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Long-term changes in loggerhead sea turtle diet indicate shifts in the benthic community associated with warming temperatures

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ABSTRACT

Long-term studies of marine communities are critical to understanding shifts in marine ecosystems in response to ecological change. We examined the diet of stranded loggerhead sea turtles (*Caretta caretta*) in New York waters between 1995 and 2014 using stomach content analysis, and quantified variability in loggerhead diet using Non-Metric Multidimensional Scaling (NMDS). Our results provide compelling evidence for a shift in the benthic community in New York waters associated with warming temperatures. We found two distinct clusters in loggerhead sea turtle diet, comprising samples in the years before and after 2000, respectively, indicating a temporal shift in prey composition after 2000. These patterns represented a shift from larger crab species such as rock crab (*Cancer irroratus*) and spider crab (*Libinia* spp.) to smaller crab species such as hermit crabs (*Pagurus* spp.) in recent years. Sea surface temperature (SST) in New York waters increased during the 20-year study period, and changes in SST and the position of the Gulf Stream were the most important environmental variables explaining variability in loggerhead sea turtle diet. Our results reflect the importance of long-term data collection in evaluating ecological responses to climate-driven warming, and highlight the utility of marine vertebrates as indicators of changes to lower trophic level organisms.

1. Introduction

Benthic communities play critical roles in marine ecosystems, regulating nutrient cycling and biogeochemical properties, controlling the decomposition of waste materials, providing habitat structure, influencing contaminant sequestering, and serving as a food source for higher trophic levels (Snelgrove, 1997; Covich et al., 1999; Reiss and Kröncke, 2005; Bremner et al., 2006; Norling et al., 2007). Further, many benthic marine organisms have limited motility and relatively long life spans, and can thus integrate environmental impacts over long time scales (Beuchel et al., 2006; Birchenough et al., 2015). Studying changes to benthic communities can therefore provide an improved understanding of biophysical links and ecosystem impacts of disturbance or environmental stress in coastal systems (Thrush and Dayton, 2002; Beuchel et al., 2006; Barnes and Conlan, 2007; Borja and Dauer, 2008; Hinz et al., 2009; Rombouts et al., 2013).

Long-term studies of benthic communities are critical to understanding the impacts of anthropogenic and environmental change on marine ecosystems (Kroncke et al., 1998; Frid et al., 2000; Currie and Small, 2005). However, collecting reliable long-term biodiversity datasets presents a number of challenges; datasets are typically time-consuming and expensive to collect, and survey objectives and methodologies may change through time (Magurran et al., 2010). The diet of marine predators can reflect underlying changes in the abundance and distribution of their prey (Montevecchi and Myers, 1996, 1997; Einoder, 2009), and can thus provide a fisheries-independent means of sampling the abundance of low- and mid-trophic level species in marine systems. Diet studies of generalist predators can be particularly useful for studying changes to the species composition of a given area since these predators vary their diet in response to fluctuations in the abundance of their prey (Korpimaki and Norrdahl, 1991; Ben-David et al., 1997; Votier et al., 2004).

Loggerhead sea turtles (*Caretta caretta*) are opportunistic carnivores that feed primarily on benthic invertebrates and freshly deceased fish (Plotkin et al., 1993; Tomas et al., 2001; Frick et al., 2009). They are long lived, slow growing, late to mature, and their lifespan is characterized by distinct ontogenetic shifts that are reflected in their habitat usage (Musick and Limpus, 1997; McClellan and Read, 2007). While loggerheads consume a variety of prey items, individual turtles have been found to specialize on a consistent mixture of prey species (Vander

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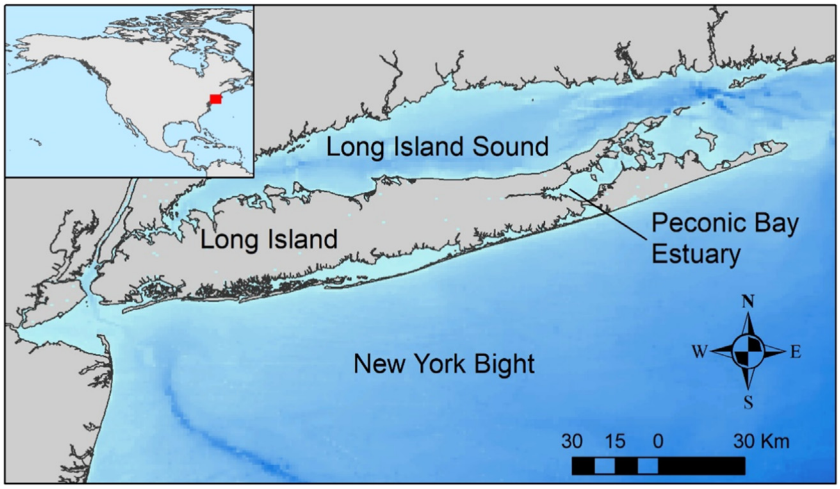

Fig. 1. Map of the study area.

Zanden et al., 2010). 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 and whelks are the predominant prey species for loggerheads in Core Sound in North Carolina (Wallace et al., 2009), while spider (*Libnia* spp.), stone (*Menippe mercenaria*), and hermit crabs (Paguridae family) are important prey species in Georgia (Frick et al., 2001; Youngkin and Wyneken, 2005), 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., 2007), to hermit crabs in the central Mediterranean (Casale et al., 2008a), to Mediterranean mussels (*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 the Northeast United States.

The Northwest Atlantic Distinct Population Segment (DPS) of loggerheads is listed as threatened under the US Endangered Species Act and faces anthropogenic threats such as fisheries bycatch, pollution and ecosystem alterations (Lutz and Musick, 1995; NMFS and USFWS, 2008; Bolten et al., 2011; USFWS and NOAA, 2011). In order to implement effective management strategies for this species, detailed knowledge of their at-sea habitat use, diet, and foraging behavior is needed. Assessing loggerhead diet and understanding the effects of trophic changes on loggerhead diet has been identified as a priority in the recovery plan for the Northwest Atlantic Population of loggerheads (NMFS and USFWS, 2008). Studying the diet of loggerhead sea turtles can not only shed light on how loggerheads are using their foraging grounds, but can also reveal shifts in benthic communities when studied over sufficiently long time frames (Youngkin and Wyneken, 2005; Seney and Musick, 2007). Decadal-scale changes to loggerhead sea turtle diet have been associated with changes in fishing pressure on benthic prey species (Seney and Musick, 2007), and variability in loggerhead diet could also be useful in assessing the impacts of environmental variability on benthic systems.

The Northeast United States Continental Shelf Large Marine Ecosystem (NEUS LME) is a highly productive coastal system that supports many commercially important fish and invertebrate species. The region has experienced rapid warming in recent decades, showing some of the highest rates of warming observed globally (Pershing et al., 2015). Effects of oceanographic and atmospheric change in the NEUS LME have been associated with distributional shifts and population dynamics of pelagic and demersal fishes (Hare and Able, 2007; Nye et al., 2009; Pershing et al., 2015; Kleisner et al., 2016), and likely have important effects on the benthic community. Within the NEUS LME, waters off the coast of Long Island, New York provide important seasonal foraging habitat for large juvenile loggerheads (Burke et al., 1993; Klinger and Musick, 1995; Morreale and Standora, 1998; Coles, 1999), though information on the diet and habitat use of loggerheads in this area is lacking (though see Burke et al., 1993). Since New York is located in the northernmost portion of the foraging range of juvenile loggerhead sea turtles (Shoop and Kenney, 1992; McClellan and Read, 2007; Mansfield et al., 2009), studying loggerheads in this region provides the opportunity to examine how climate-driven environmental variability influences their diet. Here, we evaluate samples and strandings data collected over a 20-year period to describe the diet of loggerhead sea turtles in New York waters, and to assess how changes in the diet of loggerhead sea turtles relate to oceanographic and atmospheric variability.

2. Methods

2.1. Study area

Loggerhead sea turtle foraging habitat in New York includes the offshore waters of the New York Bight, inshore estuaries and bays, as well as Long Island Sound (Fig. 1). These regions host diverse benthic habitats and support a wide array of benthic organisms (Morreale and Standora, 1998). The continental shelf in New York waters gently slopes from the shore to the shelf break (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 break (Williams et al., 2006; NYS DOS, 2013). The Long Island Sound reaches depths up to 70 m with coarse sediments in the eastern Sound and along the shoreline and finer sediments in the western and 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 (Schubel, 1991; Sagarese et al., 2011). Similarly, the Peconic Estuary system comprises a series of shallow bays composed of sand and muddy sediments, 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 and Standora, 1998; NYSDEC, 2017). Temperatures in the bays can range from 0 °C in the winter to 26 °C in the summer. Loggerheads typically arrive in these areas beginning in late May when temperatures are greater than 18 °C (Lutz et al., 2002), and leave by early November, when water temperatures decrease below 13 °C (Coles and Musick, 2000).

2.2. Sample collection

We examined 122 stomach samples collected by the Riverhead Foundation for Marine Research and Preservation from sea turtles that stranded in coastal New York and New Jersey from 1995 to 2014. Of these strandings, 29 showed definitive signs of human interaction; 23 showed evidence of boat strikes and 6 of fisheries interactions, such as fishing line or hooks. Samples up to 1999 were dried, while those from 2003 onward were frozen prior to analysis. While whole gastrointestinal (GI) tracts were preserved in some years, only prey items found in the stomach of these samples were used in the analyses to be consistent between samples. Samples that were severely decomposed or showed trauma to the abdominal cavity resulting in stomach contents outside of the GI tract were not included in the analyses. The stranding date, stranding location, sex, size (Straight Carapace Length (SCL)), and body condition were recorded both upon collection of the carcass and during a consequent necropsy, along with any evidence of human interactions (e.g., propeller scars, presence of fishing line and/or hooks, etc.).

Hard-bodied prey items, such as crab claws and gastropod opercula, were used to identify prey to the lowest possible taxonomic level. Soft tissues are more susceptible to degradation and could not be used to identify prey items (Plotkin et al., 1993; Burke et al., 1993; Godley et al., 1997; Seney and Musick, 2007). Due to difficulties in identifying some gastropod prey items to the species level, channeled (*Busycotypus canaliculatus*), waved (*Buccinum undatum*) and knobbed (*Busycon carica*) whelks were grouped together in analyses, while northern (*Euspira heros*), spotted (*Natica gualteriana*) and shark eye moonsnails (*Neverita duplicata*) were also analyzed together.

The results of our analysis (described in the Results section) suggested that smaller crab species were being taken more frequently, and larger crabs less frequently, in recent years included in the analysis. To further investigate this trend, we separated crabs into two groups in order to examine whether loggerheads were predominantly consuming large or small prey items. The actual size of consumed prey items could not be measured reliably because carapace pieces were too fragmented, and therefore groupings were based on the average size of these species in this area (Weiss, 1995; Martinez, 2003). Crabs with a maximum carapace width less than 5 cm, such as Acadian and Flat-clawed hermit crabs and Atlantic mud crabs, were considered to be small crabs, while large crabs were those greater than 5 cm, including rock, Jonah, lady, blue, and spider crabs (Supplementary Table 3).

We used species accumulation curves to determine whether a sufficient number of samples were analyzed each year in order to accurately represent loggerhead diet in New York waters. In addition, we compared strandings with stomach samples to the broader loggerhead strandings database maintained by the Riverhead Foundation for the same time period (1995–2014) to ensure that the stomach samples were representative of loggerhead sea turtles occurring in New York waters.

2.3. Environmental variables

We evaluated annual variability in the species composition of loggerhead sea turtle prey relative to several oceanographic and climatological metrics: the Atlantic Multi-decadal Oscillation (AMO), the North Atlantic Oscillation (NAO), the Gulf Stream North Wall (GSNW) index, and Sea Surface Temperature (SST) measured off the coast of Long Island. AMO is based on average SST anomalies and describes climate variability in the North Atlantic over multiple decades. The average period of the AMO is 60–80 years. Variability in AMO has been associated with fluctuations in the abundance, distribution and species composition of fish and invertebrates in the North Atlantic (Collie et al., 2008; Nye et al., 2009, 2014; Alheit et al., 2014). The NAO describes the difference in surface pressure between the subtropical high and the polar low. Positive values of the NAO reflect stronger values of the subtropical high and lower values of the polar low, and are associated with lower SSTs over the northwest Atlantic. NAO has been associated with recruitment, fluctuations and latitudinal shifts in plankton and fish populations in the North Atlantic (Sullivan et al., 2005; Lehodey et al., 2006; Dulvy et al., 2008; Collie et al., 2008). The GSNW index reflects the latitudinal position of the Gulf Stream (Taylor and Stephens, 1998). Gulf Stream dynamics have strong impacts on SST in the NEUS LME, and northward shifts in the position of the Gulf Stream result in increases in water temperatures on the continental shelf (Nye et al., 2011; Pershing et al., 2015). The position of the Gulf Stream has been associated with changes in the abundance of phytoplankton, variability in the distribution, landings, recruitment and mortality of fish, and latitudinal variability in the abundance of invertebrates in the NEUS LME (Schollaert et al., 2004; Borkman and Smayda, 2009; Nye et al., 2011; Colton et al., 2014; Pershing et al., 2015).

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). We included values of the NAO and AMO indices lagged by 0, 1 and 2 years in our analysis. We used the Taylor Index (Taylor and Stephens 1998) to indicate the position of the GSNW, downloaded from the Plymouth Marine Laboratory (http://www.pml-gulfstream.org.uk/Data%20Web2014.pdf). We used daily Group for High Resolution SST (GRHSST) images with a 0.25° resolution from June to October (when 98% of our strandings occurred) in each year. To examine how local SST in NY waters used by loggerheads varied through time, we evaluated the following variables in our analysis, calculated at the location of the center mean distribution of the sea turtle strandings: mean SST, minimum SST, maximum SST, and number of days over 15 °C (loggerhead sea turtles are thought to prefer waters above 15 °C; Witt et al., 2010).

2.4. Data analysis

We used Non-Metric Multidimensional Scaling (NMDS) to characterize variability in the species composition of prey in loggerhead stomach samples. NMDS is an ordination technique that aims to present the ranked distance relationship between samples in a small number of dimensions, with similar samples grouped closer together, and dissimilar items farther apart (Legendre and Legendre, 1998). We performed NMDS on the percent frequency of occurrence (defined as the percentage of samples in which the prey species was observed) for each prey species occurring within loggerhead sea turtle stomach samples on an annual time scale. We used the Bray-Curtis measures of dissimilarity, and included only data from years with species accumulation curves that approached or reached asymptotes in analyses to prevent spurious observations due to small sample sizes (117 samples collected over 9 years; Table 1).

In each sample, there were some prey species that could not be identified to the species level. Sea urchin parts and teleost fish vertebrae were occasionally observed in sea turtle stomach samples and could not be reliably identified to species. The categories “unidentified sea urchin” and “unidentified teleost fish” were included in the ordination since these categories were distinct from other categories of prey items. Crabs, bivalves and gastropods could typically be identified to the species level (we estimate that we were able to identify approximately 90% of crabs, 98% of bivalves and 80% of gastropods observed in our samples); however, unidentified crabs, bivalves and gastropods were not included as separate prey categories in the ordination since these categories were likely to include species that were identified and assessed separately and could therefore not be considered distinct groupings.

Table 1
Characteristics of samples used in NMDS analysis by year. N, sample size, Mean SCL = Mean Straight Carapace Length. Loggerhead sea turtles < 80 cm SCL were considered to be juveniles.

Year	N	Mean SCL	Prop. Juveniles	Prop. Females
1997	15	63.02	0.73	0.50
1998	9	65.49	0.78	1.00
1999	7	64.83	0.71	1.00
2003	15	65.53	0.93	0.67
2006	9	73.32	0.78	0.67
2007	17	67.55	0.88	0.71
2012	24	64.63	0.83	0.73
2013	12	63.04	0.83	0.70
2014	9	67.13	0.89	0.86
TOTAL	117	65.87	0.82	0.71

We estimated the goodness of fit of the ordination using the stress statistic; stress ranges from 0 to 1 and values close to zero indicate a good fit (Dangles et al., 2004). We then performed k-means cluster analysis to examine temporal trends in NMDS results and assessed differences in clusters using analysis of similarities (ANOSIM), which compares mean ranked dissimilarities within and between groups (the R parameter represents the degree of separation between the groups). We selected the best subset of environmental variables to explain variability in sea turtle diet samples by maximizing the rank correlations between similarity matrices. We then assessed effects of oceanographic and atmospheric variables on the species composition of prey in loggerhead diet by fitting vectors onto ordination plots using the “envfit” function, including only variables with strong ($r^2 > 0.50$) and significant correlations ($p < 0.10$), assessed using 1000 permutations (Strohbach et al., 2009). We also assessed the relationships between environmental variables and prey species observed in loggerhead stomach samples using Mantel's tests with 1000 permutations. All analyses were conducted in the R Version 3.3.2 (R Core Team, 2017) using the ‘vegan’ library (version 2.4–6; Oksanen, 2015).

3. Results

3.1. Loggerhead sea turtle diet

We found that strandings with stomach samples were of similar size (mean SCL of 65.5 cm for strandings with stomach samples and 62.8 cm for all recorded strandings), and that the majority of samples and strandings were juveniles (SCL < 80 cm; 82% for strandings with stomach samples, 89% for all strandings in the database; Table 1). Similarly, the majority of both groups were females (strandings with stomach samples were 71% female, while 75% of all strandings were females).

Crustaceans dominated loggerhead sea turtle diet in New York waters, occurring in 95% of the samples. Acadian hermit crab (*Pagurus acadianus*), Jonah crab (*Cancer borealis*), moonsnails, flat-clawed hermit crab (*Pagurus pollicaris*), rock crab (*Cancer irroratus*) and spider crabs (*Libinia* spp.) were the most frequently observed crustaceans (Table 2). Gastropods were also prevalent, occurring in 63% of samples, while bivalves, echinoderms, chordates and horseshoe crabs were observed less frequently (Table 2). 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. At broad taxonomic levels (e.g., crustaceans, bivalves, gastropods), there were no marked changes in the percent frequency of occurrence through time (Table 2). However, when changes in diet samples were examined at the lowest taxonomic level possible, shifts in the species composition of sea turtle diet became apparent.

3.2. Trends in loggerhead sea turtle prey species composition

A convergent solution was found for the NMDS model with a stress value of 0.11, indicating that the model had a good fit with the data. The NMDS analysis showed that loggerhead sea turtle stomach samples were grouped into two distinct clusters, one representing samples collected in the years before 2000 (n = 3), and one representing the years after 2000 (n = 6) (Fig. 2). ANOSIM results showed a significant difference between the mean ranked dissimilarities of pre-and post-2000 clusters (ANOSIM R-statistic: 0.65, p-value = 1.40×10^{-2}). The GSNW index and the number of days over 15 °C were the only variables in the final subset of environmental variables used to explain variability in sea turtle diet, and the Mantel's test indicated a significant correlation between these variables and loggerhead prey species (Mantel r-statistic = 0.51, p = 7.00×10^{-3}). SST at the center of mean distribution for loggerhead sea turtle strandings increased significantly over the 20-year study period (Pearson's correlation = 0.55, p = 0.012). GSNW varied considerably over the years in which stomach samples were collected, ranging from −0.60 in 1998 to 0.82 in 2012, representing extreme southern and northern latitudinal limits of the Gulf Stream, respectively (Borkman and Smayda, 2009). The highest values of GSNW were associated with warm SST values throughout the NEUS LME (Fig. 3). On average, in the years before 2000, there were 146 days over 15 °C, and the GSNW was negative in all years included in the analysis, while after 2000 there were 155 days over 15 °C and the GSNW was positive in 71% of years included in the analysis. The post-2000 cluster of sea turtle stomach samples was associated with higher GSNW values and a higher number of days over 15 °C and prey species closely associated with this cluster, such as Acadian and flat-clawed hermit crabs, Jonah crabs, and moonsnails, were observed more frequently (Fig. 2b). Conversely, species that clustered more closely with the pre-2000 cluster, such as blue crabs, rock crabs, and blue mussels, occurred more frequently in the years before 2000, and were associated with years with lower values of GSNW and a lower number of days of 15 °C (Fig. 2b).

We focused further analyses on crab species since these species dominated the diet of loggerhead sea turtles and because individual crab species were observed frequently enough that changes in their occurrence could be assessed through time. Individual bivalve and gastropod species were not taken frequently (occurring, on average, in less than 11% of samples for bivalves and less than 20% of samples for gastropods; Table 2). Loggerhead sea turtle diet typically included larger species before 2000, and smaller species after 2000; before 2000, small crabs occurred in 42% of samples, while large crabs occurred in 62% of samples. After 2000, small crabs were observed in 72% of samples, while large crabs were observed in 45% of samples.

4. Discussion

We found distinct clusters in the prey species of loggerhead sea turtle diet in the years before and after 2000, indicating that a shift in diet took place between these time periods. Rock crabs, blue crabs, lady crabs and blue mussels were taken by loggerheads more frequently in the late 1990s, while Acadian and flat-clawed hermit crabs, Jonah crabs and moonsnails were taken more frequently after 2000 (Fig. 2, Table 2). These findings were in agreement with trends observed in landings data; landings of rock and blue crabs have decreased, while landings of Jonah crabs have increased during this time period (NOAA, 2017). Our results were also consistent with a study using data from bottom trawls conducted in the Peconic Bay estuary on the eastern end of Long Island, which demonstrated a shift in the dominant species in the benthic community in the year 2000 (Abruzzo, 2015). Different components of the benthic community were examined in Abruzzo (2015); Abruzzo (2015) primarily observed shifts in fish species, while we observed shifts primarily in species of crustaceans. Despite the limited number of years in our analyses, restricted by the number and condition of

Table 2
Summary of percent frequency of occurrence for prey items identified in the stomachs of stranded loggerhead sea turtles used in the analysis (n = 117). Small crabs were species with a maximum carapace width < 5 cm, while large crabs were those with a maximum carapace width > 5 cm.

Taxa	Species name	Abbreviation	% Frequency Occurrence		
			Before 2000	After 2000	All years
Crustaceans			100.00%	93.33%	95.11%
Decapods			100.00%	93.33%	95.11%
Small crabs			41.93%	61.29%	54.84%
Large crabs			72.09%	44.77%	53.88%
Acadian Hermit Crab	*Pagurus acadianus*	ACHE	30.30%	60.00%	52.03%
Flat-clawed Hermit Crab	*Pagurus pollicaris*	FCHE	24.24%	38.89%	34.96%
Jonah Crab	*Cancer borealis*	JOCR	30.30%	46.67%	42.28%
Rock Crab	*Cancer irroratus*	ROCR	63.64%	23.33%	34.15%
Spider Crab	*Libinia* spp.	SPCR	33.33%	21.11%	24.39%
Blue Crab	*Callinectes sapidus*	BLCR	12.12%	5.56%	7.32%
Lady Crab	*Ovalipes ocellatus*	LACR	15.15%	3.33%	6.50%
Atlantic Mud Crab	*Panopeus herbstii*	ANCR	0.00%	2.22%	1.63%
Chelicerates					
Horseshoe Crab	*Limulus polyphemus*	HRCR	3.03%	3.33%	3.25%
Mollusks			66.67%	68.89%	68.29%
Bivalves			21.21%	12.22%	14.63%
Blue Mussel	*Mytilus edulis*	BLMU	15.15%	8.89%	10.57%
Hard Clam	*Mercenaria mercenaria*	HACL	3.03%	0.00%	0.81%
Ocean Quahog	*Arctica islandica*	OCQU	0.00%	1.11%	0.81%
Atlantic Surf Clam	*Spisula solidissima*	ASCL	0.00%	2.22%	1.63%
Waved Astarte	*Astarte undata*	WAAS	0.00%	1.11%	0.81%
Gastropods			60.61%	64.44%	63.41%
Moonsnails	Naticidae	MOON	9.09%	23.33%	19.51%
Whelks	Buccinidae	WHLK	3.03%	13.33%	10.57%
Three-lined Mudsnail	*Tritia trivittata*	TLMU	15.15%	8.89%	10.57%
Eastern Mudsnail	*Tritia obsoleta*	EAMU	6.06%	2.22%	3.25%
Atlantic Oyster Drill	*Urosalpinx cinera*	OYDR	9.09%	8.89%	8.94%
Common Atlantic Slippersnail	*Crepidula fornicata*	ALSL	6.06%	11.11%	1.63%
Eastern White Slippersnail	*Crepidula plana*	WHSL	0.00%	4.44%	3.25%
Smooth Periwinkle	*Littorina obtusata*	SMPE	0.00%	1.11%	0.81%
Chordata			9.09%	5.56%	6.50%
Lined seahorse	*Hippocampus erectus*	UNSH	0.00%	2.22%	1.63%
Teleost fish		UNFI	9.09%	3.33%	4.88%
Echinoderms			3.03%	12.22%	9.76%
Common Sand Dollar	*Echinarachnius parma*	SADO	3.03%	4.44%	4.07%
Unidentified Sea Urchin		UNUR	0.00%	7.78%	5.69%
Marine Debris			18.18%	22.22%	21.38%

samples that were available, the fact that shifts in the benthic community were observed at the same time in both studies suggests broad-scale change, impacting different functional groups, might be underlying these trends.

Within the NEUS LME, temperatures have risen dramatically in recent years in association with a northward shift in the Gulf Stream, with particularly warm conditions observed during the "heat wave" observed in this region in 2012 (Belkin, 2009; Mills et al., 2013; Pershing et al., 2015). This was also true in our study area in coastal New York; SST increased significantly over the 20-year study period and SST at the center of mean distribution of loggerhead strandings in 2012 was nearly 2 °C higher than the mean for 1995–1999. Warming conditions can cause shifts in the distribution of marine fishes and invertebrates, as well as phenological changes and effects on abundance and mortality (Edward and Richardson, 2004; Nye et al., 2009; Cheung et al., 2013a). Within the NEUS LME, a climate vulnerability assessment of fish and invertebrate species found that benthic invertebrates, along with diadromous fish, show the greatest vulnerability to change (Hare et al., 2016). Our findings suggest a shift in the benthic assemblage in New York waters that was strongly associated with variability in SST and the position of the Gulf Stream. Prey species that dominated sea turtle diets after 2000 were associated with higher SST values and higher values of the GSNW index. However, the observed change in the benthic assemblage cannot be explained simply in terms of shifts in the distribution of warm and cool water species; many of the prey species taken by sea turtles, including Jonah crabs, rock crabs, and lady crabs, occur across a wide latitudinal range, and New York occurs in the central part of their range. Rather, the shift in loggerhead sea turtle diet generally represented a decrease in size classes of crab species taken after 2000 (Table 1). The observed decrease in the proportion of turtles taking large crab species was further supported by a comparison with the results of an earlier study by Burke et al. (1993), who studied loggerhead sea turtle diet in a single year (1989) in Peconic Bay on eastern Long Island. Large crabs such as spider crabs dominated loggerhead sea turtle diet in Burke et al. (1993) and were observed in a larger proportion of samples than in our samples collected before and after 2000 (70% of samples in Burke et al. (1993), 33% in our pre-2000 samples, representing the mid-to late-1990s, and 21% in our post-2000 samples). The proportion of samples containing small crabs such as hermit crabs was considerably lower in the Burke et al. study (12%) than in our study (42% before 2000, 71% after 2000). Analyses of long-term datasets in marine and aquatic ecosystems have demonstrated decreases in body size with warming temperatures (Daufresne et al., 2009; Irie and Fischer, 2009; Sheridan and Bickford, 2011; Cheung et al., 2013a; b; Ohlberger, 2013). Warming can also lead to composition shifts that alter mean body sizes within a community due to changes in the distribution of species of different sizes (i.e., a higher abundance of small-bodied species; Daufresne et al., 2009; Ohlberger,

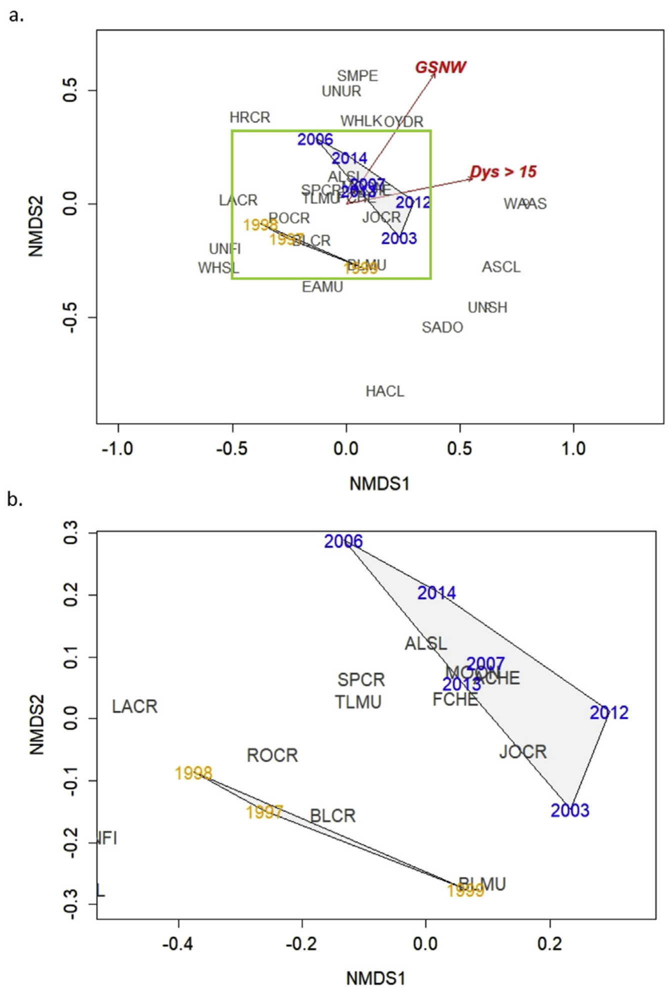

Fig. 2. Biplot of NMDS model for annual percent frequency of occurrence of loggerhead sea turtle prey items. (a) Shows the full extent of the NMDS axes, while (b) shows the region indicated by the green box in (a) in detail. There were two distinct clusters based on year, one containing samples from the years before 2000 (orange), and one with years after 2000 (blue). Species located near the clusters were more commonly observed during those time periods. Red arrows in (a) represent environmental vectors in the final model fitted into NMDS space. Species abbreviations as indicated in Table 2. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

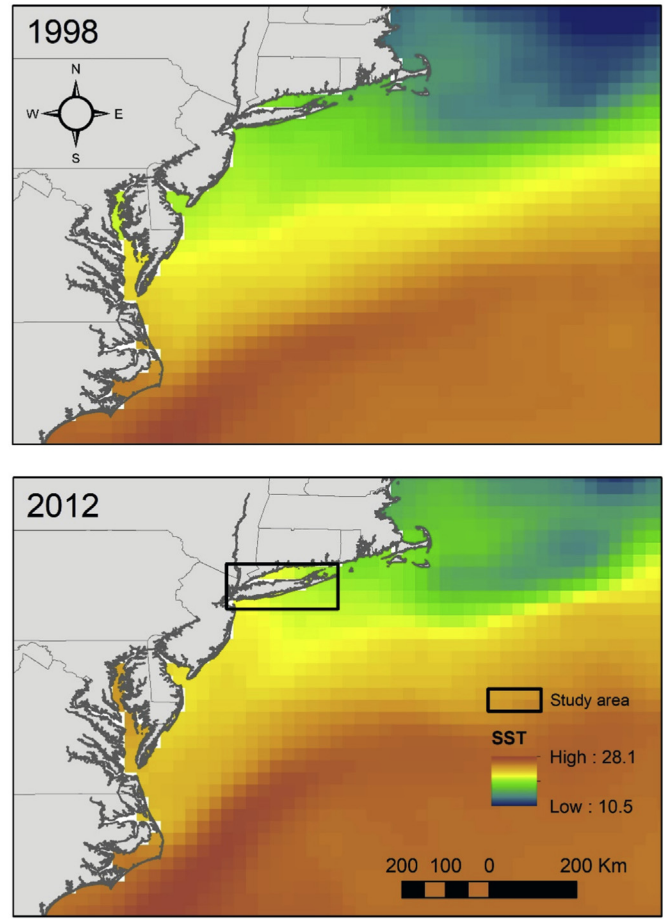

Fig. 3. Satellite Sea Surface Temperature (SST) in the Northeast United States Large Marine Ecosystem (NEUS LME) in the years with the lowest (1998) and highest values (2012) of the Gulf Stream North Wall Index during the study period (1995–2012). A heat wave occurred in the NEUS LME in 2012, and SST values in the study area were considerably higher in 2012 than in 1998 (mean SST value of 19.5 °C [range 13.2–23.6 °C] in June–October of 1998 vs. 21.40 °C [range 14.80–26.04 °C] in 2012).

2013). Several studies have suggested that a shift in the size spectrum of communities in marine and aquatic environments due to warming temperatures can lead to declines in the abundance of large organisms from species to community levels (e.g., Petchey et al., 1999; Yvon-Durocher et al., 2011; Dossena et al., 2012). Our results suggest that smaller crab species may have become more abundant in New York waters after 2000, and future targeted sampling could investigate this pattern in more detail.

Results of our analyses suggest that the diet of loggerhead sea turtles in New York waters is dominated by crustaceans and particularly by hermit crabs. While species of gastropods were observed in most sea turtle stomach samples analyzed (63% of all samples), on a species level, most gastropods observed in our samples occurred in less than 10% of samples. With the exception of moonsnails and whelks, we believe these prey items might have been accidentally consumed while turtles were preying on other more caloric species (Casale et al., 2008a; Lazar et al., 2011). Though moonsnails and whelks were observed more frequently than most other species of gastropod, the importance of these gastropods in loggerhead diet might be misleading. Hermit crabs are known to inhabit gastropod shells, so it is not possible to ascertain whether loggerheads were specifically foraging for gastropod species, or whether gastropods were taken incidentally (Frick et al., 2001; Casale et al., 2008b).

Trophic changes influencing prey availability are of concern for loggerhead sea turtles (NMFS and USFWS, 2008). Diet shifts induced by fishery-driven changes in species abundance have been demonstrated for loggerheads (Seney and Musick, 2007), and impacts of fisheries on trophic structure and habitat alteration have been identified as a threat to the species. However, our results suggest that ecological change driven by changes in oceanography can also lead to shifts in loggerhead diet. The observed diet shift, which generally represented a shift from larger to smaller crab species, merits further investigation; a diet composed of smaller prey items may require an increased handling time and could lower the energy intake per unit effort for a foraging predator (Davoren and Montevecchi, 2003; Becker and Beissinger, 2006; Norris et al., 2007; Van Deurs et al., 2015). However, it is important to consider both the prey size and the energy density of the prey in order to understand the broader implications of a diet shift. While carapace pieces were too fragmented to measure the size of individual prey items in loggerhead samples in the present study, future studies could attempt to estimate prey size using intact body parts (e.g., the length of the propodus) in order to more accurately examine prey size distribution. Further studies of loggerhead sea turtle diet along with studies of the energy density of prey items would illuminate whether loggerheads continue to take smaller crabs more frequently as NY waters become increasingly warm, and would provide a more detailed picture of the energetic consequences of the observed diet shift.

Studying the diets of marine predators can provide an effective means of assessing ecosystem change at lower trophic levels. Data from marine predators have been used to provide an index of the abundance of fish and invertebrates (Cairns, 1988; Montevecchi and Myers, 1995; Reid et al., 2005; Mills et al., 2007; Piatt et al., 2007) and to elucidate the effects of physical regime shifts on multiple trophic levels (Francis et al., 1998; Diamond and Devlin, 2003). Shifts in loggerhead sea turtle diet have previously been linked with long-term changes in prey availability associated with fishing pressure (Youngkin and Wyneken, 2005; Seney and Musick, 2007). In Virginia, Seney and Musick (2007) observed a shift in loggerhead diet from horseshoe crabs (*Limulus polyphemus*) in the 1980s, to blue crabs in the early 1990s, to finfish (*Brevoortia tyrannus* and *Micropogonias undulatus*) in the late 1990s and early 2000s, reflecting changes in the abundance of prey. In the present study, shifts in sea turtle diet were reflective of changes in the abundance of benthic organisms due to warming temperatures in coastal waters (Abruzzo, 2015), emphasizing that sea turtle diet can be used as a tool to link broad patterns in lower-trophic level species with ecological change.

Benthic organisms are typically sampled with bottom trawls and benthic grabs, which provide point data that are specific to a particular location and time. Long-lived, mobile marine vertebrates such as loggerhead sea turtles can integrate resources such as benthic prey items over space and time, and as such can provide information about broad-scale patterns of ecological change (e.g., Montevecchi and Myers, 1996, 1997; Shaffer et al., 2006; Wallace et al., 2006; Piatt et al., 2007). In addition, studying the diet of marine predators can provide information on species that are not effectively sampled by conventional methods (Olson et al., 2014). We found that loggerhead sea turtles frequently took small prey items, such as gastropods and hermit crabs, in years after 2000. Since these species are not the target of commercial fisheries and are not effectively sampled using sampling methodologies such as bottom trawls, there are limited data on their abundance and distribution. By providing a fisheries-independent means of sampling the marine environment, studies examining the diets of marine predators can also provide important information on trends in small or understudied species.

We assessed sea turtle diet at the species level, and the long-term trends that we observed would not have been evident had we examined variability in diet at a coarser scale. For example, while previous studies found differences in sea turtle diet based on broad taxonomic prey groups (e.g., horseshoe crabs, crustaceans, mollusks, fish; Seney and Musick, 2007), we found limited variability in sea turtle diet across broad taxonomic or functional groups throughout the study period. Examining sea turtle prey items at the species level and assessing patterns in diet using ordination allowed us to investigate trends in sea turtle diet relative to ecological change at the community level. Whether it is best to examine individual prey species, functional groups, or community-level variability in prey species will depend on the characteristics of the predator, the study region, and the prey community. Since the diet of loggerhead sea turtles in New York was found to be dominated by crabs, both in the present study and in previous studies (Burke et al., 1993), examining community-level metrics rather than comparing functional groups of prey items was a more appropriate means of characterizing variability in diet.

This study provided a much-needed description of loggerhead sea turtle diet in New York waters, but our approach included limitations. Firstly, this research used stomach contents analysis of dead stranded turtled to describe loggerhead sea turtle diet, which allows prey to be identified to species but could introduce a source of bias in the results. Animals might not have been foraging under normal conditions immediately before death, and thus stomach contents may not reflect the animal's typical diet (Revelles et al., 2007). In the present study, necropsied animals were robust and had adequate levels of adipose tissue; thus we believe that samples used in these analyses were likely from healthy animals who suffered acute deaths. However, stomach content analysis also tends to be biased towards benthic prey items in nearshore environments and their hard, indigestible parts (Plotkin et al., 1993; Revelles et al., 2007; Casale et al., 2008a) and only provides information on diet over short time scales (days) (Revelles et al., 2007); loggerhead sea turtles take approximately 2.5–3 days to fully digest prey items (Casale et al., 2008b). Secondly, our analysis included fewer years of observations from before the diet shift was observed (3) in comparison to the number of years of observations after the shift was observed (6). A more even distribution of samples from before and after the observed shift would have been preferable, though our study was limited by the availability of previously collected samples. Lastly, our analysis did not examine the effects of other factors, such as stranding season, size or sex in detail. Preliminary analyses suggested that prey items consumed were similar between male and female and large and small turtles, and the vast majority of the samples included in the analysis (81%) were from summer months (June through August). However, future studies could focus sampling efforts so as to investigate effects of these factors in more detail.

Together, our results provide compelling evidence for a shift in the benthic community in New York waters associated with warming sea surface temperatures over a 20-year period. Understanding links between marine communities and climate-driven change is critical to predicting ecosystem responses to future warming, and assessing the diet of marine vertebrates can provide a powerful means of examining broad patterns in lower trophic levels. Our results emphasize the importance of collecting and maintaining long-term datasets in order to understand ecological change in the context of environmental variability.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecss.2018.12.008.

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