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Feeding dynamics of Northwest Atlantic small pelagic fishes

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ABSTRACT

Small pelagic fishes represent a critical link between zooplankton and large predators. Yet, the taxonomic resolution of the diets of these important fishes is often limited, especially in the Northwest Atlantic. We examined the diets, along with stable isotope signatures, of five dominant small pelagic species of the northeast US continental shelf ecosystem (Atlantic mackerel *Scomber scombrus*, Atlantic herring *Clupea harengus*, alewife *Alosa pseudoharengus*, blueback herring *Alosa aestivalis*, and Atlantic butterfish *Peprilus triacanthus*). Diet analyses revealed strong seasonal differences in most species. Small pelagic fishes predominantly consumed *Calanus* copepods, small copepod genera (*Pseudocalanus/Paracalanus/Clausocalanus*), and *Centropages* copepods in the spring, with appendicularians also important by number for most species. Krill, primarily *Meganyctiphanes norvegica*, and hyperiid amphipods of the genera *Hyperia* and *Parathemisto* were common in the stomach contents of four of the five species in the fall, with hyperiids common in the stomach contents of butterfish in both seasons and krill common in the stomach contents of alewife in both seasons. Depth and region were also found to be sources of variability in the diets of Atlantic mackerel, Atlantic herring, and alewife (region but not depth) with krill being more often in the diet of alewife in more northerly locations, primarily the Gulf of Maine. Stable isotope data corroborate the seasonal differences in diet but overlap of isotopic niche space contrasts that of dietary overlap, highlighting the differences in the two methods. Overall, the seasonal variability and consumer-specific diets of small pelagic fishes are important for understanding how changes in the zooplankton community could influence higher trophic levels.

1. Introduction

Small pelagic fishes are also known as ‘forage fishes’ because of their important role as prey in many marine ecosystems. These fishes occupy a critical trophic position—one that links planktonic production to a high diversity of upper trophic level consumers. In the Northwest Atlantic, such consumers include ecologically and economically important piscivorous fishes such as Atlantic bluefin tuna (*Thunnus thynnus*) and cod (*Gadus morhua*), several species of sharks, seabirds, pinnipeds, and whales (Powers and Backus, 1987; Montevecchi and Myers, 1996; Baraff and Loughlin, 2000; Chase, 2002; Link and Garrison, 2002; Overholtz and Link, 2007). Small pelagic fishes have been identified as some of the most important organisms in marine food webs, as, in certain ecosystems such as upwelling regions, their abundance may affect the populations of organisms at trophic levels both above and below them (Cury et al., 2000; Lindegren et al., 2018). These “wasp-waist” ecosystems, where the low diversity of small pelagic fishes represents the narrow waist of a wasp, can also occur in coastal regions such as the Northwest Atlantic shelf, though the benthopelagic nature of many organisms in this ecosystem cause the higher trophic levels of the Northwest Atlantic to be less dependent on these planktivorous fishes than typical “wasp-waist” ecosystems (Cury et al., 2000; Link, 2002; Bakun et al., 2009).

Small pelagic fishes are often short-lived and mature early, resulting in species abundances that exhibit large fluctuations, often out of synchrony with each other (Skud, 1982; Schwartzlose and Alheit, 1999; Richardson et al., 2014). Much research has focused on understanding the drivers of these population fluctuations, primarily including how

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climatic variability results in the differential recruitment of these fishes via effects on planktonic prey availability (Toresen and Østvedt, 2000; Chavez et al., 2003). Evidence of changes to small pelagic communities comes from studies in European waters, where the distributions of small pelagics are changing throughout the Northeast Atlantic and may be responding to long-scale climatic variability such as the Atlantic Multidecadal Oscillation (ICES, 2012). Classic food web theory suggests that these organisms, when abundant enough, may exert top down control on their prey, which means subsequent regime shifts in zooplankton communities could occur if small pelagic fish populations change (Turner and Mittelbach, 1990; Pace et al., 1999; Frank et al., 2005; Frank et al., 2011). However, the impact of planktivores on zooplankton and top predators varies within the broader Northwest Atlantic region, with clear cascading top-down effects from overfishing occurring on the Scotian Shelf (Frank et al., 2005) but much more muted and intricate effects of overfishing on the ecosystems of the Gulf of Maine and Georges Bank, suggesting a more bottom-up driven system (Link, 2002; Link et al., 2009; Greene, 2013). The more complex system in the Northeast US shelf results from the large degree of omnivory and generalist feeding of many predators in this system, and thus the system is likely robust to removal of highly connected species (Link, 2002; Dunne et al., 2004).

Understanding whether changes to prey availability may result in changes to the small pelagic fish community is a pressing need, as recent studies have already demonstrated the early signs of changing zooplankton communities in the Northwest Atlantic arising from changing hydrographic patterns of the region, particularly on the Newfoundland and Scotian Shelves and in the Gulf of Maine (Greene and Pershing, 2007; Beaugrand et al., 2010; Head and Pepin, 2010). Changes on decadal time scales have included an increase in the abundance of smaller copepod taxa such as *Pseudocalanus* sp. and *Temora longicornis*, and fluctuations in the abundance of the large copepod *Calanus finmarchicus,* particularly in the Mid-Atlantic Bight region (Pershing et al., 2005; Kane, 2007; Hare and Kane, 2012; Bi et al., 2014). It is possible that these changes may affect the dynamics of the food web and energy flow in the system—and specifically the food available to zooplanktivorous small pelagics. Changes in zooplankton communities may select for different small pelagic fish species based on their life histories and feeding behaviors, including any differences in feeding apparatuses (such as the distance between gill rakers) or inherent preferences for some prey types over others (Magnuson and Heitz, 1971; Dalpadado et al., 2000; Casini et al., 2004). However, it is uncertain whether small pelagic fishes within a region truly represent different foraging niches, thus questioning the role of bottom-up trophodynamics in population fluctuations of these fishes—a topic noted as needing further research (Peck et al., 2013; Yasue et al., 2013; Chouvelon et al., 2015).

Information on the diets of small pelagic fishes may be important to understanding how these changes in the zooplankton community may influence higher trophic levels. Most recent studies, while useful for general descriptions and for particular prey taxa, have often grouped zooplankton into broad categories such as “copepod” or “fish larvae”, as well as “well digested prey” due to the collecting of food habits data at sea instead of in the laboratory (Garrison and Link, 2000; Smith and Link, 2010). One exception to this for the Northwest Atlantic was Bowman et al. (2000), who described the diets of small pelagic fishes at a usually high taxonomic resolution using samples from 1977 to 1980, describing intraspecific differences by region and size. There is little information on the diets of these species in the Northwest Atlantic in more recent decades and no detailed diet information on seasonal scales. With changes in the zooplankton community occurring in recent decades, updated information on the diets of small pelagics is needed to understand how any changes in zooplankton assemblages and abundances may influence these fishes.

The small pelagic fish complex of the Northeast United States continental shelf (NE Shelf) ecosystem, spanning from the Mid-Atlantic Bight to the Gulf of Maine and Georges Bank, largely comprises six species, of which five are the focus of this work. They are Atlantic herring (*Clupea harengus*), alewife (*Alosa pseudoharengus*), blueback herring (*Alosa aestivalis*), Atlantic mackerel (*Scomber scombrus*), Atlantic butterfish (*Peprilus triacanthus*), and northern sand lance (*Ammodytes dubius;* not discussed in this study). Three of these species, Atlantic herring, Atlantic mackerel, and butterfish represent extensive fisheries throughout this region, while alewife and blueback herring often constitute bycatch in the Atlantic herring and mackerel fisheries (Limburg and Waldman, 2009; Turner et al., 2015; Adams, 2018). While these species are classically considered to occupy a similar trophic level, they have important ecological distinctions that lead to habitat-related, and likely feeding-related, differences among them.

Atlantic herring exhibit both filter and particulate feeding on diel scales and most of their diet by weight in the Northwest Atlantic is attributed to krill, primarily *Meganyctiphanes norvegica* (Bowman et al., 2000). The diel variations in feeding include exhibiting particulate feeding on larger prey items such as fishes and mysids during the day, and consumption of almost exclusively copepods at night, though copepods dominate the diet overall (Darbyson et al., 2003). Other species of herring (Clupeidae) in the NE Shelf region include alewife and blueback herring (often collectively termed river herring). These species are anadromous and forage in offshore shelf waters, then swim up rivers to spawn in the spring (Loesch, 1987). Bowman et al. (2000) represents the only thorough description of alewife diets in the Northwest Atlantic, indicating a reliance on crustaceans, primarily a mix of krill and copepods. Diet data for blueback herring is lacking, with sample sizes too small to elucidate much aside from feeding on gelatinous zooplankton and copepods (Bowman et al., 2000). Atlantic mackerel (mackerel hereafter) are known for their larger size and general piscivory, even at the larval stage (Robert et al., 2008). However, being a small scombrid, adult mackerel have been shown to be consumers of zooplankton, including small copepods and fish larvae (Pepin et al., 1987; Langoy et al., 2012; Bachiller et al., 2016; Jansen, 2016; Óskarsson et al., 2016). Their potential role as a predator of fish larvae is important in understanding the recruitment of other fishes and understanding the dependence of mackerel on the spawning of certain taxa such as sand lance (Fogarty et al., 1991). Atlantic butterfish (butterfish hereafter) are both taxonomically and ecologically distinct from all other species of small pelagic fishes in the NE Shelf region. Unlike the generally crustacean-dominated diets of clupeids, butterfish have been shown to primarily consume soft-bodied zooplankton (Maurer and Bowman, 1975; Oviatt and Kremer, 1977; Bowman and Michaels, 1984), but major portions of stomach contents are usually unidentifiable.

While stomach content studies provide insight into the specific prey types consumed by organisms, stable isotope analysis can yield a broader and complementary understanding of energy flow in an ecosystem. Diet studies based on visual inspection of stomach contents alone have limitations such as missing soft bodied organisms and only capturing recently consumed items, while stable isotopes provide a longer-term, integrated signal of foraging behavior, albeit without information on actual prey species composition (Hyslop, 1980; Peterson and Fry, 1987). Stable isotope analysis reflects the nutritional sources, including variability and differences in these sources among consumers (Fry, 2006). Carbon stable isotope ratios are useful in an ecological context because they can provide a proxy for the base of the food web due to differential discrimination of ^{13}C among primary producers (DeNiro and Epstein, 1978). Nitrogen isotopes can also reflect base-of-the-food-web variability and, within a system, can provide a proxy for the trophic position of an organism due to the assumed trophic discrimination factor that estimates δ^{15}N values will increase approximately 3.4 per mille (‰) per trophic level, though this value has been shown to vary by trophic level (DeNiro and Epstein, 1981; Hussey et al., 2014). Stable isotopes therefore may provide a more integrated signal of nutrient and carbon transfer through food webs, information that is

Table 1
Number of specimens and mean (± SD) fork length (mm) by species and cruise on which stomach content analysis (SCA) and stable isotope analysis (SIA; both $\delta^{13}C$ and $\delta^{15}N$) were performed, as well as the feeding incidence (FI; proportion with prey present) of specimens analyzed for stomach contents.

	Atlantic mackerel			Atlantic butterfish			Atlantic herring			Alewife			Blueback herring			All species	
	SCA	SIA	FL	SCA	SIA	FL	SCA	SIA	FL	SCA	SIA	FL	SCA	SIA	FL	SCA	SIA
Spring 2013	19	23	253 (27)	27	26	126 (25)	25	26	198 (32)	0	0	–	0	0	–	71	75
Spring 2014	33	27	246 (42)	30	28	136 (28)	35	40	203 (35)	38	37	202 (37)	41	45	190 (27)	177	177
Fall 2014	25	24	232 (31)	53	49	132 (33)	40	38	219 (10)	23	22	249 (9)	21	21	216 (9)	162	154
Fall 2015	25	24	272 (30)	20	21	135 (15)	23	22	247 (7)	20	18	222 (36)	4	10	214 (5)	92	95
Total	102	98		130	124		123	126		81	77		66	76		502	501
FI spring	0.96			0.98			1.0			1			1.0				
FI fall	1.0			1.0			0.89			0.95			1.0				

critical in a changing ecosystem.

Here, we assess the hypotheses that the small pelagic fishes in the NE Shelf region have consumer-specific diets and that these diets vary by season. We test these hypotheses through multivariate analysis of detailed, high-resolution stomach contents and compare and contrast stomach contents with consumer stable isotope signatures. Understanding energy pathways within the small pelagic fish complex can provide important information on the potential resilience of these species to shifts in zooplankton communities and their control on lower trophic levels.

2. Methods

2.1. Field methods

Alewife, blueback herring, mackerel, Atlantic herring, and butterfish were collected from four NOAA Northeast Fisheries Science Center (NEFSC) trawl surveys: spring 2013, spring 2014, fall 2014, and fall 2015 (Table 1; Fig. S1). Each survey spanned the continental shelf from the northern Gulf of Maine to Cape Hatteras, with spring sampling encompassing March through May and fall sampling extending from September through early November. Details on the sampling methodology of the surveys and approach for selecting station locations can be found in Stauffer (2004) and Reid et al. (1999). The fish we analyzed were selected randomly from those available within each of 4 regions: Mid-Atlantic Bight, Southern New England, Georges Bank, and Gulf of Maine (Walsh et al., 2015). The number of fish analyzed per species per station ranged from 1 to 5. Fish were frozen shipboard in a −80 °C freezer to minimize digestion occurring postmortem, and samples were stored at −80 °C until processed in the laboratory.

2.2. Diet analysis

Fish were thawed to near room temperature before dissection. Fork lengths were recorded for each fish, and the gastrointestinal tract (esophagus through intestine) was removed and weighed. The entire gastrointestinal tract was used due to the lack of a defined stomach in clupeids. The gastrointestinal tract was then opened, and contents were placed in 95% ethanol for preservation. Gut contents were identified to the lowest taxonomic unit practical (see below) using a Leica M60 dissecting microscope. A subsample of 10 individuals of common prey types was measured for length to estimate consumed biomass of each prey taxon using published length-to-dry weight relationships, though the number of prey taxa used for this analysis was limited by the availability of such relationships (Table S1). In cases of extremely high gut fullness, a known subsample of prey items was taken with a Hensen-Stempel pipette and enumerated, and this value was divided by the fraction of total volume that the subsample represented to yield an approximation for total stomach contents. Diet analyses were largely focused at the genus level (and hereafter only genera are named) due to partially digested prey and inherent difficulties in identifying zooplankton to the species level. The exceptions to this were the small calanoid copepods in the genera *Pseudocalanus*, *Paracalanus*, and *Clausocalanus*, which were grouped together (hereafter referred to as *PPC*), the copepod species *Temora longicornis*, and appendicularians. Appendicularians were always of the genus *Oikopleura* when identifiable, and consist of the organism itself and often a gelatinous ‘house’ within which the organism lives (Alldredge and Madin, 1982). Both were enumerated, but numbers rarely matched, likely due to a combination of reasons: appendicularians sometimes lack a house, abandoned houses could be consumed on their own, or houses in a fish’s gut digest more slowly than the organisms (pers. obs.). As such, appendicularian counts were taken to be the maximum of the number of houses or organisms in each fish. Fecal pellets of appendicularians were not counted, as the number of fecal pellets per appendicularian varies. Many fish, particularly butterfish (> 90% frequency of occurrence; Table S8), contained unidentifiable prey items that were often soft-bodied. These prey were enumerated but no biomass estimation could be calculated. Infrequently observed prey items, including fish eggs, squid eggs, and bivalve larvae, were grouped in one category labeled “other”.

Diets were described by the proportion of prey consumed by species with station as the sampling unit (i.e. the prey consumed by multiple specimens of the same species were pooled for each station). Biomass and numerical descriptors of diet allow for interpreting two different functions in trophic ecology. Biomass of prey represents the prey items that likely contribute most to consumer growth and development, as energy transferred up the food web is more accurately represented by biomass (Hyslop, 1980). Numbers of individuals consumed provides an opportunity to quantify and compare the top down effects of consumers on their prey species. Feeding incidences were calculated as the fraction of analyzed fish that contained prey.

To assess overlap in the diet of small pelagic fishes by species and season, the diets of consumers in each season were compared using hierarchical cluster analysis based on the Bray-Curtis dissimilarity matrix constructed from the average arc-sine transformed proportions of prey using the “vegan” package in R statistical software (Version 3.4.0; Oksanen et al., 2018). Prey categories that composed greater than 1% of the diet of any of the consumer-season groupings were included in the analysis, except the categories of other and unknown, which were excluded. Butterfish were excluded from cluster analysis owing to the high proportion of unknown prey in their diet. Hierarchical clustering used the unweighted arithmetic average method (Legendre and Legendre, 2012).

Canonical correspondence analysis (CCA) was employed to assess diet variability within a consumer species. CCAs are a direct gradient analysis that serves as a multivariate equivalent to a multiple non-linear regression where a set of explanatory variables is used to predict species or community composition (ter Braak, 1986; Garrison and Link, 2000). The response variables for the CCAs were the prey consumed by fish within the same cruise-station-fork length bin (1 cm) grouping. A detrended correspondence analysis was performed to ensure that the response variables followed a unimodal distribution, an assumption of CCA (Lepš and Šmilauer, 2003). Season, region (Gulf of Maine, Georges Bank, Southern New England Shelf, and Middle-Atlantic Bight), day/night, and depth of collection were included as explanatory factors to explain variability in the diet of the small pelagic fishes. Season, region, and day/night were converted to nominal variables for inclusion in the CCA (spring to fall, north to south, and day to night). Explanatory factors were chosen through forward stepwise selection (ter Braak, 1986), only keeping factors that represented a significant contribution to explaining the variance in the diet as determined through permutation tests.

CCAs were visualized through ordination diagrams. Arrows represent significant explanatory factors and the weighted means of prey items are located along these gradients. The angle between two arrows indicates correlation of those explanatory factors. The location of prey items along these arrows indicate how much above/below the weighted mean of the prey item is along that explanatory factor.

2.3. Stable isotope analysis

Small sections of dorsal musculature of the 5 small pelagic species were analyzed for bulk carbon and nitrogen stable isotopes. Samples were dried at 60 °C in a drying oven for at least 48 h and then pulverized to a powder. Subsamples (1.2–1.5 mg) were weighed, wrapped in tin foil, and then analyzed with a PDZ Europa ANCA-GSL elemental analyzer interfaced to a PDZ Europa 20-20 isotope ratio mass spectrometer (Sercon Ltd., Cheshire, UK) by the University of California Davis Stable Isotope Facility. Analyses yielded carbon to nitrogen ratios (C:N) and the isotopic ratios of ^{13}C:^{12}C and ^{15}N:^{14}N in each sample. We report stable isotope ratios using the conventional delta notation (i.e. $\delta^{13}C$ and $\delta^{15}N$; Fry, 2006), with the reference standards of Pee Dee belemnite (for $\delta^{13}C$) and atmospheric nitrogen (for $\delta^{15}N$), calculated with the following equation:

$$\delta^{13}C\text{or}\delta^{15}N = \left(\frac{R_{sample}}{R_{standard}} - 1\right) * 1000$$

where R is either $^{13}C/^{12}C$ or $^{15}N/^{14}N$. A lipid correction curve was applied to each sample using the C:N ratio from the mass spectrometry results. This correction was made using the model created for fish muscle tissue (Logan et al., 2008):

$$\delta^{13}\text{C corrected} = \delta^{13}\text{C} - 4.763 + 4.401 * \ln(\text{C: N})$$

Linear regression analysis was used to compare each isotope with latitude and depth. The water column depth at each station was extracted from the NOAA Center for Environmental Information bathymetry raster (0.03° resolution; http://maps.ngdc.noaa.gov/viewers/wcs-client/). Student's t-tests were used to compare differences within species by season with the exception of seasonal comparisons in $\delta^{13}C$ and $\delta^{15}N$ for butterfish, which were compared using Wilcoxon ranked sum test due to unequal variances.

Isotopic niche widths for each species and season were compared using standard ellipse areas with a sample size correction. The standard ellipse is the bivariate equivalent of standard deviation and the standard ellipse area is calculated using the variance and covariance of $\delta^{13}C$ and $\delta^{15}N$ values, encompassing 40% of the data for each species (Batschelet, 1981; Ricklefs and Nealen, 1998). The area of this ellipse is then corrected with the equation:

$$SEA_c = SEA * (n-1) / (n-2)$$

where SEA is the standard ellipse area, SEA_c is the sample size corrected ellipse area, and n is the number of samples for a species (Jackson et al., 2011; Jackson et al., 2012). While SEA_c values allow a comparison of isotopic niche width, comparisons in the overlap of these ellipses quantifies the overlap in isotopic niche space between two species (Jackson et al., 2012). Further, Bayesian inference was used to create credible intervals around the Bayesian standard ellipse areas (SEA_B). This Bayesian framework allows for the assumption that the isotopic data are not completely representative of the populations of these fishes and are merely a subset of data from a greater distribution, allowing for the formation of credible intervals around estimations of isotopic niche width. Details of this method are described in Jackson et al. (2011), but, briefly, vague normal priors are assigned to the means and an Inverse-Wishart prior is used as the covariance matrix of isotope values for each species. The isotope data are then used to form likelihood values, which are then combined with the priors to form posterior distributions (in this case the posterior estimate of the covariance matrix is simulated using the Markov Chain Monte Carlo method). From these posterior distributions, a set of 4000 estimates of the standard ellipse area is calculated to provide the mode of the Bayesian standard ellipse areas and credible intervals.

3. Results

3.1. Diet composition

Feeding incidences were high for all species in both seasons, ranging from 0.89 to 1.0 (Table 1). Spring-collected fish had a higher number of prey items than in the fall for both blueback and Atlantic herring ($p < 0.001$; not shown) with no significant differences between seasons for alewife, mackerel, or butterfish ($p = 0.47$; $p = 0.38$; $p = 0.48$). Biomass of consumed prey was also significantly higher in the spring for blueback herring and Atlantic herring ($p < 0.001$; not shown) and was significantly higher in the fall than in the spring for mackerel and butterfish with no significant difference in consumed prey biomass for alewife ($p < 0.05$ for Atlantic herring, blueback herring, mackerel, and butterfish; $p = 0.73$ for alewife). Dominant prey taxa varied by consumer species, by season, and by cruise in some cases (Fig. 1; Tables S2 and S3). In the spring, copepods represented substantial proportions of the number of prey items for all species except butterfish. However, the importance of each copepod taxon varied by consumer species, with *Pseudo-/Para-/Clausocalanus* (*PPC*) copepods being prominent in the diet of mackerel (though driven by 2014) and alewife (14% by number (N) for both species) but slightly less so for Atlantic herring and blueback herring (11% and 10% N). *Centropages* represented a moderate portion of the spring diet of all five of these species, with the highest abundance in the diet of Atlantic herring, the only species to show a greater number of *Centropages* than *PPC* copepods in the spring. *Calanus* represented a nearly equivalent proportion of the diet by number as smaller genera of copepods for Atlantic herring, but was less common in the diet of Atlantic mackerel while representing a higher percentage of total prey items for alewife and blueback herring. *Temora longicornis* was much less prevalent than the other taxa of copepods. It is important to note, however, that spring diet information for alewife and blueback solely stem from 2014 as no fish were collected in the spring of 2013.

Appendicularians were only present in the spring diets of small pelagic species and were more common in 2013 than 2014 (Table S6). They were prevalent in the diet by both number and biomass of all species aside from alewife. *Ammodytes* (sand lance) larvae were present in the stomachs of mackerel during the spring and contributed a substantial portion of the biomass of their diet (32% BM).

Fall diets contrasted sharply with those in spring for many species, particularly mackerel, Atlantic herring, and alewife. Mackerel exhibited a shift from a diet dominated by *PPC* copepods in both biomass and

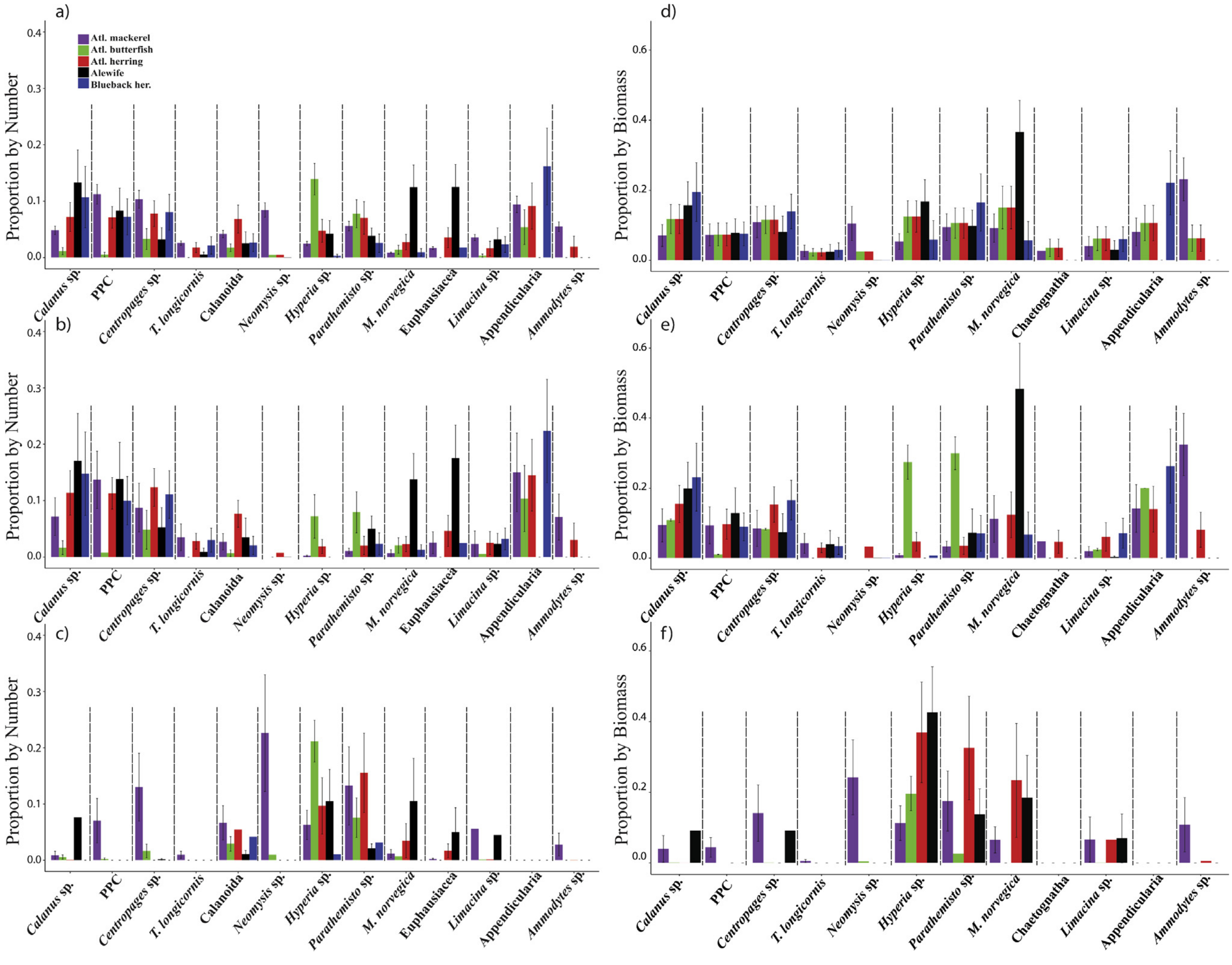

Fig. 1. *Proportion of Prey in the Diets of Small Pelagic Fishes*. Mean proportions of common prey taxa in stomach contents by number (a–c) and biomass (d–f) in total (a, d), the spring (b, e), and the fall, (c, f) of five species of small pelagic fishes. *T. longicornis = Temora longicornis, M. norvegica = Meganyctiphanes norvegica.*

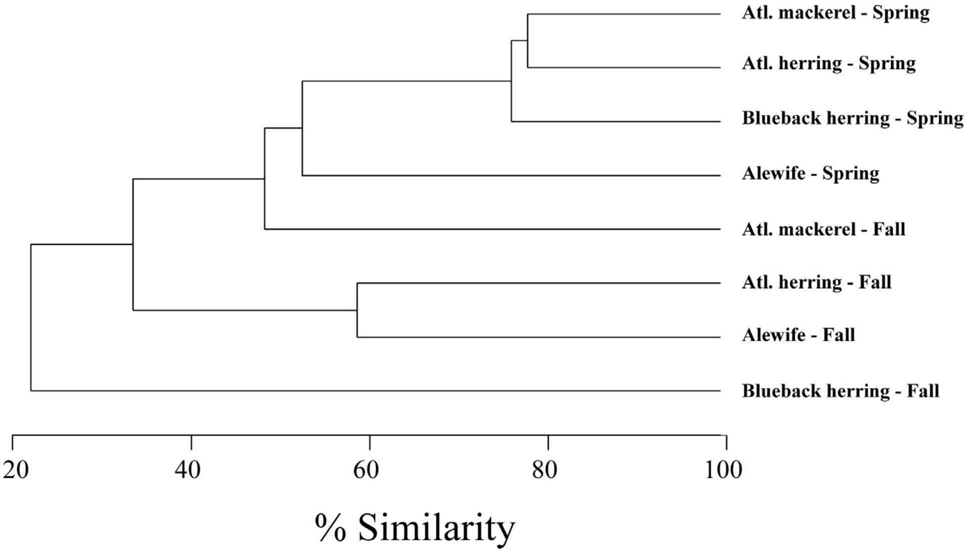

Fig. 2. *Hierarchical Cluster Analysis of Diet Similarity*. Dendrogram of a hierarchical cluster analysis indicating diet similarity of small pelagic fishes separated by spring and fall.

number in the spring to one dominated by *Neomysis* by both number and biomass in the fall. *Centropages* was also common in the fall diet of mackerel but was more prevalent in 2015 than 2014 (Table S6). Consumption of *Meganyctiphanes norvegica* and unidentifiable Euphaisiacea increased in the fall for Atlantic herring and alewife, though Atlantic herring primarily consumed hyperiid amphipods. Alewife was the only species to consume primarily Euphausiacea (mostly *Meganyctiphanes norvegica*) by biomass in both the spring and the fall. Of the identifiable prey, Hyperiidea (both *Hyperia* and *Parathemisto*) were the dominant prey by biomass and number for butterfish in both seasons. Little could be concluded for blueback herring in the fall due to low sample sizes and a diet dominated by Salpida (93.3%) that was due to two fish containing a remarkable 556 salps between them, resulting in the remainder of non-salp prey (n = 40) being a small fraction of the total.

3.2. Hierarchical cluster analysis

Hierarchical cluster analysis revealed 6 clusters and corroborate diet proportion data described above. Spring Atlantic herring, spring blueback herring, and spring mackerel compose a cluster at 75% similarity owing to the dominance of copepods in their diet. Spring alewife was separate due to the greater portion of krill in their spring diet. Blueback in the fall showed the least similarity to other groups, while fall Atlantic herring and alewife were similar. Fall mackerel, however, was more similar to spring Atlantic herring, spring blueback herring, and spring mackerel (Fig. 2). This is likely a result of high proportions of copepods in the diet of mackerel in both the fall and the spring.

3.3. Canonical correspondence analysis

The CCA for mackerel accounted for 22.4% of the variation in diets and the first two canonical axes explained 80.5% of this variance. Season, day/night, depth, and region were significant explanatory factors. *Neomysis* was important in the diet in the fall, while *Calanus* and appendicularians were important in the spring. Appendicularia and *PPC* were more common in the diet in deeper waters while *Ammodytes* was found in shallower waters (Fig. 3a). *PPC* copepods and Appendicularia were also more common at night while *Ammodytes* and *Calanus* were more common during daylight hours (Fig. 3a). The CCA for Atlantic herring accounted for 32.6% of the total variance, with the first two canonical axes explaining 94.9% of this variation (Fig. 3b). The CCA for Atlantic herring showed three significant explanatory variables: region, season, and depth. Krill showed an association with greater depths and hyperiid amphipods showed association with the fall. The CCA for alewife explained 24.8% of the variation and only retained season and region (thus 100% of variance is explained by the first two canonical axes; Fig. 3c). The CCA shows *Hyperia* being strongly associated with fall while *PPC* was associated with more southerly regions (Fig. 3c). Blueback herring had a low number of samples described by each explanatory factor and thus CCA was not performed on their diet. CCA was also not performed on the diet of butterfish as their diet contained many unidentifiable prey items.

3.4. Stable isotope analysis

Clear latitudinal trends were apparent for $\delta^{13}C$ and $\delta^{15}N$ values for certain species (Fig. S2). Significant negative correlations were present for $\delta^{13}C$ and latitude for mackerel ($r = -0.32$, $p < 0.01$), blueback herring ($r = -0.37$, $p < 0.01$), and Atlantic herring ($r = -0.37$, $p < 0.001$; Fig. S2a). Significant negative correlations of $\delta^{15}N$ with latitude were present in mackerel ($r = -0.53$, $p < 0.001$), alewife ($r = -0.57$, $p < 0.001$), Atlantic herring ($r = -0.25$, $p < 0.01$), and blueback herring ($r = -0.26$, $p < 0.01$, Fig. S2b). Two of 5 relationships of $\delta^{15}N$ with bottom depth (Fig. S3) were observed to be significant while no relationships between $\delta^{13}C$ and bottom depth were

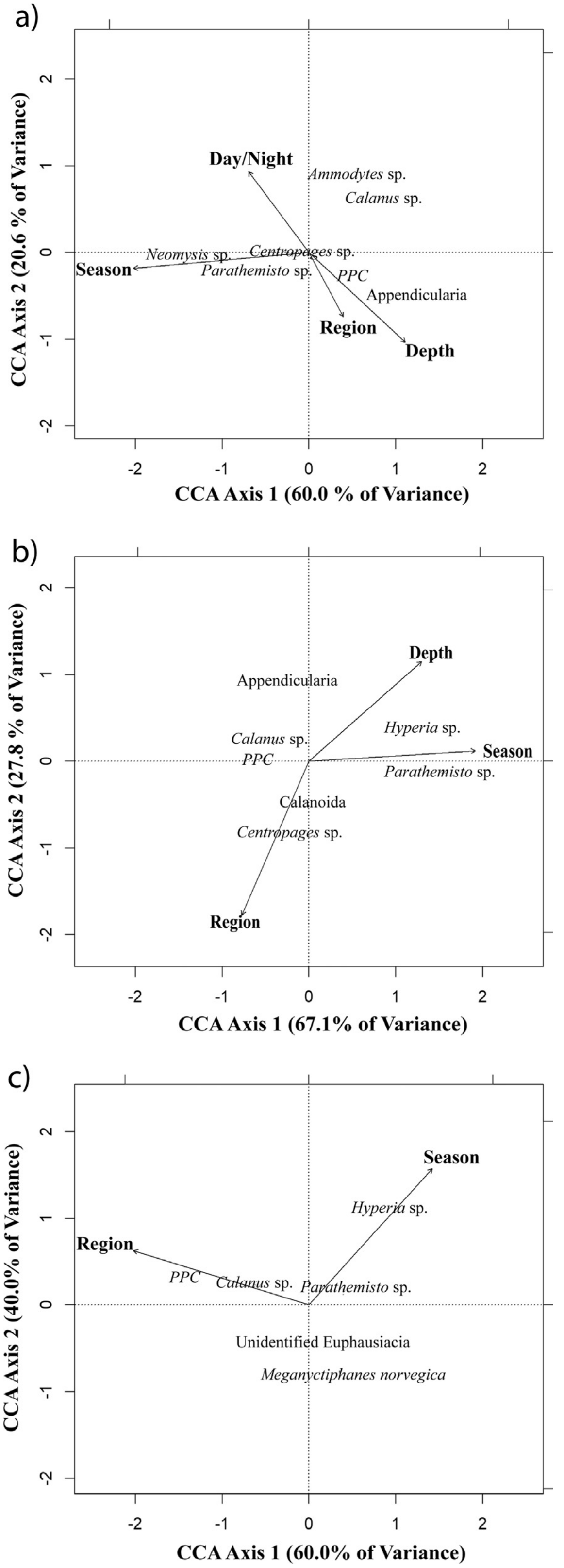

Fig. 3. *Canonical Correspondence Analyses.* Ordination biplots from results of canonical correspondence analysis of diets of (a) Atlantic mackerel, (b) Atlantic herring, and (c) alewife with explanatory variables of season, depth, and region. Arrows indicate explanatory variables that significantly accounted for the variability in diet. Locations of prey types represent the weighted mean proportions in the diet and can be related to where along the explanatory variables the prey type tended to be consumed.

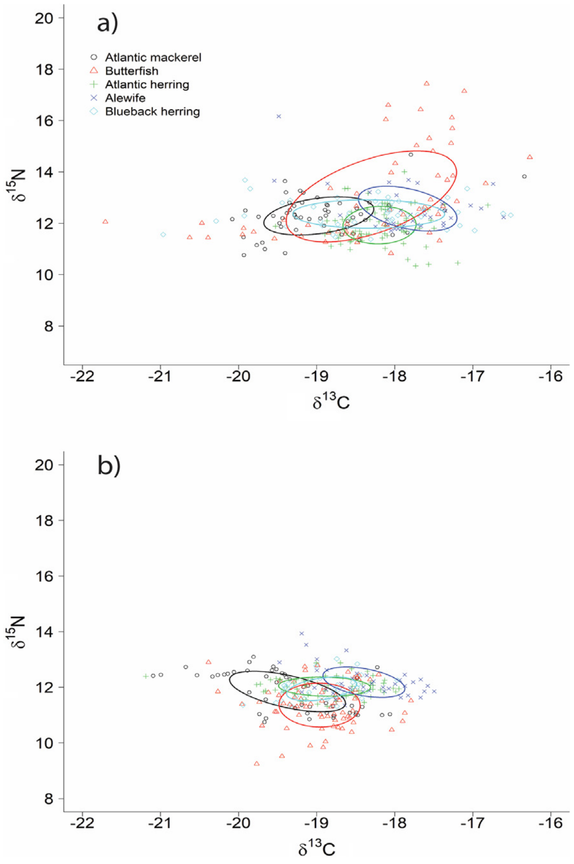

Fig. 4. *Stable Isotope Ratios and Standard Ellipses.* Stable isotope ratios (δ^{13}C and δ^{15}N) of small pelagic fishes in the (a) spring and (b) fall, along with each species' standard ellipse corrected for sample size.

observed to be significant. There was no significant trend between bottom depth or latitude and fork length for any species, and thus it was assumed that the size of the fish was not the cause of these trends.

Differences in isotopic values primarily occurred between seasons and not by cruises within the same season. The exceptions to this are δ^{13}C values of Atlantic mackerel in the fall and butterfish in the spring, which showed significant differences between cruises within a season ($p < 0.01$). However, due to the similarities in δ^{13}C within a season for all other species and for δ^{15}N in all species, comparisons in isotopes were focused on the seasonal level, where seasonal differences in isotopic values were apparent (Fig. 4). Mackerel, Atlantic herring, blueback herring, alewife, and butterfish had more enriched mean δ^{13}C values in the spring than fall ($p < 0.01$). Mackerel, alewife, blueback herring, and butterfish had more enriched mean δ^{15}N values in the spring relative to the fall ($p < 0.05$ for all).

Standard ellipse areas corrected for sample size (SEA_c; Table S9; Fig. 4) and Bayesian ellipse areas (SEA_B; Fig. 5) were different among species and between seasons, with butterfish showing the largest SEA_c both overall and in the spring, and mackerel having the greatest SEA_c in the fall (though only slightly larger than butterfish). Atlantic herring showed the lowest SEA_c values in the spring, fall, and overall. SEA_c was substantially lower for all species in the fall than the spring with the exception of mackerel, which showed little change in SEA_c between seasons.

Overlap among species was variable by species and season but greater overlap among species generally occurred in the fall (Fig. 4; Tables S10 and S11). The clupeids (Atlantic herring, alewife, and blueback herring) showed a large degree of overlap in both seasons but greater overlap in the fall.

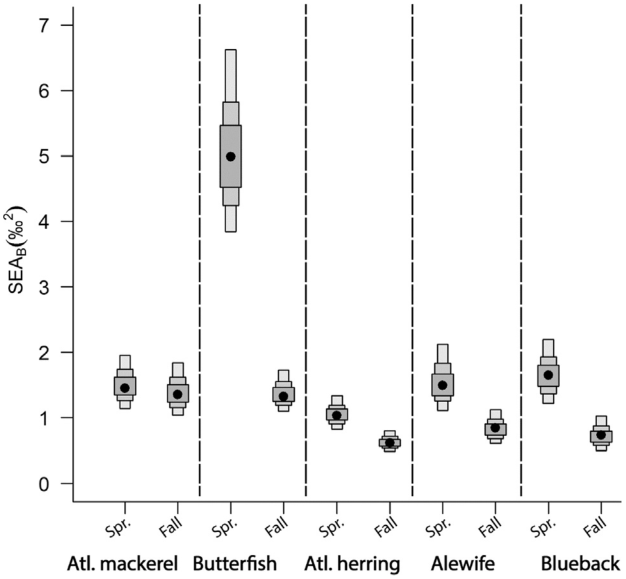

Fig. 5. *Bayesian Ellipse Areas.* Density plot of Bayesian standard ellipse areas (SEA_B) for small pelagic fishes in the spring and fall. Black dots represent the mode of posterior distribution of SEA_B values with grey boxes presenting 50%, 75%, and 95% credible intervals.

4. Discussion

Small pelagic fishes of the NE Shelf ecosystem showed diet differences among species but most noticeably by season, illustrating that these fishes exhibit variable diets throughout the year. Stable isotope data corroborate these seasonal differences in diet, displaying differences in the isotopic niche size by season, while at the same time showing that the ultimate carbon source at the base of the food web is similar for most species, as evidenced by high overlap in isotopic niche. Additionally, mackerel showed the smallest change in isotopic niche size between seasons, which corroborates their fairly small change in diets by season. However, isotopic niche overlap was higher among small pelagic fishes in the fall despite less diet similarity, emphasizing differences in stable isotope and stomach content analysis.

Differences in spring diets among consumer species and between seasons within a species were evident due to the identification of copepod prey usually to the genus level, thereby improving our understanding of food webs in the NE Shelf region. However, hierarchical cluster analysis grouped spring Atlantic herring, spring mackerel and spring blueback herring at the 75% similarity level owing to the large proportion of copepods in their diets. Alewife were less similar due to krill composing a large proportion of their diet in the spring in addition to copepods. Differences in the relative abundance of each copepod taxon in the diet among consumer species are noteworthy, though the CCA of mackerel, Atlantic herring, and alewife make the cause of this variability difficult to elucidate. Explanatory factors associated with each copepod taxon varied by fish species with the exception of a weak association of *PPC* and *Calanus* with spring. This suggests that these copepod taxa are likely consumed in similar locations that vary by small pelagic species with no obvious spatial differences.

The similar levels of small genera (*PPC*) of copepods and the larger genus *Calanus* in the spring diets of small pelagics is a notable observation when considering the observed decadal-scale changes in the zooplankton community of the NE Shelf (Pershing et al., 2005; Greene and Pershing, 2007; Kane, 2007; Beaugrand et al., 2015). These observations have shown an increase in the abundance and diversity of small copepods in the Northwest Atlantic, while the abundance of larger genera, particularly the lipid-rich *Calanus finmarchicus*, has fluctuated (Mid-Atlantic Bight) or decreased (in the case of the

Newfoundland and Scotian Shelves) on regional scales and is projected to decrease throughout much of the NE Shelf (Kane, 2007; Beaugrand et al., 2010; Head and Pepin, 2010; Grieve et al., 2017). Thus, we are uncertain if the prominence of these smaller copepod genera in the diet of small pelagic fishes is a response to relatively high levels of availability and the rapidly shifting hydrography of the region (Chen et al., 2014; Forsyth et al., 2015), and more importantly what the consequences are for small pelagic fish nutritional condition. Bowman et al. (2000), who report on diets of small pelagics from the same regions here but during 1977–1980, found *Calanus* to be important in the diet of alewife and Atlantic herring, but they classified most copepods as unidentifiable or Calanoida, and thus we cannot fairly assess changes in the diet between our study and theirs. It is also worth noting that studies from Europe show a much greater reliance on *Calanus* in the diet of Atlantic herring than our results (Holst et al., 1997; Kennedy et al., 2009; Langoy et al., 2012). Thus, if Atlantic herring are adapted to be at optimal condition—including reproductive condition—when *Calanus* prey are heavily consumed, changes in dominant zooplankton taxa to smaller, more lipid-poor genera could have large implications for the growth, survival, reproduction, and food quality of this important forage fish species in the NE Shelf region. Alewife also showed a higher proportion of *Calanus* by proportion of number in their diet than that of the other small pelagic fishes, and *Calanus* was found in the diet of alewife in both spring and fall. Thus it is also possible that alewife may be susceptible to changes in *Calanus* abundance throughout the Northwest Atlantic. However, both Atlantic herring and alewife may be able to rely on krill during times of low *Calanus* abundance, but projected changes to abundances of *Meganyctiphanes norvegica* in the Gulf of Maine remain uncertain due to difficulties in assessing their presence and abundance (Wiebe et al., 2013; Lowe et al., 2018). Bowman et al. (2000) showed a very high abundance of *Meganyctiphanes norvegica* (> 80%) in the diet of Atlantic herring and alewife (> 65%) in the Gulf of Maine, corroborating the suggestion that these fishes may be able to rely on krill as a major prey source in the Gulf of Maine. Our results further substantiate this, as krill were most abundant in the diet of alewife in the northerly regions of our study, including the Gulf of Maine. Long-term monitoring of small pelagic fish diets and condition (e.g. lipid content) as they relate to zooplankton abundance and, importantly, composition would likely prove fruitful for effective ecosystem-based management of the NE Shelf region in the face of rapid ecosystem change (Pershing et al., 2015).

The prevalence of krill (Euphausiacea, namely *Meganyctiphanes norvegica*) in the fall diets of blueback herring, Atlantic herring, and the fall and spring diets of alewife may be a result of increased coupling of predators and prey during the absence of other prey items. Though krill were present in the diet of small pelagics in the spring as well, the substantially larger amounts in the fall may be a result of the lack of availability of many copepods during this time as they begin to enter diapause, particularly *Calanus finmarchicus* (Pershing et al., 2004; Johnson et al., 2007). This lack of copepod availability is evident in the diet shift of the clupeids studied, which consumed primarily copepods and few krill by number in the spring, despite higher environmental abundances of krill in the spring in the Gulf of Maine region (NOAA NEFSC, unpub. data). Copepods entering diapause in the fall, where they sink to depths in excess of 200 m, creates a vertical decoupling of their range and that of many of the small pelagic fishes (Hirche, 1996; Pershing et al., 2004). Further*, Meganyctiphanes norvegica* are abundant in the eastern Gulf of Maine, which may represent an increased spatial coupling of krill with the clupeids, particularly Atlantic herring in the fall as they spawn throughout waters of the Gulf of Maine and Georges Bank (Sinclair and Tremblay, 1984; Hay et al., 2001; Stephenson et al., 2009; Johnson et al., 2011). It is also possible that the increased importance of krill in the diet of clupeids in the fall was a result of the larger size of fall clupeids used in this study, indicating an ontogenetic shift to larger prey items. Bowman et al. (2000) observed higher abundances of krill in diets of larger alewife and Atlantic herring, though this was likely an artifact of larger fish being caught in the Gulf of Maine as regional differences in krill consumption were much greater than ontogenetic differences in their study. Given the association of krill with more northerly stations in the diet of alewife and that fork length was not a significant explanatory factor in the CCA of alewife or Atlantic herring in our study, we believe that differences in the consumption of krill by season were more likely due to regional differences than size differences.

Hyperiid amphipods were found in the diet of all species in this study in both seasons, indicating their importance as prey items for small pelagic fishes in the NE Shelf ecosystem. All species studied consumed both *Hyperia* and *Parathemisto* and in much higher abundances than documented by Bowman et al. (2000) and by Hanson (2017) in the Gulf of St. Lawrence, particularly for alewife and Atlantic herring. Either one or both genera (*Hyperia* and *Parathemisto*) were associated with the fall season in the CCA for mackerel, Atlantic herring, and alewife, indicating they may be an important prey source in the fall during low copepod abundances. While there is very limited data on hyperiid amphipods, their abundance increased in the Gulf of Maine-Georges Bank region from the early 1990s through 2004, which may play a role in their increased prevalence in this diet study when compared to older data (Bowman et al., 2000; Kane 2007).

Hyperiids composed the majority of the identified prey of butterfish, a finding that is not surprising since hyperiid amphipods are often found within gelatinous zooplankton, which butterfish are known to consume (Harbison et al., 1977; Laval, 1980). Therefore, it is possible that the hyperiids were consumed incidentally along with gelatinous zooplankton, which were qualitatively very abundant in the diet of butterfish (but unable to be incorporated in the prey number and biomass calculations). *Hyperia*, in particular, being common in the diet of butterfish may indicate feeding on scyphozoan jellies, as scyphozoans are often the host of this genus of amphipod (Buecher et al., 2001). Ctenophores have previously been described as prey of butterfish and likely represent a large portion of their diet as well (Oviatt and Kremer, 1977). Salps were also an important soft-bodied zooplankton in the diet of small pelagics, namely in the fall diet of blueback herring. The nearly monotypic diet of blueback herring consisting of salps in the fall is the reason that fall blueback herring show the lowest percent similarity to any other consumer, though our limited sample size inhibits our ability to elucidate much about the importance of salps to blueback herring.

Evidence of intra-guild predation was apparent in the diet of mackerel, with sand lance larvae constituting a large portion of their diet by biomass in the spring. This has been documented before by Smith and Link (2010) with both mackerel and alewife consuming sand lance larvae in their study and is significant enough to suggest that mackerel and sand lance populations may oscillate out of phase owing to this phenomenon (Fogarty et al., 1991). Bowman et al. (2000) did not show sand lance in the diet of mackerel, which is surprising given their study years (1977–1980) co-occurred with a dramatic population increase in sand lance (Nelson and Ross, 1991). In our study, sand lance larvae primarily occurred in the diet of mackerel during the day and at shallower depths, though these were collinear and it is impossible to know which is important or if there is a mechanism behind those patterns. Sand lance juveniles were also found in the stomachs of four mackerel from two stations in fall of 2015, indicating intra-guild predation goes beyond adults feeding on larvae. However, the low frequency of occurrence of juvenile sand lance in the diet of mackerel limits our capacity to determine if feeding on juveniles contributes to top-down pressure on sand lance populations by mackerel. Intra-guild predation has been cited as an important topic of study in forage fish science and it is thus important to document intra-guild predation in this system (Peck et al., 2013). Variability in evidence of intra-guild predation among studies of the diet of small pelagics substantiates the need for additional study on this topic.

Isotopic niche widths were substantially lower in the fall than in the spring for all species except mackerel. This finding suggests that the carbon and nitrogen sources for these organisms were more homogenous during the fall than the spring. The small decrease in isotopic niche space in the fall by mackerel may arise from their continued feeding on *Centropages* in the fall and the addition of *Neomysis* as a major source of their diet by biomass. This observation suggests that copepods, particularly the more nearshore *Centropages*, may represent a different source of carbon and nitrogen than the krill and hyperiids consumed by the clupeids in the fall (Durbin and Kane, 2007; Ji et al., 2009; Kürten et al., 2013). Baseline δ^{15}N data from zooplankton and particulate organic matter across the NE Shelf ecosystem substantiates this claim, as differences in δ^{15}N are primarily seen inshore-to-offshore with more depleted δ^{15}N values offshore and no trend with latitude (McKinney et al., 2010; J. Lueders-Dumont, pers. comm.). These data suggest that the difference in stable isotope values of these fishes by season originates from different prey sources and not solely from spatial effects in the fall, despite the series of significant correlations of isotopic values with latitude and depth. However, Atlantic herring and alewife may be an exception since they were collected at stations with deeper waters in the fall, when they showed depleted δ^{15}N values. Thus the difference in δ^{15}N values for Atlantic herring and alewife by season may originate from utilization of more offshore nitrogen sources. Diet data contrast isotopic niche overlap results because there was more dietary similarity in the spring among mackerel and the three clupeids studied, while isotopic overlap was lower. This indicates that dietary differences, even when examined with high taxonomic resolution, may not fully reflect differences in energy flow through small pelagics on the NE Shelf. Our findings of greater seasonal than inter-specific differences in isotopic niches of small pelagics are consistent with similar studies on small pelagics from other regions, indicating that the role of energy flow to these fishes may vary more with time and location than species (Costalago et al., 2012; Yasue et al., 2013). Some of these seasonal differences may be driven by factors such as small-scale spatial and temporal variability at the base of the food web that we were unable to thoroughly assess in this study.

Appendicularians, which are a soft-bodied (often referred to as gelatinous) zooplankter, were also common in the spring diet of the small pelagics studied (with the exception of alewife), particularly in 2013. Appendicularians feed through filtering nanoplankton via a gelatinous house they build, and thus represent a notable direct link to the microbial loop (Azam et al., 1983; Jaspers et al., 2015). Owing to this feeding strategy, appendicularians may be important during spring seasons that have low salinity and high stratification, which limit blooms of larger phytoplankters and favor microbial based primary productivity. Such conditions have been shown to occur in the Gulf of Maine during negative phases of the North Atlantic Oscillation (Townsend et al., 2015). This phenomenon likely occurred in the Gulf of Maine in 2013, as there was a negative winter NAO phase (2-year lag, as suggested by Townsend et al., (2015)), which may have led to the increase in appendicularians in the diets of small pelagic fishes in spring of 2013. While appendicularians and gelatinous zooplankton generally constituted a low proportion of the biomass of the diet of these fishes, they represent a link to a different carbon and nitrogen source from most crustacean zooplankton, possibly resulting in an increased isotopic niche width for species that consume them. Butterfish substantiate this possibility as they display the largest overall isotopic niche width and have a diet that is dominated by soft-bodied organisms. While the diversity in their consumption of soft bodied organisms is unknown, the varied feeding pathways and trophic levels that gelatinous zooplankton represent may cause an increase in the carbon and nitrogen sources utilized by butterfish (Jaspers et al., 2015). Previous data from Puget Sound show that the isotopic niche of jellyfish and fish may overlap less than 50% and be variable with time (Naman et al., 2016), corroborating the suggestion that gelatinous zooplankton may represent different nutrient sources. However, data on gelatinous zooplankton isotopes on the NE shelf and comparisons of gelatinous zooplankton and crustacean zooplankton are lacking.

We have shown that zooplanktivorous small pelagic fishes of the NE Shelf ecosystem display distinct seasonal differences in diets, as a whole and within the same species, as well as some clear differences among species, illustrating how zooplanktivorous fishes can represent different carbon and nutrient pathways in the NE Shelf ecosystem. Differences were also apparent in the diet of some fishes when compared to data from 1977 to 1980 (Bowman et al., 2000), suggesting changes in the feeding of these fishes that specifically include a decrease in the frequency of krill and an increase in the abundance of hyperiid amphipods and copepods in the diet of Atlantic herring and alewife. These findings are important for our understanding and prediction of how changes to zooplankton communities will impact small pelagic fishes and higher trophic levels. It also highlights a need to increase our focus on the trophic linkages between small pelagics and planktonic production, specifically including how these relationships will change in the future and impact the overall NE Shelf ecosystem.

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Contributors

Justin Suca led the data analyses and writing of the manuscript with assistance from Joel Llopiz, who also designed the study and led its implementation. Julie Pringle analyzed the diets of all examined fish, Zophia Knorek and Sara Hamilton performed dissections, prepared samples for isotope preparation, and performed preliminary data analyses, David Richardson provided zooplankton data, assisted with obtaining fish specimens, assisted with data analysis, and all co-authors provided editorial assistance and approve the submission of this version of the manuscript.

Declaration of interest

None.

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.pocean.2018.04.014.

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