index explained 23.5% of the species-environment relationship for percent frequency of occurrence, and 27.2% for relative abundance. As with the principal component analyses, all samples before 2000 showed negative values on the first axis of the redundancy analysis (RDA1) for both models, while samples after 2000 showed positive values of RDA1 (Figures 14 & 15), and both showed clustering of years before and after 2000, similar to NMDS results. GSNW index was positively correlated with RDA1, indicating that prey species associated with positive values of RDA1, such as Acadian hermit

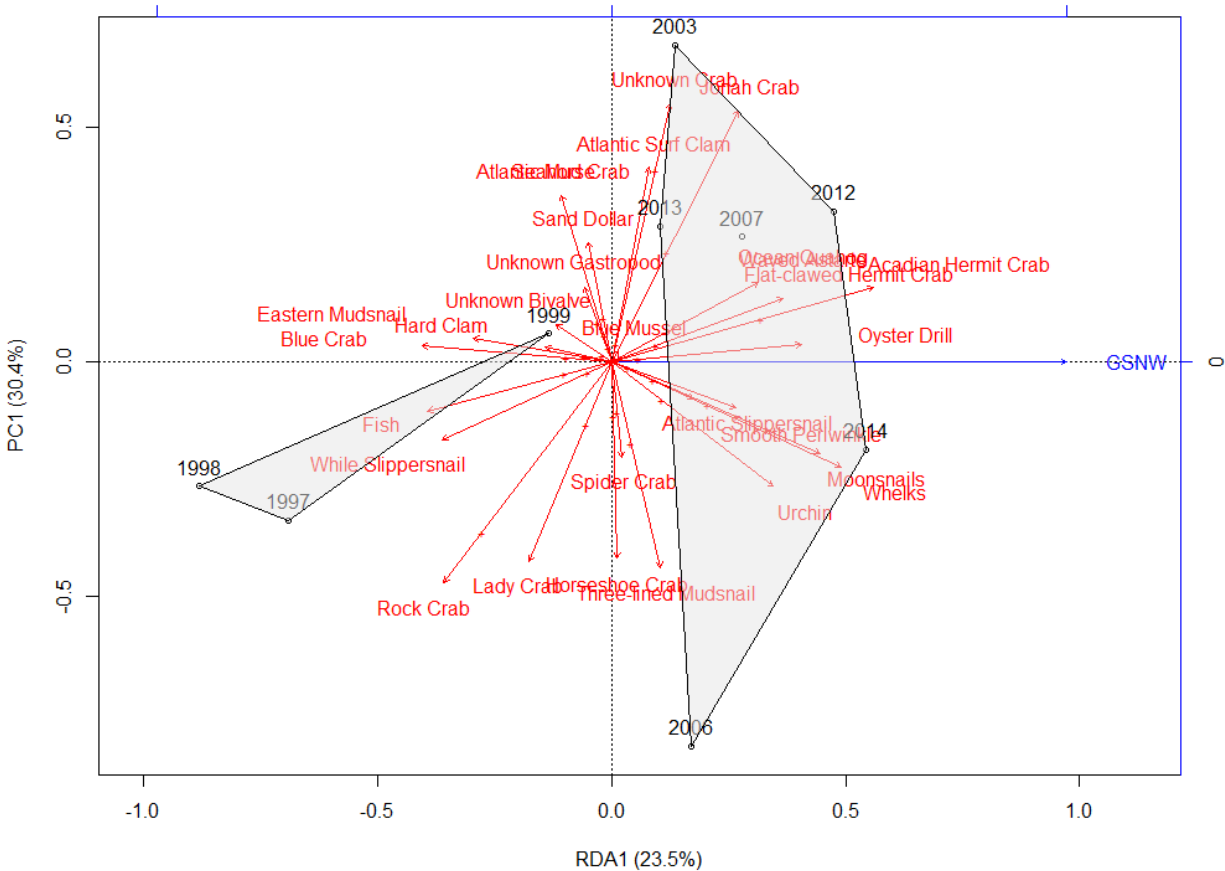


FIGURE 14. Biplot of RDA model with lowest AICc value for annual percent frequency of occurrence of loggerhead prey items. Red arrows denote species loadings relative to RDA1 and PC1 and blue arrow represents the environmental variable (GSNW). Grey polygons represent year clusters as observed in NMDS analysis.

crab and moonsnails and whelks in percent frequency of occurrence (Table 7a), and Acadian hermit crab and whelks in relative abundance (Table 7b), were not only associated with years after 2000, but also with higher values of the GSNW. Conversely, rock crab and blue crab were negatively associated with RDA1, for both percent frequency of occurrence and relative abundance, indicating that these species were more abundant in loggerhead diet in years before 2000 and were associated with lower values of the GSNW (Tables 7a & b).

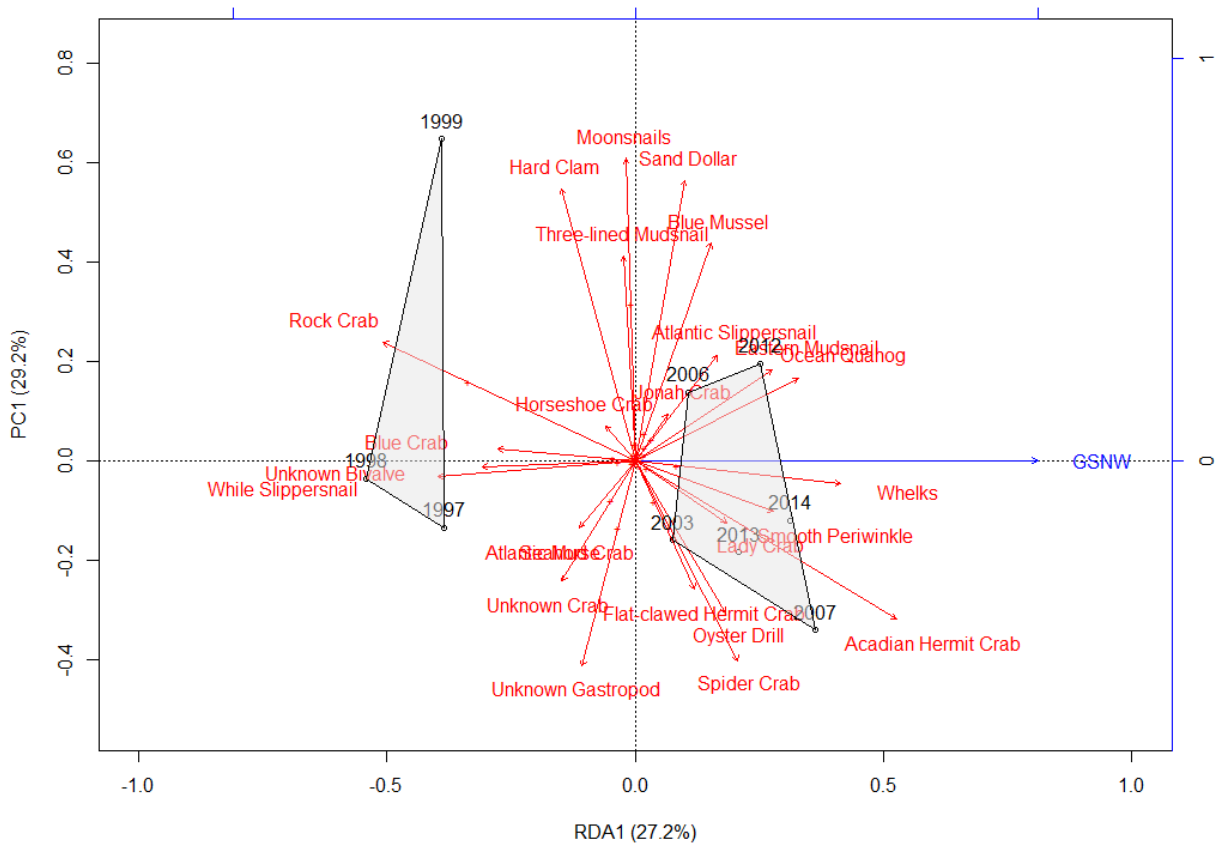


FIGURE 15. Biplot of RDA model with lowest AICc value for annual relative abundance of loggerhead prey items. Red arrows denote species loadings relative to RDA1 and PC1 and blue arrow represents the environmental variable (GSNW). Grey polygons represent year clusters as observed in NMDS analysis.

TABLE 7a. Species loading for RDA1 for annual percent frequency of occurrence RDA. Species are sorted from highest to lowest loading on RDA1

| | RDA1 |
|-------------------------|--------|
| Acadian Hermit Crab | 0.516 |
| Moonsnails | 0.430 |
| Whelks | 0.330 |
| Jonah Crab | 0.191 |
| Urchin | 0.173 |
| Flat-clawed Hermit Crab | 0.152 |
| Unknown Crab | 0.149 |
| Atlantic Slippersnail | 0.144 |
| Oyster Drill | 0.092 |
| Three-lined Mudsnaill | 0.067 |
| Smooth Periwinkle | 0.056 |
| Ocean Quahog | 0.025 |
| Waved Astarte | 0.025 |
| Spider Crab | 0.017 |
| Atlantic Surf Clam | 0.011 |
| Blue Mussel | 0.009 |
| Horseshoe Crab | 0.005 |
| Atlantic Mud Crab | -0.014 |
| Seahorse | -0.027 |
| Sand Dollar | -0.030 |
| Unknown Bivalve | -0.032 |
| Hard Clam | -0.039 |
| Unknown Gastropod | -0.050 |
| White Slippersnail | -0.084 |
| Lady Crab | -0.090 |
| Eastern Mudsnaill | -0.096 |
| Blue Crab | -0.161 |
| Fish | -0.167 |
| Rock Crab | -0.453 |

TABLE 7b. Species loading for RDA1 for annual relative abundance RDA. Species are sorted from highest to lowest loading on RDA1

| | RDA1 |
|-------------------------|--------|
| Acadian Hermit Crab | 0.518 |
| Whelks | 0.194 |
| Spider Crab | 0.161 |
| Flat-clawed Hermit Crab | 0.088 |
| Atlantic Slippersnail | 0.076 |
| Lady Crab | 0.051 |
| Blue Mussel | 0.043 |
| Jonah Crab | 0.041 |
| Eastern Mudsnaill | 0.035 |
| Oyster Drill | 0.014 |
| Smooth Periwinkle | 0.006 |
| Sand Dollar | 0.005 |
| Ocean Quahog | 0.000 |
| Three-lined Mudsnaill | -0.004 |
| Hard Clam | -0.006 |
| Seahorse | -0.008 |
| Atlantic Mud Crab | -0.013 |
| Horseshoe Crab | -0.014 |
| Unknown Bivalve | -0.019 |
| Moonsnails | -0.022 |
| Unknown Gastropod | -0.081 |
| White Slippersnail | -0.082 |
| Blue Crab | -0.105 |
| Unknown Crab | -0.113 |
| Rock Crab | -0.780 |

Spatial patterns in loggerhead sea turtle strandings

Analyses conducted on all loggerhead strandings in the Riverhead Foundation’s stranding database (1982 – 2016) showed that the vast majority of loggerhead sea turtles that stranded along Long Island Sound and Peconic and Gardiners Bays were juveniles (SCL < 80 cm), while mature sea turtles (>80 cm SCL) primarily stranded along beaches on the south shore of Long Island (Figure 16; 50.7% of juveniles stranded in Long Island Sound and Peconic and Gardiners Bays while 94.7% of adults stranded on the south shore).

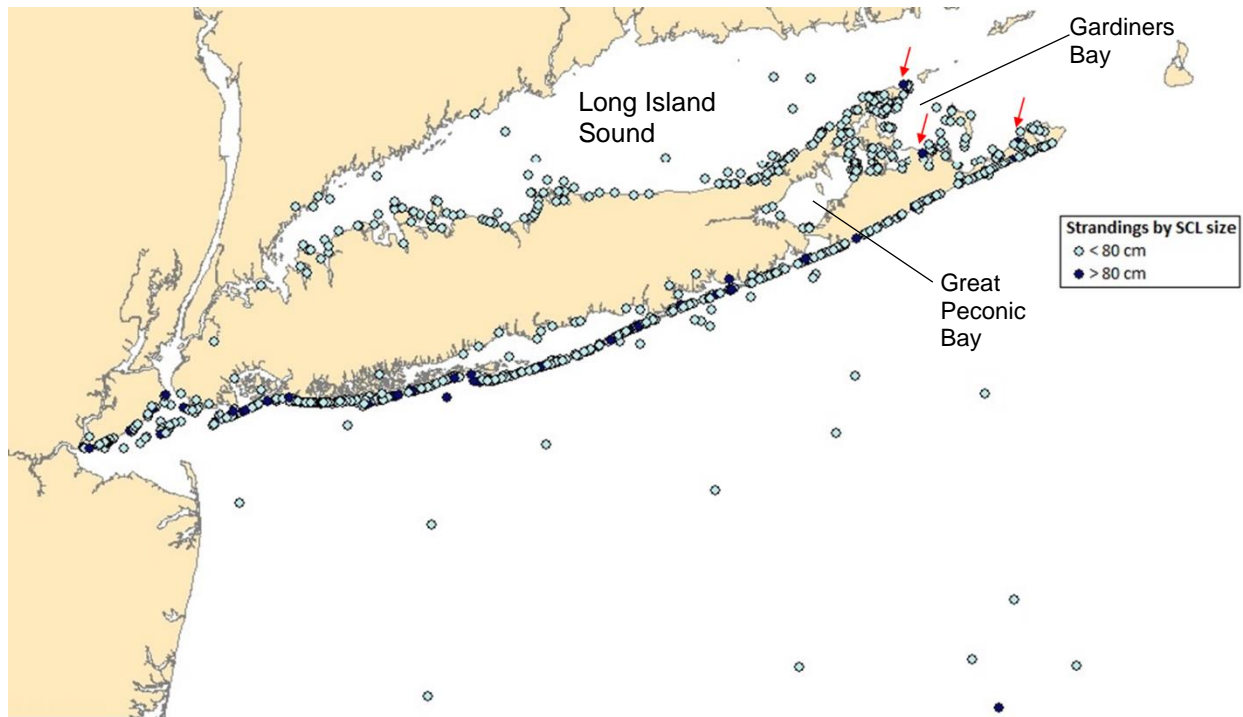


FIGURE 16. Map of all loggerhead strandings from 1982 – 2016 showing that all strandings occurring in Long Island Sound, Peconic Bay, and Gardiners Bay were turtles with a SCL of less than 80 cm (light blue circles), with the exception of three individuals (red arrows). Turtles with carapaces larger than 80 cm are dark blue circles.

DISCUSSION

Loggerhead sea turtle prey species

Results of my analysis suggest that the diet of loggerhead sea turtles in New York waters is dominated by crustaceans, particularly by hermit crabs, in terms of both the percent frequency of occurrence and the relative abundance of prey items observed. My results differed slightly from those observed in a previous study of loggerhead sea turtle diet on Long Island, which examined only a small number (25) of fecal samples from individuals captured in a single year (1989) in eastern Long Island bays (Burke et al. 1993). By only sampling loggerheads captured in the eastern bays of Long Island, the results of Burke et al. (1993) might not reflect the full range of prey items on which loggerheads are scavenging in New York waters. Burke et al. found that spider crabs were the most frequently observed prey item (occurring in approximately 70% of samples), followed by rock crabs and hermit crabs (occurring in 50% and 12% of samples, respectively). The prevalence of hermit crabs (size 2.5 cm) in my analysis suggests that loggerhead sea turtles may be consuming a larger number of smaller crustaceans more frequently in recent years, potentially due to a shift in available prey species in the benthic communities in loggerhead foraging habitat (Seney & Musick 2007, Younkin & Wyneken 2007; discussed in more detail below). This is further supported by the high relative abundance of small crabs (39.4% of diet) compared to medium and large crabs (15.2% combined).

Moonsnails were frequently observed in loggerhead sea turtle stomachs in the present study, however, the relative abundance of these gastropods might be misleading since hermit crabs are known to inhabit gastropods shells (Casale 2008b). The minimum number of moonsnails was calculated by the presence of opercula and/or shell spires, however only samples that had opercula present (54%) could be used to indicate that the mollusk was present in the

shell when the turtle ate it (Frick et al. 2001). Estimates of prey abundance in samples that included shell fragments containing the apex of the spire, but where opercula were not present, could lead to overestimation of the importance of moonsnails in loggerhead sea turtle diet. Moreover, with the exception of moonsnails and whelks, many of the gastropod species that were encountered in our samples were small species (e.g., the three-lined mud snail typically has a size of 1.9 cm, slipper snails are usually around 4 cm, etc.), indicating these prey items might have been accidentally consumed while turtles were preying on other more caloric species (Casale et al. 2008b, Lazar et al. 2011). For example, eastern mudsnails (*Tritia obsoleta*) are common in estuaries and are known scavengers of carrion (Kelaher et al. 2003). Loggerheads may forage for the same, larger prey items on which the mudsnail is scavenging. Similarly, slippersnails are known epibionts and can be found on top of shells that house hermit crabs (*C. fornicata*) or can even be present on the inside of shells inhabited by hermit crabs (*C. plana*) (Shenk & Karlson 1986). Thus, it is not possible to ascertain whether loggerheads were specifically foraging for these species, or whether these species were taken incidentally (Frick et al. 2001, Casale et al. 2008b).

Fish species and portunid crabs, such as blue crabs and lady crabs, were not frequently observed in loggerhead sea turtle stomachs. Blue crabs and lady crabs were each observed in 7% of the samples examined, and together made up less than 1% of the relative abundance of prey items observed. Similarly, while fish vertebrae were only found in 5% of the samples analyzed, the lack of otoliths and the large number of vertebrae present in the stomach samples (83 in one sample) suggests that loggerheads are not catching these fish alive and consuming them whole, but are probably opportunistically scavenging on carcasses of larger animals instead. This is likely because loggerheads are not believed to be fast enough to maneuver and catch fast-

swimming animals such as blue crabs and fish (Plotkin et al. 1993, Burke et al. 1994, Frick et al. 2001, Tomas et al. 2001, Youngkin & Wyneken 2007).

Stage-specific differences in diet and foraging habitat

As observed in previous studies, larger loggerhead sea turtles were found to have consumed a greater mean number of prey items than smaller turtles (Tomas et al. 2001, Youngkin & Wyneken 2007, Frick et al. 2009; though note that I could not compare the results of my multivariate analysis between large and small turtles because PCAs were performed on annually averaged data). This was expected, as large turtles have a greater stomach capacity and greater access to different foraging areas (Tomas et al. 2001, Frick et al. 2009). In addition, larger turtles on average ate significantly more gastropods overall, and particularly more moonsnails. Significant differences in the prey species consumed between larger and smaller individuals suggests that loggerheads might be partitioning their foraging habitats in New York waters, particularly since juvenile loggerheads are more frequently observed in shallow inshore estuaries, while adult turtles forage along the continental shelf (NMFS & USFWS 2008, NYSDOS 2013). Shark eye and northern moonsnails are extremely common in the coastal waters of the New York Bight (Quijón et al. 2007), supporting the idea that resource partitioning might be occurring between size classes of loggerheads.

Studies documenting intraspecific resource partitioning based on size-classes have also shown that larger animals forage at higher trophic levels and for larger sized prey items (Ortiz-Serrato et al. 2014, Nifong et al. 2015, Cloyed & Eason 2017). Larger loggerheads also ate significantly more horseshoe crabs than smaller turtles. Larger turtles have stronger jaws (Marshall et al. 2012), allowing them to eat larger and harder prey items such as horseshoe crabs,

whose size typically ranges from 30-60 cm (Weiss 1995, Martinez & Martinez 2003). I found no evidence that male and female loggerheads partition resources since no significant differences were observed in the mean number of prey consumed between large and small turtles based on sex, likely because loggerhead sea turtles do not exhibit sexual dimorphism in carapace size (Wibbbels et al. 1987, Casale et al. 2005, Ishihara & Kamezaki 2011). Comparisons between and among large and small female turtles and large and small male turtles also showed no significant difference in diversity. Diet diversity, however, is not necessarily a product of size alone. Scheel et al. (2016) proposed that substrate diversity, the size and abundance of prey items, and competition among predators are all factors that can affect prey diversity.

In addition to the observed differences in diet between juvenile and adult loggerheads, strandings of juvenile and adult loggerheads occurred in different locations, with juveniles stranding primarily along Long Island Sound and in shallow coastal bays, and adult turtles occurring along beaches on the south shore of Long Island. In the Atlantic loggerhead population, the shift from an oceanic life stage to a neritic one usually occurs in turtles of approximately 48.5 – 51.1 cm SCL (Snover 2000); however, the transition from oceanic to neritic waters might not be an instantaneous shift, but instead might take several attempts (McClellan et al. 2010). As loggerheads grow larger, their increased diving capacity allows them to forage in progressively deeper benthic habitats (Hochscheid et al. 2007, Casale et al. 2008b). As a result, smaller juveniles tend to start foraging in shallower inshore habitats (Hawkes et al. 2007, McClellan et al. 2010). The shallow, enclosed estuarine waters of Long Island Sound and Peconic and Gardiners Bays provide the environment necessary for juvenile turtles to transition into foraging in neritic habitats, while adult turtles that can dive deeper and for longer periods of time forage along the continental shelf (NMFS & USFWS 2008, NYSDOS 2013). Together, the

diet analysis and location of strandings suggest that loggerheads show intraspecific habitat partitioning based on life stage.

Temporal trends in loggerhead sea turtle diet

Multivariate analyses of loggerhead sea turtle diet between years indicated that distinct clusters were present in the years before and after 2000, indicating that a shift in diet took place between these time periods. This trend was consistently observed in the different analyses that I conducted, with similar findings observed in the PCA and RDA biplots for percent frequency of occurrence (samples in the 1990s loaded negatively on PC1 and RDA1 while samples after 2000 loaded positively with these axes). In terms of the most frequently observed prey items, this represents a shift in diet from rock crabs and spider crabs in the late 1990s to Acadian and flat-clawed hermit crabs, Jonah crabs and moonsnails after 2000. A similar trend was observed for the relative abundance of prey items, with a shift from rock crabs and moonsnails in the late 1990s to Acadian and flat-clawed hermit crabs, Jonah crabs, and whelks after 2000.

The high percent frequency of occurrence of rock crab and the lower percent frequency of occurrence of hermit crabs observed in the present study during the late 1990s are consistent with the findings of Burke et al. (1993). Abruzzo (2015) documented an increase in spider crabs in the Peconic from 1987 – 2012, which I observed in the NMDS results for percent frequency of occurrence, showing spider crabs clustered more closely with samples from after 2000. However, in terms of percent frequency of occurrence, spider crabs loaded slightly negatively on PC1 and were neutral with respect to RDA1, suggesting that spider crabs remained relatively constant in loggerhead sea turtle diet over the time period examined during this study.

The GSNW index correlated positively with RDA1 of both percent frequency of occurrence and relative abundance biplots, suggesting that observed interannual variability in prey items associated with these axes is related to the oscillating movement of the GSNW. Changes in species abundance due to movement of the GSNW have been documented along the northeast American coast in pelagic species: off Newfoundland, an increase in short-finned squid (*Illex illecebrosus*) abundance was correlated with the southward movement of the GSNW, as well as with a negative NAO phase (Dawe et al. 2000). Similarly, Atlantic salmon abundance in Georges Bank increased during cool AMO phases, which were correlated with the southward movement of the GSNW (Condron et al. 2005). In the Gulf of Maine, warming SST, which was related to the northward movement of the GSNW, negatively affected recruitment and resulted in increased mortality of Atlantic cod (*Gadus morhua*; Pershing et al. 2015). In the Slope Sea, increased duration and magnitude of phytoplankton blooms on the shelf break have been correlated with northward movements of the GSNW (Schollaerts et al. 2004), whereas the opposite trend was observed in offshore waters near the Gulf Stream (Sanchez-Franks & Zhang 2015). Lastly, in Narragansett Bay, an increased abundance in the diatom *Skeletonema costatum* was related to the southward movement of the GSNW (Borkman & Smayda 2009).

Some studies have documented changes in benthic species abundance correlated with environmental variables: in the Gulf of Mexico there were two distinct changes in blue crab abundance, which were linked to shifting hydrological conditions driven by AMO and NAO regime shifts (Sanchez-Rubio et al. 2011) and Colton et al. (2014) established there was a synchrony in interannual variability in blue crabs from Delaware Bay to Florida, and correlated that variability with changes in GSNW and southern winter temperatures. However, most studies predominantly examined the effects of temperature, without investigating possible relationships

with broader climate variables. In the Mid Atlantic Bight, warmer temperatures have been correlated with increased mortality in Atlantic surf clams (*Spisula solidissima*; Weinberg 2005, Narvaéz et al. 2015) and American lobster (*Homarus americanus*; Wahle et al. 2015), leading to bathymetric distributional shifts in both species (Weinberg 2005, Wahle et al. 2015). Johnson (2015), also documented blue crabs in the Gulf of Maine, where water temperatures have been rapidly increasing (Johnson 2015, Pershing et al. 2015), indicating a possible northward range expansion for this species. Vulnerability assessments by Hare et al. (2016) showed that overall, benthic invertebrates had very high climate vulnerability and had a moderate to high potential for distribution change, particularly in cancer crabs (rock and Jonah) and blue crabs.

The movement of the GSNW can influence the distribution of benthic organisms, and thus the composition of the benthic community in loggerhead foraging habitat. Rock crab and blue crab loaded negatively with GSNW for both percent frequency of occurrence and relative abundance, while Acadian hermit crab, moonsnails, whelks, and Jonah crab loaded positively with GSNW in the analysis of percent frequency of occurrence. With the exception of moonsnails, those same species loaded positively with GSNW for relative abundance. This indicates that species such as rock and blue crabs might be occurring less frequently or in lower numbers in NY waters when the GSNW index, and thus water temperature in this region, is high. Both rock crabs and Jonah crabs exhibit some form of thermotaxis, adjusting their position relative to their preferred temperature range of 15 – 18°C (Johns 1981, Lewis & Ayers 2004) and annual mean June – October temperatures were regularly higher than 18°C throughout the study period (19-23°C). Jonah crab larvae, however, are more resilient than rock crab larvae to higher temperatures (Sastry & McCarthy 1973), and Jonah crabs were found to occur in loggerhead sea turtle diet more frequently and in greater abundance when GSNW was high. Thus, it follows that

positive values of the GSNW index and higher temperatures observed since the early 2000's were associated with lower abundance and percent frequency of occurrence of rock crab in loggerhead sea turtle diet. This decreasing trend in rock crabs and increasing trend in Jonah crab in loggerhead diet are consistent with landings data for these species in New York (NOAA 2017). My analysis also showed that blue crabs occurred less frequently and at lower abundance after 2000, however, it is more difficult to explain the decrease in blue crabs in loggerhead diet. Blue crabs are a tropical species which can tolerate a wide range of temperatures and salinities (Cadman & Weinstein 1988, Rome et al. 2005). The abundance of this species should therefore not be negatively affected by increasing temperatures and the northward movement of the GSNW. Blue crabs were not frequently observed in the stomach samples analyzed, occurring in only 9 of the 123 samples analyzed, and thus loggerhead sea turtle diet might not be an ideal indicator for this particular species. However, results of my analysis are in agreement with landings data for blue crabs in New York, which show that the species has been steadily declining since the mid 1990's (NOAA 2017). Further research must be done to better understand drivers of the observed trends in blue crab abundance.

It is interesting to note that while GSNW was selected as an environmental variable for the best fit RDA models, AMO and NAO were not. The ecological effects of NAO and AMO shifts on community structure have been observed throughout the Northeastern Atlantic (Collie et al. 2008, Nye et al. 2009, Sanchez-Rubio et al. 2011, O'Connor et al. 2012, Nye et al. 2014, Friedland et al. 2014, Abruzzo 2015), with effects not only observed on an individual species level, but also through various trophic levels (Greene & Pershing 2003). Furthermore, both NAO and AMO are drivers of the latitudinal movement of the Gulf Stream (Taylor & Stephens 1998, Hurrell & Deser 2009, Nye et al 2014), so I expected these variables to also be included in the

optimal RDA model as explanatory variables of changes in loggerhead diet. In particular, I expected AMO to be an important predictor of loggerhead sea turtle diet since this variable was correlated with changes to the benthic community in Peconic Bay (Abruzzo 2015). It is possible that the effects of AMO are not evident in this study because the AMO shifted to a positive phase in the 1990's (Nye et al. 2014) and the samples in this study do not go back far enough to capture changes that might have occurred in the benthic community due to a shift in AMO. Similarly, effects of NAO may not have been evident in our samples since the effects of NAO are more pronounced in winter months (Hurrell 2003, Stenseth et al. 2003) and most of the samples in my analysis were from summer months.

Conclusions

My thesis research provides a much-needed description of loggerhead sea turtle diet in New York waters, and, importantly, describes variability in loggerhead diet over a 20-year period. A spatial assessment of loggerhead sea turtle strandings suggested that the majority of juvenile loggerheads use Long Island Sound and Peconic and Gardiners Bays as foraging areas, while mature loggerheads appear to forage in offshore waters, indicating that these habitats provide important stage-specific foraging habitats for loggerhead sea turtles. My analyses also indicate that observed diet shifts were likely temperature-driven, and in particular, were associated with variability in the Gulf Stream North Wall index. Results suggested that loggerhead diet showed two temporal clusters, before 2000 and after 2000, and that loggerhead diet shifted from larger prey species, such as rock crab, to smaller species, such as hermit crabs and moonsnails, between these time periods. Shifts in loggerhead diet reflected the availability of prey species in their benthic foraging grounds, indicating that prey species, rather than sea

turtles, show responses to changes in the position of the Gulf Stream. These findings are consistent with other studies investigating links between benthic communities and environmental variability in this region, suggesting that loggerhead diet can be used as an indicator of the relative abundance of benthic organisms. This work emphasizes the importance of analyzing long-term datasets in order to understand ecological change in the context of environmental variability, despite the obstacles associated with analyzing historical datasets.

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