

## Feeding dynamics of Northwest Atlantic small pelagic fishes

Justin J. Suca<sup>1,2</sup>, Julie W. Pringle<sup>1,3</sup>, Zofia R. Knorek<sup>1,4</sup>, Sara L. Hamilton<sup>1,5</sup>, David E. Richardson<sup>6</sup>, Joel K. Llopiz<sup>1,\*</sup>

<sup>1</sup> Biology Department, Woods Hole Oceanographic Institution, 266 Woods Hole Road, Woods Hole, MA 02543, USA

<sup>2</sup> MIT-WHOI Joint Program in Oceanography, Woods Hole, MA 02543, USA

<sup>3</sup> Current address: Department of Marine Sciences, University of Connecticut, 1080 Shennecossett Road, Groton, CT 06340, USA

<sup>4</sup> Current address: Oregon Institute of Marine Biology, University of Oregon, P.O. Box 5389 Charleston, OR 97420, USA

<sup>5</sup> Current address: Department of Integrative Biology, Oregon State University, 3029 Cordley Hall, Corvallis, OR 97330, USA

<sup>6</sup> NOAA National Marine Fisheries Service, Northeast Fisheries Science Center, 28 Tarzwell Drive, Narragansett, RI 02882, USA

\*Corresponding author: [jllopiz@whoi.edu](mailto:jllopiz@whoi.edu), 1-508-289-3845

1 **Abstract**

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

20

21 *Key words:* forage fish, zooplankton, feeding, copepods, stable isotopes, trophodynamics, Northeast US  
22 Shelf

## 23 1.1 Introduction

24 Small pelagic fishes are also known as ‘forage fishes’ because of their important role as prey in  
25 many marine ecosystems. These fishes occupy a critical trophic position—one that links planktonic  
26 production to a high diversity of upper trophic level consumers. In the Northwest Atlantic, such  
27 consumers include ecologically and economically important piscivorous fishes such as Atlantic bluefin  
28 tuna (*Thunnus thynnus*) and cod (*Gadus morhua*), several species of sharks, seabirds, pinnipeds, and  
29 whales (Powers and Backus, 1987; Montevecchi and Myers, 1996; Baraff and Loughlin, 2000; Chase,  
30 2002; Link and Garrison, 2002; Overholtz and Link, 2007). Small pelagic fishes have been identified as  
31 some of the most important organisms in marine food webs, as, in certain ecosystems such as upwelling  
32 regions, their abundance may affect the populations of organisms at trophic levels both above and below  
33 them (Cury et al., 2000; Lindegren et al., 2018). These “wasp-waist” ecosystems, where the low diversity  
34 of small pelagic fishes represents the narrow waist of a wasp, can also occur in coastal regions such as the  
35 Northwest Atlantic shelf, though the benthic-pelagic nature of many organisms in this ecosystem cause the  
36 higher trophic levels of the Northwest Atlantic to be less dependent on these planktivorous fishes than  
37 typical “wasp-waist” ecosystems (Cury et al., 2000; Bakun et al., 2009).

38 Small pelagic fishes are often short-lived and mature early, resulting in species abundances that  
39 exhibit large fluctuations, often out of synchrony with each other (Skud, 1982; Schwartzlose and Alheit,  
40 1999; Richardson et al., 2014). Much research has focused on understanding the drivers of these  
41 population fluctuations, primarily including how climatic variability results in the differential recruitment  
42 of these fishes via effects on planktonic prey availability (Torensen and Østvedt, 2000; Chavez et al.,  
43 2003). Evidence of changes to small pelagic communities comes from studies in European waters where  
44 the distributions of small pelagics are changing throughout the Northeast Atlantic and may be responding  
45 to long-scale climatic variability such as the Atlantic Multidecadal Oscillation (ICES, 2012). Classic food  
46 web theory suggests that these organisms, when abundant enough, may exert top down control on their  
47 prey, which means subsequent regime shifts in zooplankton communities could occur if small pelagic fish  
48 populations change (Turner and Mittelbach, 1990; Pace et al., 1999; Frank et al., 2005; Frank et al.,

49 2011). However, the impact of planktivores on zooplankton and top predators varies within the broader  
50 Northwest Atlantic region, with clear cascading top-down effects from overfishing occurring on the  
51 Scotian Shelf (Frank et al., 2005) but much more muted and intricate effects of overfishing on the  
52 ecosystems of the Gulf of Maine and Georges Bank, suggesting a more bottom-up driven system (Link,  
53 2002; Link et al., 2009; Greene, 2013). The more complex system in the Northeast US shelf results from  
54 the large degree of omnivory and generalist feeding of many predators in this system, and thus the system  
55 is likely robust to removal of highly connected species (Link, 2002; Dunne et al., 2004).

56         Understanding whether changes to prey availability may result in changes to the small pelagic  
57 fish community is a pressing need, as recent studies have already demonstrated the early signs of  
58 changing zooplankton communities in the Northwest Atlantic arising from changing hydrographic  
59 patterns of the region, particularly on the Newfoundland and Scotian Shelves and in the Gulf of Maine  
60 (Greene and Pershing, 2007; Beaugrand et al., 2010; Head and Pepin, 2010). Changes on decadal time  
61 scales have included an increase in the abundance of smaller copepod taxa such as *Pseudocalanus* sp. and  
62 *Temora longicornis*, and fluctuations in the abundance of the large copepod *Calanus finmarchicus*,  
63 particularly in the Mid-Atlantic Bight region (Pershing et al., 2005; Kane, 2007; Hare and Kane, 2012; Bi  
64 et al., 2014). It is possible that these changes may affect the dynamics of the food web and energy flow in  
65 the system—and specifically the food available to zooplanktivorous small pelagics. Changes in  
66 zooplankton communities may select for different small pelagic fish species based on their life histories  
67 and feeding behaviors, including any differences in feeding apparatuses (such as the distance between gill  
68 rakers) or inherent preferences for some prey types over others (Magnuson and Heitz, 1971; Dalpadado et  
69 al., 2000; Casini et al., 2004). However, it is uncertain whether small pelagic fishes within a region truly  
70 represent different foraging niches, thus questioning the role of bottom-up trophodynamics in population  
71 fluctuations of these fishes—a topic noted as needing further research (Peck et al., 2013; Yasue et al.,  
72 2013; Chauvelon et al., 2015).

73         Information on the diets of small pelagic fishes may be important to understanding how these  
74 changes in the zooplankton community may influence higher trophic levels. Most recent studies, while

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

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

96         Atlantic herring exhibit both filter and particulate feeding on diel scales and most of their diet by  
97 weight in the Northwest Atlantic is attributed to krill, primarily *Meganyctiphanes norvegica* (Bowman et  
98 al., 2000). The diel variations in feeding include exhibiting particulate feeding on larger prey items such  
99 as fishes and mysids during the day, and consumption of almost exclusively copepods at night, though  
100 copepods dominate the diet overall (Darbyson et al., 2003). Other species of herring (Clupeidae) in the

101 NE Shelf region include alewife and blueback herring (often collectively termed river herring). These  
102 species are anadromous and forage in offshore shelf waters, then swim up rivers to spawn in the spring  
103 (Loesch, 1987). Bowman et al. (2000) represents the only thorough description of alewife diets in the  
104 Northwest Atlantic, indicating a reliance on crustaceans, primarily a mix of krill and copepods. Diet data  
105 for blueback herring is lacking, with sample sizes too small to elucidate much aside from feeding on  
106 gelatinous zooplankton and copepods (Bowman et al., 2000). Atlantic mackerel (mackerel hereafter) are  
107 known for their larger size and general piscivory, even at the larval stage (Robert et al., 2008). However,  
108 being a small scombrid, adult mackerel have been shown to be consumers of zooplankton, including  
109 small copepods and fish larvae (Pepin et al., 1987; Langoy et al., 2012; Bachiller et al., 2016; Jansen,  
110 2016; Óskarsson et al., 2016). Their potential role as a predator of fish larvae is important in  
111 understanding the recruitment of other fishes and understanding the dependence of mackerel on the  
112 spawning of certain taxa such as sand lance (Fogarty et al., 1991). Atlantic butterfish (butterfish hereafter)  
113 are both taxonomically and ecologically distinct from all other species of small pelagic fishes in the NE  
114 Shelf region. Unlike the generally crustacean-dominated diets of clupeids, butterfish have been shown to  
115 primarily consume soft-bodied zooplankton (Maurer and Bowman, 1975; Oviatt and Kremer, 1977;  
116 Bowman and Michaels, 1984), but major portions of stomach contents are usually unidentifiable.

117 While stomach content studies provide insight into the specific prey types consumed by  
118 organisms, stable isotope analysis can yield a broader and complementary understanding of energy flow  
119 in an ecosystem. Diet studies based on visual inspection of stomach contents alone have limitations such  
120 as missing soft bodied organisms and only capturing recently consumed items, while stable isotopes  
121 provide a longer-term, integrated signal of foraging behavior, albeit without information on actual prey  
122 species composition (Hyslop, 1980; Peterson and Fry, 1987). Stable isotope analysis reflects the  
123 nutritional sources, including variability and differences in these sources among consumers (Fry, 2006).  
124 Carbon stable isotope ratios are useful in an ecological context because they can provide a proxy for the  
125 base of the food web due to differential discrimination of  $^{13}\text{C}$  among primary producers (DeNiro and  
126 Epstein, 1978). Nitrogen isotopes can also reflect base-of-the-food-web variability and, within a system,

127 can provide a proxy for the trophic position of an organism due to the assumed trophic discrimination  
128 factor that estimates  $\delta^{15}\text{N}$  values will increase approximately 3.4 per mille (‰) per trophic level, though  
129 this value has been shown to vary by trophic level (DeNiro and Epstein, 1981; Hussey et al., 2014).  
130 Stable isotopes therefore may provide a more integrated signal of nutrient and carbon transfer through  
131 food webs, information that is critical in a changing ecosystem.

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

## 138 **2. Methods**

### 139 2.1 Field methods

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

### 151 2.2 Diet analysis 152

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



178 Diets were described by the proportion of prey consumed by species with station as the sampling  
179 unit (i.e. the prey consumed by multiple specimens of the same species were pooled for each station).  
180 Biomass and numerical descriptors of diet allow for interpreting two different functions in trophic  
181 ecology. Biomass of prey represents the prey items that likely contribute most to consumer growth and  
182 development, as energy transferred up the food web is more accurately represented by biomass (Hyslop,  
183 1980). Numbers of individuals consumed provides an opportunity to quantify and compare the top down  
184 effects of consumers on their prey species. Feeding incidences were calculated as the fraction of analyzed  
185 fish that contained prey.

186 To assess overlap in the diet of small pelagic fishes by species and season, the diets of consumers  
187 in each season were compared using hierarchical cluster analysis based on the Bray-Curtis dissimilarity  
188 matrix constructed from the average arc-sine transformed proportions of prey using the “vegan” package  
189 in R statistical software (Version 3.4.0; Oksanen et al., 2018). Prey categories that composed greater than  
190 1% of the diet of any of the consumer-season groupings were included in the analysis, except the  
191 categories of other and unknown, which were excluded. Butterfish were excluded from cluster analysis  
192 owing to the high proportion of unknown prey in their diet. Hierarchical clustering used the unweighted  
193 arithmetic average method (Legendre and Legendre, 2012).

194 Canonical correspondence analysis (CCA) was employed to assess diet variability within a  
195 consumer species. CCAs are a direct gradient analysis that serves as a multivariate equivalent to a  
196 multiple non-linear regression where a set of explanatory variables is used to predict species or  
197 community composition (ter Braak, 1986; Garrison and Link, 2000). The response variables for the CCAs  
198 were the prey consumed by fish within the same cruise-station-fork length bin (1 cm) grouping. A  
199 detrended correspondence analysis was performed to ensure that the response variables followed a  
200 unimodal distribution, an assumption of CCA (Lepš and Šmilauer, 2003). Season, region (Gulf of Maine,  
201 Georges Bank, Southern New England Shelf, and Middle-Atlantic Bight), day/night, and depth of  
202 collection were included as explanatory factors to explain variability in the diet of the small pelagic  
203 fishes. Season, region, and day/night were converted to nominal variables for inclusion in the CCA

204 (spring to fall, north to south, and day to night). Explanatory factors were chosen through forward  
205 stepwise selection (ter Braak, 1986), only keeping factors that represented a significant contribution to  
206 explaining the variance in the diet as determined through permutation tests.

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

### 211 2.3 Stable isotope analysis

212 Small sections of dorsal musculature of the 5 small pelagic species were analyzed for bulk carbon  
213 and nitrogen stable isotopes. Samples were dried at 60°C in a drying oven for at least 48 hours and then  
214 pulverized to a powder. Subsamples (1.2-1.5 mg) were weighed, wrapped in tin foil, and then analyzed  
215 with a PDZ Europa ANCA-GSL elemental analyzer interfaced to a PDZ Europa 20-20 isotope ratio mass  
216 spectrometer (Sercon Ltd., Cheshire, UK) by the University of California Davis Stable Isotope Facility.  
217 Analyses yielded carbon to nitrogen ratios (C:N) and the isotopic ratios of <sup>13</sup>C:<sup>12</sup>C and <sup>15</sup>N:<sup>14</sup>N in each  
218 sample. We report stable isotope ratios using the conventional delta notation (i.e. δ<sup>13</sup>C and δ<sup>15</sup>N; Fry,  
219 2006), with the reference standards of Pee Dee belemnite (for δ<sup>13</sup>C) and atmospheric nitrogen (for δ<sup>15</sup>N),  
220 calculated with the following equation:

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

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

$$224 \quad \delta^{13}C \text{ corrected} = \delta^{13}C - 4.763 + 4.401 * \ln(\text{C:N})$$

225 Linear regression analysis was used to compare each isotope with latitude and depth. The water  
226 column depth at each station was extracted from the NOAA Center for Environmental Information  
227 bathymetry raster (0.03° resolution; <http://maps.ngdc.noaa.gov/viewers/wcs-client/>). Student's t-tests

228 were used to compare differences within species by season with the exception of seasonal comparisons in  
229  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  for butterfish, which were compared using Wilcoxon ranked sum test due to unequal  
230 variances.

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

$$236 \quad \text{SEA}_c = \text{SEA} * (n-1) / (n-2)$$

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

### 251 **3. Results**

#### 252 3.1 Diet composition

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

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

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

279 and number in the spring to one dominated by *Neomysis* by both number and biomass in the fall.  
280 *Centropages* was also common in the fall diet of mackerel but was more prevalent in 2015 than 2014  
281 (Table S6). Consumption of *Meganyctiphanes norvegica* and unidentifiable Euphausiacea increased in the  
282 fall for Atlantic herring and alewife, though Atlantic herring primarily consumed hyperiid amphipods.  
283 Alewife was the only species to consume primarily Euphausiacea (mostly *Meganyctiphanes norvegica*)  
284 by biomass in both the spring and the fall. Of the identifiable prey, Hyperiidea (both *Hyperia* and  
285 *Parathemisto*) were the dominant prey by biomass and number for butterfish in both seasons. Little could  
286 be concluded for blueback herring in the fall due to low sample sizes and a diet dominated by Salpida  
287 (93.3%) that was due to two fish containing a remarkable 556 salps between them, resulting in the  
288 remainder of non-salp prey (n = 40) being a small fraction of the total.

### 289 3.2 Hierarchical cluster analysis

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

### 297 3.3 Canonical correspondence analysis

298 The CCA for mackerel accounted for 22.4% of the variation in diets and the first two canonical  
299 axes explained 80.5 % of this variance. Season, day/night, depth, and region were significant explanatory  
300 factors. *Neomysis* was important in the diet in the fall, while *Calanus* and appendicularians were  
301 important in the spring. Appendicularia and PPC were more common in the diet in deeper waters while  
302 *Ammodytes* was found in shallower waters (Fig. 3a). PPC copepods and Appendicularia were also more  
303 common at night while *Ammodytes* and *Calanus* were more common during daylight hours (Fig. 3a). The  
304 CCA for Atlantic herring accounted for 32.6% of the total variance, with the first two canonical axes

305 explaining 94.9% of this variation (Fig. 3b). The CCA for Atlantic herring showed three significant  
306 explanatory variables: region, season, and depth. Krill showed an association with greater depths and  
307 hyperiid amphipods showed association with the fall. The CCA for alewife explained 24.8% of the  
308 variation and only retained season and region (thus 100% of variance is explained by the first two  
309 canonical axes; Fig. 3c). The CCA shows *Hyperia* being strongly associated with fall while *PPC* was  
310 associated with more southerly regions (Fig. 3c). Blueback herring had a low number of samples  
311 described by each explanatory factor and thus CCA was not performed on their diet. CCA was also not  
312 performed on the diet of butterfish as their diet contained many unidentifiable prey items.

### 313 3.4 Stable isotope analysis

314 Clear latitudinal trends were apparent for  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values for certain species (Fig. S2).  
315 Significant negative correlations were present for  $\delta^{13}\text{C}$  and latitude for mackerel ( $r=-0.32$ ,  $p<0.01$ ),  
316 blueback herring ( $r=-0.37$ ,  $p<0.01$ ), and Atlantic herring ( $r=-0.37$ ,  $p<0.001$ ; Fig. S2a). Significant  
317 negative correlations of  $\delta^{15}\text{N}$  with latitude were present in mackerel ( $r=-0.53$ ,  $p<0.001$ ), alewife ( $r=-0.57$ ,  
318  $p<0.001$ ), Atlantic herring ( $r=-0.25$ ,  $p<0.01$ ), and blueback herring ( $r=-0.26$ ,  $p<0.01$ , Fig. S2b). Two of 5  
319 relationships of  $\delta^{15}\text{N}$  with bottom depth (Fig. S3) were observed to be significant while no relationships  
320 between  $\delta^{13}\text{C}$  and bottom depth were observed to be significant. There was no significant trend between  
321 bottom depth or latitude and fork length for any species, and thus it was assumed that the size of the fish  
322 was not the cause of these trends.

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

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

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

#### 340 **4. Discussion**

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

349 Differences in spring diets among consumer species and between seasons within a species were  
350 evident due to the identification of copepod prey usually to the genus level, thereby improving our  
351 understanding of food webs in the NE Shelf region. However, hierarchical cluster analysis grouped spring  
352 Atlantic herring, spring mackerel and spring blueback herring at the 75% similarity level owing to the  
353 large proportion of copepods in their diets. Alewife were less similar due to krill composing a large  
354 proportion of their diet in the spring in addition to copepods. Differences in the relative abundance of  
355 each copepod taxon in the diet among consumer species are noteworthy, though the CCA of mackerel,  
356 Atlantic herring, and alewife make the cause of this variability difficult to elucidate. Explanatory factors

357 associated with each copepod taxon varied by fish species with the exception of a weak association of  
358 *PPC* and *Calanus* with spring. This suggests that these copepod taxa are likely consumed in similar  
359 locations that vary by small pelagic species with no obvious spatial differences.

360         The similar levels of small genera (*PPC*) of copepods and the larger genus *Calanus* in the spring  
361 diets of small pelagics is a notable observation when considering the observed decadal-scale changes in  
362 the zooplankton community of the NE Shelf (Pershing et al., 2005; Greene and Pershing, 2007; Kane,  
363 2007; Beaugrand et al., 2015). These observations have shown an increase in the abundance and diversity  
364 of small copepods in the Northwest Atlantic, while the abundance of larger genera, particularly the lipid-  
365 rich *Calanus finmarchicus*, has fluctuated (Mid-Atlantic Bight) or decreased (in the case of the  
366 Newfoundland and Scotian Shelves) on regional scales and is projected to decrease throughout much of  
367 the NE Shelf (Kane, 2007; Beaugrand et al., 2010; Head and Pepin, 2010; Grieve et al., 2017). Thus, we  
368 are uncertain if the prominence of these smaller copepod genera in the diet of small pelagic fishes is a  
369 response to relatively high levels of availability and the rapidly shifting hydrography of the region (Chen  
370 et al., 2014; Forsyth et al., 2015), and more importantly what the consequences are for small pelagic fish  
371 nutritional condition. Bowman et al. (2000), who report on diets of small pelagics from the same regions  
372 here but during 1977-1980, found *Calanus* to be important in the diet of alewife and Atlantic herring, but  
373 they classified most copepods as unidentifiable or Calanoida, and thus we cannot fairly assess changes in  
374 the diet between our study and theirs. It is also worth noting that studies from Europe show a much  
375 greater reliance on *Calanus* in the diet of Atlantic herring than our results (Holst et al., 1997; Kennedy et  
376 al., 2009; Langoy et al., 2012). Thus, if Atlantic herring are adapted to be at optimal condition—including  
377 reproductive condition—when *Calanus* prey are heavily consumed, changes in dominant zooplankton  
378 taxa to smaller, more lipid-poor genera could have large implications for the growth, survival,  
379 reproduction, and food quality of this important forage fish species in the NE Shelf region. Alewife also  
380 showed a higher proportion of *Calanus* by proportion of number in their diet than that of the other small  
381 pelagic fishes, and *Calanus* was found in the diet of alewife in both spring and fall. Thus it is also  
382 possible that alewife may be susceptible to changes in *Calanus* abundance throughout the Northwest



383 Atlantic. However, both Atlantic herring and alewife may be able to rely on krill during times of low  
384 *Calanus* abundance, but projected changes to abundances of *Meganyctiphanes norvegica* in the Gulf of  
385 Maine remain uncertain due to difficulties in assessing their presence and abundance (Wiebe et al., 2013;  
386 Lowe et al., 2018). Bowman et al. (2000) showed a very high abundance of *Meganyctiphanes norvegica*  
387 (>80%) in the diet of Atlantic herring and alewife (>65%) in the Gulf of Maine, corroborating the  
388 suggestion that these fishes may be able to rely on krill as a major prey source in the Gulf of Maine. Our  
389 results further substantiate this, as krill were most abundant in the diet of alewife in the northerly regions  
390 of our study, including the Gulf of Maine. Long-term monitoring of small pelagic fish diets and condition  
391 (e.g. lipid content) as they relate to zooplankton abundance and, importantly, composition would likely  
392 prove fruitful for effective ecosystem-based management of the NE Shelf region in the face of rapid  
393 ecosystem change (Pershing et al., 2015).

394         The prevalence of krill (Euphausiacea, namely *Meganyctiphanes norvegica*) in the fall diets of  
395 blueback herring, Atlantic herring, and the fall and spring diets of alewife may be a result of increased  
396 coupling of predators and prey during the absence of other prey items. Though krill were present in the  
397 diet of small pelagics in the spring as well, the substantially larger amounts in the fall may be a result of  
398 the lack of availability of many copepods during this time as they begin to enter diapause, particularly  
399 *Calanus finmarchicus* (Pershing et al., 2004; Johnson et al., 2007). This lack of copepod availability is  
400 evident in the diet shift of the clupeids studied, which consumed primarily copepods and few krill by  
401 number in the spring, despite higher environmental abundances of krill in the spring in the Gulf of Maine  
402 region (NOAA NEFSC, unpub. data). Copepods entering diapause in the fall, where they sink to depths in  
403 excess of 200 m, creates a vertical decoupling of their range and that of many of the small pelagic fishes  
404 (Hirche, 1996; Pershing et al., 2004). Further, *Meganyctiphanes norvegica* are abundant in the eastern  
405 Gulf of Maine, which may represent an increased spatial coupling of krill with the clupeids, particularly  
406 Atlantic herring in the fall as they spawn throughout waters of the Gulf of Maine and Georges Bank  
407 (Sinclair and Tremblay, 1984; Hay et al., 2001; Stephenson et al., 2009; Johnson et al., 2011). It is also  
408 possible that the increased importance of krill in the diet of clupeids in the fall was a result of the larger

409 size of fall clupeids used in this study, indicating an ontogenetic shift to larger prey items. Bowman et al.  
410 (2000) observed higher abundances of krill in diets of larger alewife and Atlantic herring, though this was  
411 likely an artifact of larger fish being caught in the Gulf of Maine as regional differences in krill  
412 consumption were much greater than ontogenetic differences in their study. Given the association of krill  
413 with more northerly stations in the diet of alewife and that fork length was not a significant explanatory  
414 factor in the CCA of alewife or Atlantic herring in our study, we believe that differences in the  
415 consumption of krill by season were more likely due to regional differences than size differences.

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

426         Hyperiid amphipods composed the majority of the identified prey of butterfish, a finding that is not  
427 surprising since hyperiid amphipods are often found within gelatinous zooplankton, which butterfish are  
428 known to consume (Harbison et al., 1977; Laval, 1980). Therefore, it is possible that the hyperiid amphipods were  
429 consumed incidentally along with gelatinous zooplankton, which were qualitatively very abundant in the  
430 diet of butterfish (but unable to be incorporated in the prey number and biomass calculations). *Hyperia*, in  
431 particular, being common in the diet of butterfish may indicate feeding on scyphozoan jellies, as  
432 scyphozoans are often the host of this genus of amphipod (Buecher et al., 2001). Ctenophores have  
433 previously been described as prey of butterfish and likely represent a large portion of their diet as well  
434 (Oviatt and Kremer, 1977). Salps were also an important soft-bodied zooplankton in the diet of small

435 pelagics, namely in the fall diet of blueback herring. The nearly monotypic diet of blueback herring  
436 consisting of salps in the fall is the reason that fall blueback herring show the lowest percent similarity to  
437 any other consumer, though our limited sample size inhibits our ability to elucidate much about the  
438 importance of salps to blueback herring.

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

455 Isotopic niche widths were substantially lower in the fall than in the spring for all species except  
456 mackerel. This finding suggests that the carbon and nitrogen sources for these organisms were more  
457 homogenous during the fall than the spring. The small decrease in isotopic niche space in the fall by  
458 mackerel may arise from their continued feeding on *Centropages* in the fall and the addition of *Neomysis*  
459 as a major source of their diet by biomass. This observation suggests that copepods, particularly the more  
460 nearshore *Centropages*, may represent a different source of carbon and nitrogen than the krill and

461 hyperiids consumed by the clupeids in the fall (Durbin and Kane, 2007; Ji et al., 2009; Kürten et al.,  
462 2013). Baseline  $\delta^{15}\text{N}$  data from zooplankton and particulate organic matter across the NE Shelf ecosystem  
463 substantiates this claim, as differences in  $\delta^{15}\text{N}$  are primarily seen inshore-to-offshore with more depleted  
464  $\delta^{15}\text{N}$  values offshore and no trend with latitude (McKinney et al., 2010; J. Lueders-Dumont, pers. comm.).  
465 These data suggest that the difference in stable isotope values of these fishes by season originates from  
466 different prey sources and not solely from spatial effects in the fall, despite the series of significant  
467 correlations of isotopic values with latitude and depth. However, Atlantic herring and alewife may be an  
468 exception since they were collected at stations with deeper waters in the fall, when they showed depleted  
469  $\delta^{15}\text{N}$  values. Thus the difference in  $\delta^{15}\text{N}$  values for Atlantic herring and alewife by season may originate  
470 from utilization of more offshore nitrogen sources. Diet data contrast isotopic niche overlap results  
471 because there was more dietary similarity in the spring among mackerel and the three clupeids studied,  
472 while isotopic overlap was lower. This indicates that dietary differences, even when examined with high  
473 taxonomic resolution, may not fully reflect differences in energy flow through small pelagics on the NE  
474 Shelf. Our findings of greater seasonal than inter-specific differences in isotopic niches of small pelagics  
475 are consistent with similar studies on small pelagics from other regions, indicating that the role of energy  
476 flow to these fishes may vary more with time and location than species (Costalago et al., 2012; Yasue et  
477 al., 2013). Some of these seasonal differences may be driven by factors such as small-scale spatial and  
478 temporal variability at the base of the food web that we were unable to thoroughly assess in this study.

479         Appendicularians, which are a soft-bodied (often referred to as gelatinous) zooplankter, were  
480 also common in the spring diet of the small pelagics studied (with the exception of alewife), particularly  
481 in 2013. Appendicularians feed through filtering nanoplankton via a gelatinous house they build, and thus  
482 represent a notable direct link to the microbial loop (Azam et al., 1983; Jaspers et al., 2015). Owing to this  
483 feeding strategy, appendicularians may be important during spring seasons that have low salinity and high  
484 stratification, which limit blooms of larger phytoplankters and favor microbial based primary  
485 productivity. Such conditions have been shown to occur in the Gulf of Maine during negative phases of  
486 the North Atlantic Oscillation (Townsend et al., 2015). This phenomenon likely occurred in the Gulf of

487 Maine in 2013, as there was a negative winter NAO phase (2-year lag, as suggested by Townsend et al.,  
488 (2015)), which may have led to the increase in appendicularians in the diets of small pelagic fishes in  
489 spring of 2013. While appendicularians and gelatinous zooplankton generally constituted a low  
490 proportion of the biomass of the diet of these fishes, they represent a link to a different carbon and  
491 nitrogen source from most crustacean zooplankton, possibly resulting in an increased isotopic niche width  
492 for species that consume them. Butterfish substantiate this possibility as they display the largest overall  
493 isotopic niche width and have a diet that is dominated by soft-bodied organisms. While the diversity in  
494 their consumption of soft bodied organisms is unknown, the varied feeding pathways and trophic levels  
495 that gelatinous zooplankton represent may cause an increase in the carbon and nitrogen sources utilized  
496 by butterfish (Jaspers et al., 2015). Previous data from Puget Sound show that the isotopic niche of  
497 jellyfish and fish may overlap less than 50% and be variable with time (Naman et al., 2016),  
498 corroborating the suggestion that gelatinous zooplankton may represent different nutrient sources.  
499 However, data on gelatinous zooplankton isotopes on the NE shelf and comparisons of gelatinous  
500 zooplankton and crustacean zooplankton are lacking.

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

512

513  
514  
515  
516  
517  
518  
519  
520  
521  
522  
523  
524  
525  
526  
527  
528  
529  
530  
531  
532  
533  
534  
535  
536

**Acknowledgments**

This work would not have been possible without the samples provided by NOAA’s Northeast Fisheries Science Center, specifically including Jakub Kircun and the many other scientists and crewmembers on the NOAA’s *Henry B. Bigelow* during the spring and fall trawl surveys. We are thankful for the laboratory assistance of Sarah Glancy, Marissa Lerner, Katie Swoap, and Isabelle Stewart. Funding for this work was primarily through a US National Science Foundation (NSF) OCE-RIG grant (OCE 1325451) to JKL, with additional support from NOAA through the Cooperative Institute for the North Atlantic Region (CINAR) under Cooperative Agreement NA14OAR4320158 in the form a CINAR Fellow Award (JKL), an NSF Long-term Ecological Research grant for the Northeast US Shelf Ecosystem (OCE 1655686; JKL), a Hendrix College summer research award (ZRK), and an NSF REU-supported Woods Hole Oceanographic Institution Summer Student Fellowship (SLH). Funding agencies had no role in the study design, data collection and analysis, or writing of the manuscript.

**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.

**Conflict of interest:** none.

**References**

537 Adams, C.F., 2018. Butterfish 2017 Stock Assessment Update. Northeast Fisheries Science  
538 Center Reference Document 18-05.

539 Alldredge, A., Madin, L., 1982. Pelagic tunicates: unique herbivores in the marine plankton.  
540 BioScience, 32, 655-663.

541 Azam, F., Fenchel, T., Field, J.G., Gray, J.S., Meyer-Reil, L.A., Thingstad, F., 1983. The  
542 ecological role of water-column microbes in the sea. Marine Ecology Progress Series, 10,  
543 257-263.

544 Bachiller, E., Skaret, G., Nøttestad, L., Slotte, A., 2016. Feeding ecology of Northeast Atlantic  
545 mackerel, Norwegian spring-spawning herring and blue whiting in the Norwegian Sea.  
546 PLoS One, 11, e0149238.

547 Bakun, A., Babcock, E.A., Santora, C., 2009. Regulating a complex adaptive system via its  
548 wasp-waist: grappling with ecosystem-based management of the New England herring  
549 fishery. ICES Journal of Marine Science, 66, 1768-1775.

550 Baraff, L.S., Loughlin, T.R., 2000. Trends and potential interactions between pinnipeds and  
551 fisheries of New England and the US West Coast. Marine Fisheries Review, 62, 1-39.

552 Batschelet, E., 1981. *Circular statistics in biology*: Academic Press, New York.

553 Beaugrand, G., Conversi, A., Chiba, S., Edwards, M., Fonda-Umani, S., Greene, C., Mantua, N.,  
554 Otto, S., Reid, P., Stachura, M., 2015. Synchronous marine pelagic regime shifts in the  
555 Northern Hemisphere. Philosophical Transactions of the Royal Society B, 370,  
556 20130272.

557 Beaugrand, G., Edwards, M., Legendre, L., 2010. Marine biodiversity, ecosystem functioning,  
558 and carbon cycles. Proceedings of the National Academy of Sciences, 107, 10120-10124.

559 Bi, H., Ji, R., Liu, H., Jo, Y.-H., Hare, J.A., 2014. Decadal changes in zooplankton of the  
560 northeast US continental shelf. PLoS One, 9, e87720.

561 Bowman, R.E., Michaels, W.L., 1984. *Food of seventeen species of northwest Atlantic fish*: US  
562 Department of Commerce, National Oceanic and Atmospheric Administration, National  
563 Marine Fisheries Service, Northeast Fisheries Center.

564 Bowman, R.E., Stillwell, C.E., Michaels, W.L., Grosslein, M.D., 2000. Food of northwest  
565 Atlantic fishes and two common species of squid. NOAA Tech. Memo. NMFS-NE-155.

566 Buecher, E., Sparks, C., Brierley, A., Boyer, H., Gibbons, M., 2001. Biometry and size  
567 distribution of *Chrysaora hysoscella* (Cnidaria, Scyphozoa) and *Aequorea aequorea*  
568 (Cnidaria, Hydrozoa) off Namibia with some notes on their parasite *Hyperia medusarum*.  
569 Journal of Plankton Research, 23, 1073-1080.

570 Casini, M., Cardinale, M., Arrhenius, F., 2004. Feeding preferences of herring (*Clupea*  
571 *harengus*) and sprat (*Sprattus sprattus*) in the southern Baltic Sea. ICES Journal of  
572 Marine Science, 61, 1267-1277.

573 Chase, B.C., 2002. Differences in diet of Atlantic bluefin tuna (*Thunnus thynnus*) at five seasonal  
574 feeding grounds on the New England continental shelf. Fishery Bulletin, 100, 168-180.

575 Chavez, F.P., Ryan, J., Lluch-Cota, S.E., Niquen, M., 2003. From anchovies to sardines and  
576 back: multidecadal change in the Pacific Ocean. Science, 299, 217-221.

577 Chen, K., Gawarkiewicz, G.G., Lentz, S.J., Bane, J.M., 2014. Diagnosing the warming of the  
578 Northeastern US Coastal Ocean in 2012: A linkage between the atmospheric jet stream  
579 variability and ocean response. Journal of Geophysical Research: Oceans, 119, 218-227.

580 Chauvelon, T., Violamer, L., Dessier, A., Bustamante, P., Mornet, F., Pignon-Mussaoud, C.,  
581 Dupuy, C., 2015. Small pelagic fish feeding patterns in relation to food resource



582 variability: an isotopic investigation for *Sardina pilchardus* and *Engraulis encrasicolus*  
583 from the Bay of Biscay (Northeast Atlantic). *Marine Biology*, 162, 15-37.

584 Costalago, D., Navarro, J., Álvarez-Calleja, I., Palomera, I., 2012. Ontogenetic and seasonal  
585 changes in the feeding habits and trophic levels of two small pelagic fish species. *Marine*  
586 *Ecology Progress Series*, 460, 169-181.

587 Cury, P., Bakun, A., Crawford, R.J.M., Jarre, A., Quinones, R.A., Shannon, L.J., Verheye, H.M.,  
588 2000. Small pelagics in upwelling systems: patterns of interaction and structural changes  
589 in "wasp-waist" ecosystems. *ICES Journal of Marine Science*, 57, 603-618.

590 Dalpadado, P., Ellertsen, B., Melle, W., Dommasnes, A., 2000. Food and feeding conditions of  
591 Norwegian spring-spawning herring (*Clupea harengus*) through its feeding migrations.  
592 *ICES Journal of Marine Science*, 57, 843-857.

593 Darbyson, E., Swain, D., Chabot, D., Castonguay, M., 2003. Diel variation in feeding rate and  
594 prey composition of herring and mackerel in the southern Gulf of St Lawrence. *Journal of*  
595 *Fish Biology*, 63, 1235-1257.

596 DeNiro, M.J., Epstein, S., 1978. Influence of diet on the distribution of carbon isotopes in  
597 animals. *Geochimica Et Cosmochimica Acta*, 42, 495-506.

598 DeNiro, M.J., Epstein, S., 1981. Influence of diet on the distribution of nitrogen isotopes in  
599 animals. *Geochimica Et Cosmochimica Acta*, 45, 341-351.

600 Dunne, J.A., Williams, R.J., Martinez, N.D., 2004. Network structure and robustness of marine  
601 food webs. *Marine Ecology Progress Series*, 273, 291-302.

602 Durbin, E., Kane, J., 2007. Seasonal and spatial dynamics of *Centropages typicus* and *C.*  
603 *hamatus* in the western North Atlantic. *Progress in Oceanography*, 72, 249-258.

604 Fogarty, M., Cohen, E., Michaels, W., Morse, W., 1991. Predation and the regulation of sand  
605 lance populations: An exploratory analysis. *ICES Mar. Sci. Symp*, Vol. 193 (pp. 0-124).

606 Forsyth, J.S.T., Andres, M., Gawarkiewicz, G.G., 2015. Recent accelerated warming of the  
607 continental shelf off New Jersey: Observations from the CMV Oleander expendable  
608 bathythermograph line. *Journal of Geophysical Research: Oceans*, 120, 2370-2384.

609 Frank, K.T., Petrie, B., Choi, J.S., Leggett, W.C., 2005. Trophic cascades in a formerly cod-  
610 dominated ecosystem. *Science*, 308, 1621-1623.

611 Frank, K.T., Petrie, B., Fisher, J.A., Leggett, W.C., 2011. Transient dynamics of an altered large  
612 marine ecosystem. *Nature*, 477, 86.

613 Fry, B., 2006. *Stable isotope ecology*. New York: Springer.

614 Garrison, L.P., Link, J.S., 2000. Dietary guild structure of the fish community in the Northeast  
615 United States continental shelf ecosystem. *Marine Ecology Progress Series*, 202, 231-  
616 240.

617 Greene, C.H., 2013. Towards a more balanced view of marine ecosystems. *Fisheries*  
618 *Oceanography*, 22, 140-142.

619 Greene, C.H., Pershing, A.J., 2007. Climate drives sea change. *Science*, 315, 1084-1085.

620 Grieve, B.D., Hare, J.A., Saba, V.S., 2017. Projecting the effects of climate change on *Calanus*  
621 *finmarchicus* distribution within the US Northeast Continental Shelf. *Scientific Reports*,  
622 7, 6264.

623 Hanson, J.M., 2017. Feeding interactions between fishes in a coastal ecosystem in the southern  
624 Gulf of St. Lawrence, Atlantic Canada. *Transactions of the American Fisheries Society*,  
625 10.1002/tafs.10021.

626 Harbison, G., Biggs, D., Madin, L., 1977. The associations of Amphipoda Hyperiidia with  
627 gelatinous zooplankton—II. Associations with Cnidaria, Ctenophora and Radiolaria.  
628 Deep Sea Research, 24, 465-488.

629 Hare, J.A., Kane, J., 2012. Zooplankton of the Gulf of Maine—a changing perspective.  
630 American Fisheries Society Symposium, 79, 115-137.

631 Hay, D., Toresen, R., Stephenson, R., Thompson, M., Claytor, R., Funk, F., Ivshina, E.,  
632 Jakobsson, J., Kobayashi, T., McQuinn, I., 2001. Taking stock: an inventory and review  
633 of world herring stocks in 2000. Herring: Expectations for a new millennium, 381-454.

634 Head, E.J., Pepin, P., 2010. Spatial and inter-decadal variability in plankton abundance and  
635 composition in the Northwest Atlantic (1958–2006). Journal of Plankton Research, 32,  
636 1633-1648.

637 Hirche, H.-J., 1996. Diapause in the marine copepod, *Calanus finmarchicus*—a review. Ophelia,  
638 44, 129-143.

639 Holst, J., Salvanes, A., Johansen, T., 1997. Feeding, *Ichthyophonus* sp. infection, distribution and  
640 growth history of Norwegian spring-spawning herring in summer. Journal of Fish  
641 Biology, 50, 652-664.

642 Hussey, N.E., MacNeil, M.A., McMeans, B.C., Olin, J.A., Dudley, S.F., Cliff, G., Wintner, S.P.,  
643 Fennessy, S.T., Fisk, A.T., 2014. Rescaling the trophic structure of marine food webs.  
644 Ecology Letters, 17, 239-250.

645 Hyslop, E.J., 1980. Stomach content analysis: a review of methods and their application. Journal  
646 of Fish Biology, 17, 411-429.

647 ICES, 2012. Report of the working group on small pelagic fishes, their ecosystems and climate  
648 impact (WGSPEC). ICES CM 2012/ SSGEF: 10.

649 Jackson, A.L., Inger, R., Parnell, A.C., Bearhop, S., 2011. Comparing isotopic niche widths  
650 among and within communities: SIBER—Stable Isotope Bayesian Ellipses in R. *Journal of*  
651 *Animal Ecology*, 80, 595-602.

652 Jackson, M.C., Donohue, I., Jackson, A.L., Britton, J.R., Harper, D.M., Grey, J., 2012.  
653 Population-level metrics of trophic structure based on stable isotopes and their  
654 application to invasion ecology. *PLoS One*, 7, e31757.

655 Jansen, T., 2016. First-year survival of North East Atlantic mackerel (*Scomber scombrus*) from  
656 1998 to 2012 appears to be driven by availability of *Calanus*, a preferred copepod prey.  
657 *Fisheries Oceanography*, 25, 457-469.

658 Jaspers, C., Acuña, J.L., Brodeur, R.D., 2015. Interactions of gelatinous zooplankton within  
659 marine food webs. Oxford University Press.

660 Ji, R., Davis, C.S., Chen, C., Beardsley, R.C., 2009. Life history traits and spatiotemporal  
661 distributional patterns of copepod populations in the Gulf of Maine-Georges Bank region.  
662 *Marine Ecology Progress Series*, 384, 187-205.

663 Johnson, C.L., Leising, A.W., Runge, J.A., Head, E.J., Pepin, P., Plourde, S., Durbin, E.G., 2007.  
664 Characteristics of *Calanus finmarchicus* dormancy patterns in the Northwest Atlantic.  
665 *ICES Journal of Marine Science*, 65, 339-350.

666 Johnson, C.L., Runge, J.A., Curtis, K.A., Durbin, E.G., Hare, J.A., Incze, L.S., Link, J.S.,  
667 Melvin, G.D., O'Brien, T.D., Van Guelpen, L., 2011. Biodiversity and ecosystem  
668 function in the Gulf of Maine: pattern and role of zooplankton and pelagic nekton. *PLoS*  
669 *One*, 6, e16491.

670 Kane, J., 2007. Zooplankton abundance trends on Georges Bank, 1977-2004. *ICES Journal of*  
671 *Marine Science: Journal du Conseil*, 64, 909-919.

672 Kennedy, J., Skjæraasen, J.E., Nash, R.D., Thorsen, A., Slotte, A., Hansen, T., Kjesbu, O.S.,  
673 2009. Do capital breeders like Atlantic herring (*Clupea harengus*) exhibit sensitive  
674 periods of nutritional control on ovary development and fecundity regulation? Canadian  
675 Journal of Fisheries and Aquatic Sciences, 67, 16-27.

676 Kürten, B., Painting, S.J., Struck, U., Polunin, N.V., Middelburg, J.J., 2013. Tracking seasonal  
677 changes in North Sea zooplankton trophic dynamics using stable isotopes.  
678 Biogeochemistry, 113, 167-187.

679 Langoy, H., Nottestad, L., Skaret, G., Broms, C., Ferno, A., 2012. Overlap in distribution and  
680 diets of Atlantic mackerel (*Scomber scombrus*), Norwegian spring-spawning herring  
681 (*Clupea harengus*) and blue whiting (*Micromesistius poutassou*) in the Norwegian Sea  
682 during late summer. Marine Biology Research, 8, 442-460.

683 Laval, P., 1980. Hyperiid amphipods as crustacean parasitoids associated with gelatinous  
684 zooplankton. Oceanography and Marine Biology: An Annual Review, 18, 11-56.

685 Legendre, P., Legendre, L.F., 2012. *Numerical ecology*: Elsevier.

686 Lepš, J., Šmilauer, P., 2003. *Multivariate analysis of ecological data using CANOCO*:  
687 Cambridge University Press.

688 Limburg, K.E., Waldman, J.R., 2009. Dramatic declines in North Atlantic diadromous fishes.  
689 BioScience, 59, 955-965.

690 Lindegren, M., Checkley, D.M., Koslow, J.A., Goericke, R., Ohman, M.D., 2018. Climate-  
691 mediated changes in marine ecosystem regulation during El Niño. Global Change  
692 Biology, 24, 796-809.

693 Link, J., 2002. Does food web theory work for marine ecosystems? Marine Ecology Progress  
694 Series, 230, 1-9.

695 Link, J.S., Bogstad, B., Sparholt, H., Lilly, G.R., 2009. Trophic role of Atlantic cod in the  
696 ecosystem. *Fish and Fisheries*, 10, 58-87.

697 Link, J.S., Garrison, L.P., 2002. Trophic ecology of Atlantic cod *Gadus morhua* on the northeast  
698 US continental shelf. *Marine Ecology Progress Series*, 227, 109-123.

699 Loesch, J.G., 1987. Overview of life history aspects of anadromous alewife and blueback herring  
700 in freshwater habitats. *American Fisheries Society Symposium*, 1, 89-103.

701 Logan, J.M., Jardine, T.D., Miller, T.J., Bunn, S.E., Cunjak, R.A., Lutcavage, M.E., 2008. Lipid  
702 corrections in carbon and nitrogen stable isotope analyses: comparison of chemical  
703 extraction and modelling methods. *Journal of Animal Ecology*, 77, 838-846.

704 Lowe, M.R., Lawson, G.L., Fogarty, M.J., 2018. Drivers of euphausiid distribution and  
705 abundance in the Northeast US Shelf Large Marine Ecosystem. *ICES Journal of Marine  
706 Science*, fsx247, doi.org/10.1093/icesjms/fsx247.

707 Magnuson, J.J., Heitz, J.G., 1971. Gill raker apparatus and food selectivity among mackerels,  
708 tunas, and dolphins. *Fishery Bulletin*, 69, 361-370.

709 Maurer, R.O., Bowman, R.E., 1975. *Food habits of marine fishes of the northwest Atlantic—data  
710 report*: NOAA/NMFS Northeast Fisheries Center.

711 McKinney, R., Oczkowski, A., Prezioso, J., Hyde, K., 2010. Spatial variability of nitrogen  
712 isotope ratios of particulate material from Northwest Atlantic continental shelf waters.  
713 *Estuarine, Coastal and Shelf Science*, 89, 287-293.

714 Montevecchi, W., Myers, A., 1996. Dietary changes of seabirds indicate shifts in pelagic food  
715 webs. *Sarsia*, 80, 313-322.

716 Naman, S.M., Greene, C.M., Rice, C.A., Chamberlin, J., Conway-Cranos, L., Cordell, J.R., Hall,  
717 J.E., Rhodes, L.D., 2016. Stable isotope-based trophic structure of pelagic fish and

718 jellyfish across natural and anthropogenic landscape gradients in a fjord estuary. *Ecology*  
719 and *Evolution*, 6, 8159-8173.

720 Nelson, G.A., Ross, M.R., 1991. Biology and population changes of northern sand lance  
721 (*Ammodytes dubius*) from the Gulf of Maine to the Middle Atlantic Bight. *Journal of*  
722 *Northwest Atlantic Fishery Science*, 11, 11-27.

723 Oksanen, J., Blanchet, F., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P.,  
724 O'Hara, R., Simpson, G., Solymos, P., 2018. *Vegan: Community Ecology Package*  
725 *Version 2.4-4*.

726 Óskarsson, G.J., Gudmundsdottir, A., Sveinbjörnsson, S., Sigurðsson, Þ., 2016. Feeding ecology  
727 of mackerel and dietary overlap with herring in Icelandic waters. *Marine Biology*  
728 *Research*, 12, 16-29.

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

732 Oviatt, C.A., Kremer, P.M., 1977. Predation on the ctenophore, *Mnemiopsis leidyi*, by butterflyfish,  
733 *Peprilus triacanthus*, in Narragansett Bay, Rhode Island. *Chesapeake Science*, 18, 236-  
734 240.

735 Pace, M.L., Cole, J.J., Carpenter, S.R., Kitchell, J.F., 1999. Trophic cascades revealed in diverse  
736 ecosystems. *Trends in Ecology & Evolution*, 14, 483-488.

737 Peck, M.A., Neuenfeldt, S., Essington, T.E., Trenkel, V.M., Takasuka, A., Gislason, H., Dickey-  
738 Collas, M., Andersen, K.H., Ravn-Jonsen, L., Vestergaard, N., 2013. Forage fish  
739 interactions: a symposium on “Creating the tools for ecosystem-based management of  
740 marine resources”. *ICES Journal of Marine Science*, 71, 1-4.

741 Pepin, P., Pearre Jr, S., Koslow, J., 1987. Predation on larval fish by Atlantic mackerel (*Scomber*  
742 *scombrus*), with a comparison of predation by zooplankton. Canadian Journal of  
743 Fisheries and Aquatic Sciences, 44, 2012-2018.

744 Pershing, A.J., Alexander, M.A., Hernandez, C.M., Kerr, L.A., Le Bris, A., Mills, K.E., Nye,  
745 J.A., Record, N.R., Scannell, H.A., Scott, J.D., 2015. Slow adaptation in the face of rapid  
746 warming leads to collapse of the Gulf of Maine cod fishery. Science, 350, 809-812.

747 Pershing, A.J., Greene, C.H., Jossi, J.W., O'Brien, L., Brodziak, J.K., Bailey, B.A., 2005.  
748 Interdecadal variability in the Gulf of Maine zooplankton community, with potential  
749 impacts on fish recruitment. ICES Journal of Marine Science: Journal du Conseil, 62,  
750 1511-1523.

751 Pershing, A.J., Greene, C.H., Planque, B., Fromentin, J.-M., 2004. The influence of climate  
752 variability on North Atlantic zooplankton populations. Marine Ecosystems and Climate  
753 Variation: the North Atlantic—a Comparative Perspective, 59-94.

754 Peterson, B.J., Fry, B., 1987. Stable isotopes in ecosystem studies. Annual Review of Ecology  
755 and Systematics, 18, 293-320.

756 Powers, K.D., Backus, R.H., 1987. Energy transfer to seabirds. In R.H. Backus, K.D. Powers  
757 (Eds.), *Georges Bank* (pp. 372-374). Cambridge, MA: MIT Press.

758 Reid, R.N., Almeida, F.P., Zetlin, C.A., 1999. Essential fish habitat source document: Fishery-  
759 independent surveys, data sources, and methods. NOAA Technical Memorandum NMFS-  
760 NE-122.

761 Richardson, D.E., Palmer, M.C., Smith, B.E., 2014. The influence of forage fish abundance on  
762 the aggregation of Gulf of Maine Atlantic cod (*Gadus morhua*) and their catchability in  
763 the fishery. Canadian Journal of Fisheries and Aquatic Sciences, 71, 1349-1362.



764 Ricklefs, R., Nealen, P., 1998. Lineage-dependent rates of evolutionary diversification: analysis  
765 of bivariate ellipses. *Functional Ecology*, 12, 871-885.

766 Robert, D., Castonguay, M., Fortier, L., 2008. Effects of intra- and inter-annual variability in  
767 prey field on the feeding selectivity of larval Atlantic mackerel (*Scomber scombrus*).  
768 *Journal of Plankton Research*, 30, 673-688.

769 Schwartzlose, R., Alheit, J., 1999. Worldwide large-scale fluctuations of sardine and anchovy  
770 populations. *African Journal of Marine Science*, 21.

771 Sinclair, M., Tremblay, M., 1984. Timing of spawning of Atlantic herring (*Clupea harengus*  
772 *harengus*) populations and the match-mismatch theory. *Canadian Journal of Fisheries and*  
773 *Aquatic Sciences*, 41, 1055-1065.

774 Skud, B.E., 1982. Dominance in fishes: the relation between environment and abundance.  
775 *Science*, 216, 144-158.

776 Smith, B.E., Link, J.S., 2010. The trophic dynamics of 50 finfish and 2 squid species on the  
777 northeast US continental shelf. NOAA Technical Memorandum NMFS-NE-216.

778 Stauffer, G., 2004. NOAA protocols for groundfish bottom trawl surveys of the nation's fishery  
779 resources. NOAA Technical Memorandum NMFS-F/SPO-65.

780 Stephenson, R.L., Melvin, G.D., Power, M.J., 2009. Population integrity and connectivity in  
781 Northwest Atlantic herring: a review of assumptions and evidence. *ICES Journal of*  
782 *Marine Science*, 66, 1733-1739.

783 ter Braak, C.J., 1986. Canonical correspondence analysis: a new eigenvector technique for  
784 multivariate direct gradient analysis. *Ecology*, 67, 1167-1179.

785 Toresen, R., Østvedt, O.J., 2000. Variation in abundance of Norwegian spring-spawning herring  
786 (*Clupea harengus*, Clupeidae) throughout the 20th century and the influence of climatic  
787 fluctuations. *Fish and Fisheries*, 1, 231-256.

788 Townsend, D.W., Pettigrew, N.R., Thomas, M.A., Neary, M.G., McGillicuddy, J., Dennis, J.,  
789 O'Donnell, J., 2015. Water masses and nutrient sources to the Gulf of Maine. *Journal of*  
790 *Marine Research*, 73, 93-122.

791 Turner, A.M., Mittelbach, G.G., 1990. Predator avoidance and community structure: interactions  
792 among piscivores, planktivores, and plankton. *Ecology*, 71, 2241-2254.

793 Turner, S.M., Manderson, J.P., Richardson, D.E., Hoey, J.J., Hare, J.A., 2015. Using habitat  
794 association models to predict alewife and blueback herring marine distributions and  
795 overlap with Atlantic herring and Atlantic mackerel: can incidental catches be reduced?  
796 *ICES Journal of Marine Science*, 73, 1912-1924.

797 Walsh, H.J., Richardson, D.E., Marancik, K.E., Hare, J.A., 2015. Long-term changes in the  
798 distributions of larval and adult fish in the northeast US shelf ecosystem. *PLoS One*, 10,  
799 e0137382.

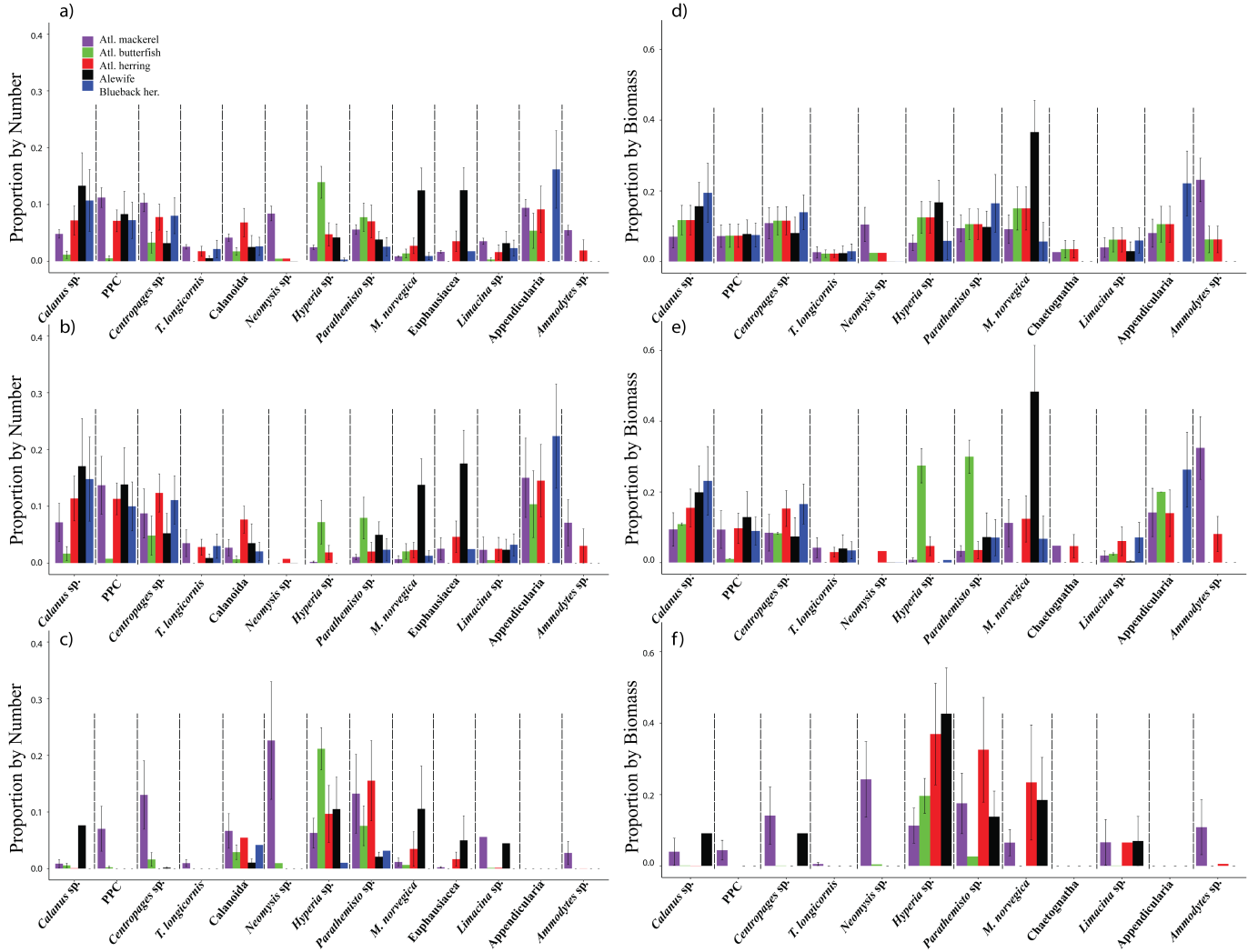
800 Wiebe, P.H., Lawson, G.L., Lavery, A.C., Copley, N.J., Horgan, E., Bradley, A., 2013. Improved  
801 agreement of net and acoustical methods for surveying euphausiids by mitigating  
802 avoidance using a net-based LED strobe light system. *ICES Journal of Marine Science*,  
803 70, 650-664.

804 Yasue, N., Doiuchi, R., Takasuka, A., 2013. Trophodynamic similarities of three sympatric  
805 clupeoid species throughout their life histories in the Kii Channel as revealed by stable  
806 isotope approach. *ICES Journal of Marine Science*, 71, 44-55.

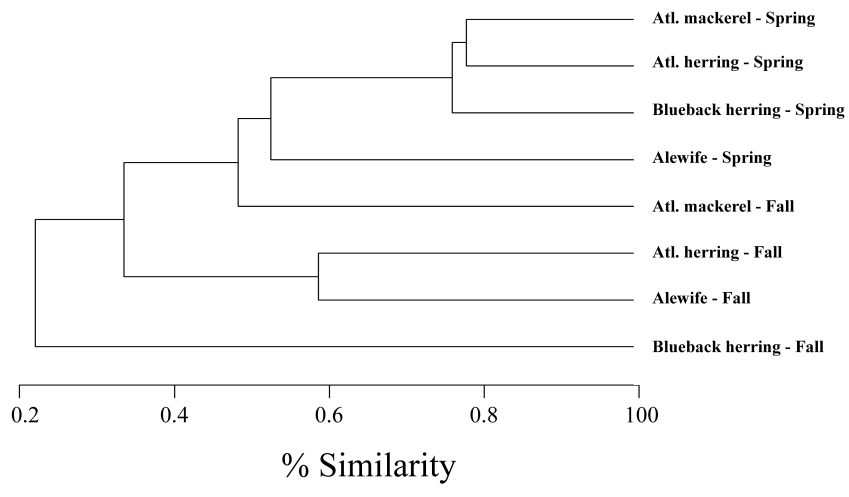
807

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

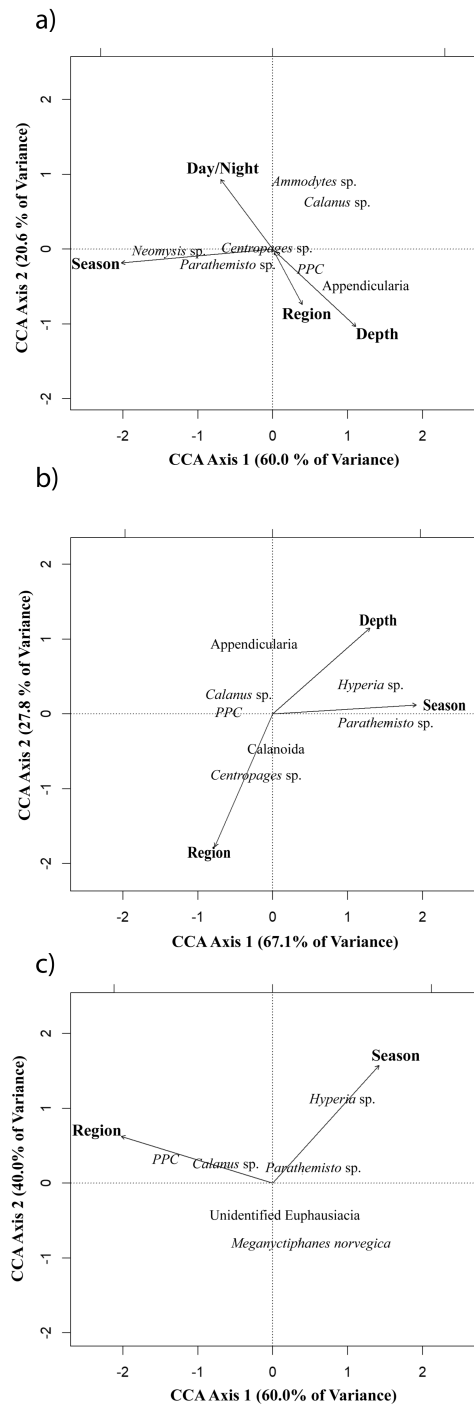
	Atlantic mackerel			Atlantic butterfish			Atlantic herring			Alewife			Blueback herring			All species	
	SCA	SIA	FL	SCA	SIA	FL	SCA	SIA	FL	SCA	SIA	FL	SCA	SIA	FL	SCA	SIA
Spring 2013	19	23	253 (27)	27	26	126 (25)	25	26	198 (32)	0	0	-	0	0	-	71	75
Spring 2014	33	27	246 (42)	30	28	136 (28)	35	40	203 (35)	38	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				



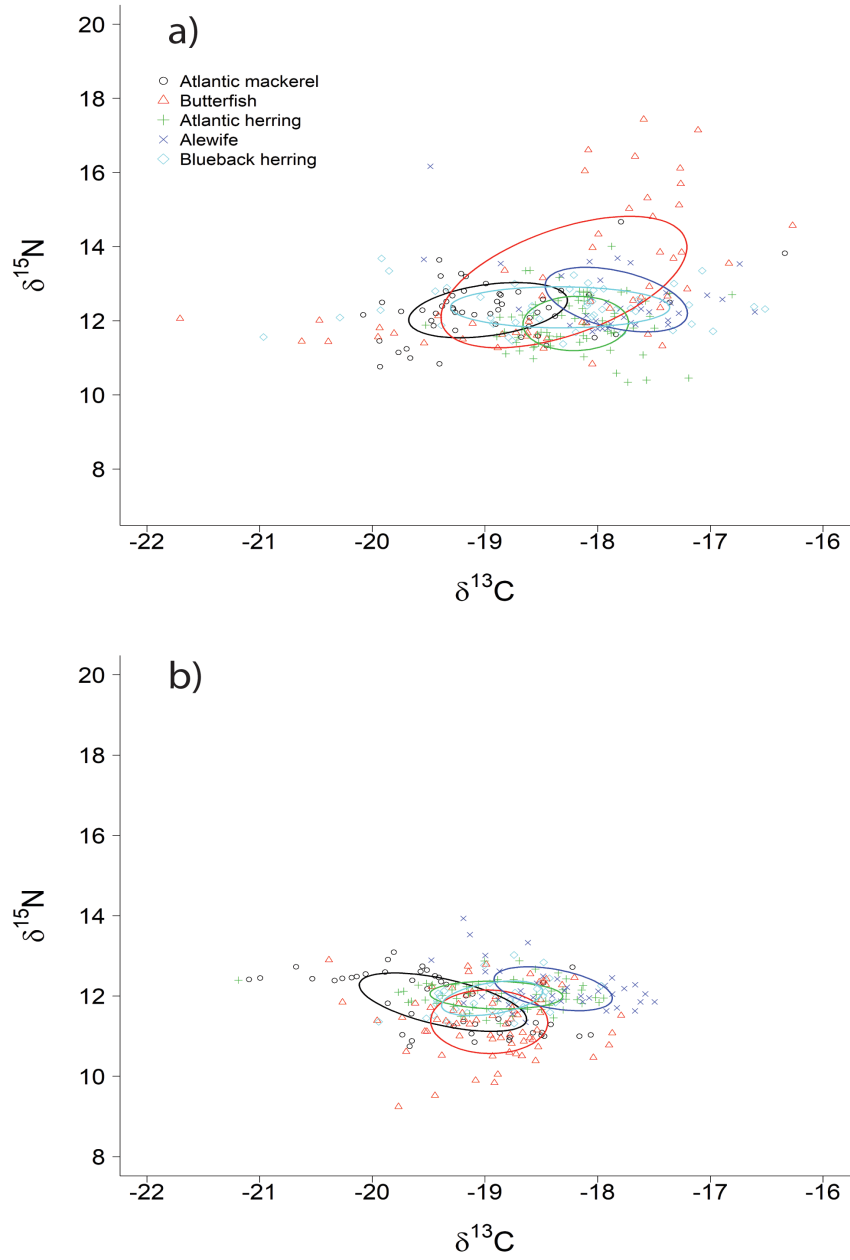
**Figure 1.** Proportion of Prey in the Diets of Small Pelagic Fishes. Mean proportions of common prey taxa in stomach contents by number (a-c) and biomass (d-f) in total (a, d), the spring (b, e), and the fall, (c, f) of five species of small pelagic fishes. *T. longicornis* = *Temora longicornis*,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



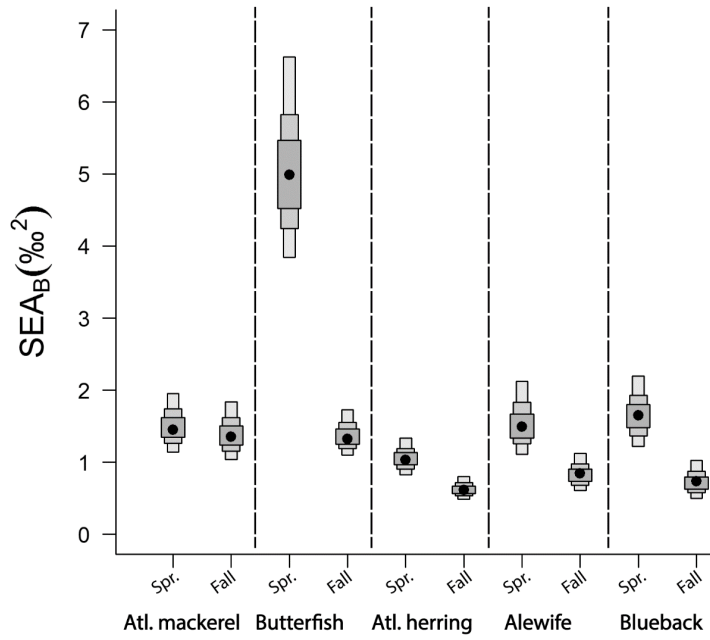
**Figure 2.** *Hierarchical Cluster Analysis of Diet Similarity.* Dendrogram of a hierarchical cluster analysis indicating diet similarity of small pelagic fishes separated by spring and fall.



**Figure 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.



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



**Figure 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.



**Supplementary Material**

**Feeding dynamics of Northwest Atlantic small pelagic fishes**

Suca et al.

**Table S1.** Prey length-to-dry weight conversions and references used to estimate consumed prey biomass from measured lengths.

Prey Taxon	Length to dry weight formula	Reference
<i>Calanus</i> sp.	$W=0.01816 * L^{2.39}$	Robertson 1968
<i>Pseudocalanus</i> sp.	$W=0.01816 * L^{2.39}$	Robertson 1968
<i>Centropages</i> sp.	$W=0.01816 * L^{2.39}$	Robertson 1968
<i>Temora longicornis</i>	$W=0.01816 * L^{2.39}$	Robertson 1968
Chaetognath	$W=0.54 * L^{2.75}$	Coston-Clements et al. 2009
<i>Oikopleura</i> sp.	$W=0.000794 * L^{2.47}$	Hopcroft et al. 1998
<i>Limacina</i> sp.	$W=0.137 * L^{1.5005}$	Bednarsek et al. 2012
<i>Hyperia</i> sp.	$W=0.0049 * L^{2.957}$	Hopcroft et al. 1998
<i>Parathemisto</i> sp.	$W=0.0049 * L^{2.957}$	Hopcroft et al. 1998
<i>Meganyctiphanes norvegica</i>	$W=0.00287 * L^{2.91}$	Harvey et al. 2012
<i>Neomysis</i> sp.	$W=0.00436 * L^{2.77}$	Clutter and Theilacker 1971
<i>Ammodytes</i> sp.	$W=0.000389L^{2.97}$	Pepin 1995

**Table S2.** Mean numerical percentage by station of the dominant prey items for five species of Northeast US continental shelf small pelagic fishes by season.

Prey taxon	Atlantic mackerel			Atlantic butterfish			Atlantic herring			Alewife			Blueback herring		
	Tot.	Spr.	Fall	Tot.	Spr.	Fall	Tot.	Spr.	Fall	Tot.	Spr.	Fall	Tot.	Spr.	Fall
Polychaeta	0.9	1.5	0.1	2.3	3.6	0.9	0	0	0	0.1	0.1	0	0.1	0.2	0
Cladocera	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Calanus</i> sp.	4.8	7.2	0.9	1.1	1.7	0.6	7.2	11.4	0.1	13.3	17	7.6	10.7	14.8	0
<i>Pseudo-/Para-/Clausocalanus</i>	11.2	13.7	7	0.5	0.8	0.2	7.1	11.3	0	8.3	13.8	0	7.2	10	0
<i>Centropages</i> sp.	10.3	8.7	13	3.3	4.8	1.6	7.8	12.3	0	3.2	5.2	0.2	8	11.1	0
<i>T. longicornis</i>	2.6	3.5	1	0	0	0	1.8	2.8	0	0.5	0.9	0	2.2	3	0
Calanoida	4.2	2.7	6.7	1.8	0.7	2.9	6.8	7.7	5.5	2.5	3.5	1.1	2.6	2.1	4.2
<i>Candacia</i> sp.	0.1	0	0.3	1	0	2	0.2	0	0.6	3.2	0	8.1	0	0	0
<i>Caligus</i> sp.	1.2	1.9	0	0.2	0	0.5	0	0	0	0	0	0	0.1	0.2	0
<i>Mysis mixta</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Mysis bigelowi</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Neomysis</i> sp.	8.4	0	22.6	0.5	0	1	0.5	0.7	0	0	0	0	0	0	0
Mysidae	0	0	0	0	0	0	0	0	0	0	0.1	0	0.2	0.2	0
Cumacea	0	0	0	0	0	0	0.4	0.7	0	1.6	2.6	0	0	0	0
<i>Gammaria</i> sp.	0.3	0.5	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Gammarus</i> sp.	0.5	0.1	1.1	0.5	0	1	0	0	0	1	1.6	0	0.3	0.5	0
Ampithoidae	0	0	0	0	0	0	0.1	0.2	0	0	0	0	0	0	0
Aoridae	0	0	0	0	0.1	0	0	0	0	0.1	0.2	0	0	0	0
Haustoriidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Melitidae	0	0.1	0	0	0	0	0	0	0	0	0	0	0	0	0
Corophiidae	0.2	0.3	0	0	0	0	0	0	0	2.4	4	0	0	0	0
<i>Hyperia</i> sp.	2.5	0.2	6.3	13.9	7.2	21.2	4.8	1.9	9.7	4.2	0	10.5	0.3	0	1
<i>Parathemisto</i> sp.	5.6	1.1	13.2	7.8	7.9	7.6	7	2	15.5	3.8	5	2.1	2.6	2.3	3.1
Lycaeidae	0	0	0	0.3	0	0.6	0	0	0	0	0	0	0	0	0
Phronimidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pronoidea	0	0	0	0.2	0	0.4	0	0	0	0	0	0	0	0	0
Hyperidea	0.1	0	0.2	2.8	4.6	0.8	2.6	0	6.9	0.1	0	0.3	0	0	0
<i>Euphausia</i> sp.	3.4	1.9	6.1	0	0	0	1.2	0.7	2.2	2.7	4	0.8	0.5	0.6	0
<i>M. norvegica</i>	1.7	2.5	0.2	0	0	0	3.5	4.6	1.7	12.5	17.5	5	1.8	2.5	0
<i>Nematoscelis</i> sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Thysanopoda</i> sp.	0.8	1.2	0.1	0	0	0	0.8	1	0.3	0.4	0	0.9	0.2	0.2	0
<i>Thysanoessa</i> sp.	0	0	0	0	0	0	0.1	0.2	0	1.1	1.9	0	0	0	0
Euphausiacea	0.9	0.7	1.2	1.4	2.1	0.7	2.7	2.3	3.5	12.5	13.8	10.5	0.9	1.3	0
Ostracoda	0	0	0	0	0	0	2.9	4.6	0	0.4	0.7	0	1.8	2.5	0
Isopoda	0	0	0	0	0	0	0	0	0	0	0	0.1	0	0	0
Crustacean larvae	0.6	0	1.5	1.1	1.6	0.6	0.1	0.1	0	3.3	5.6	0	0.9	0	3.1
Chaetognatha	2.2	3.6	0	0	0	0	0.5	0.8	0	0	0	0	0	0	0
<i>Limacina</i> sp.	3.5	2.3	5.6	0.3	0.5	0.1	1.6	2.5	0.1	3.2	2.4	4.5	2.3	3.2	0
<i>Clione</i> sp.	0.6	0.9	0	0.1	0.1	0	0	0	0	0	0	0	0	0	0
Salpida	0	0	0	0	0	0	0	0	0	0	0	0	6.9	0	25
Appendicularia	9.4	15	0	5.4	10.4	0	9.1	14.5	0	0	0	0	16.2	22.3	0
<i>Ammodytes</i> sp.	5.5	7.1	2.8	0	0	0	1.9	3	0	0	0	0	0	0	0
Fish Larva	0	0.1	0	0	0	0	0	0	0	0	0	0	0.5	0.6	0
Fish Remains	1.2	1.9	0.1	0.4	0	0.9	0.9	0	2.4	0.1	0	0.1	0	0	0
Other	4.3	2.2	7.8	2.1	0.1	4.2	0.1	0.2	0	0	0	0	0	0	0
Unknown	13	19.3	2.3	53	53.8	52.1	28	14.2	51.6	19.3	0	48.3	33.8	22.4	63.5
Total prey	187,570	90,728	278,298	482	1191	1,673	86,587	775	87362	30,185	3120	33,305	122,319	596	122,915

**Table S3.** Mean biomass (dry weight) percentage by station of the dominant prey items for five species of Northeast US continental shelf small pelagic fishes by season. Values were calculated for prey taxa with known length-to-weight relationships (Table S1).

Prey taxon	Atlantic mackerel			Atlantic butterfish			Atlantic herring			Alewife			Blueback herring		
	Tot.	Spr.	Fall	Tot.	Spr.	Fall	Tot.	Spr.	Fall	Tot.	Spr.	Fall	Tot.	Spr.	Fall
<i>Calanus</i> sp.	7.0	9.4	4.0	11.7	10.8	0.1	11.7	15.4	0.0	15.6	19.8	9.1	19.4	23.0	-
<i>Pseudo-/Para-/Clausocalanus</i>	7.2	9.4	4.4	7.3	1.0	0.0	7.3	9.7	0	7.8	12.8	0	7.5	8.9	-
<i>Centropages</i> sp.	10.8	8.4	14.0	11.5	8.3	0.1	11.5	15.2	0	8.0	7.4	9.1	13.9	16.5	-
<i>T. longicornis</i>	2.6	4.2	0.5	2.2	0	0.0	2.2	3.0	0	2.4	3.9	0	2.9	3.5	-
<i>Neomysis</i> sp.	10.4	0.0	24.2	2.5	0	0.4	2.5	3.3	0	0.1	0.1	0	0.1	0.1	-
<i>Hyperia</i> sp.	5.3	0.8	11.2	12.4	27.4	19.6	12.4	4.7	36.9	16.7	0	42.6	5.9	0.7	-
<i>Parathemisto</i> sp.	9.4	3.3	17.5	10.5	29.9	2.6	10.5	3.5	32.5	9.8	7.2	13.7	16.4	7.0	-
<i>M. norvegica</i>	9.2	11.1	6.5	15.0	0	0	15.0	12.3	23.3	36.6	48.3	18.4	5.7	6.7	-
Chaetognatha	2.7	4.7	0	3.5	0	0	3.5	4.6	0	0	0	0	0	0	-
<i>Limacina</i> sp.	4.0	2.0	6.6	6.2	2.5	0.1	6.2	6.1	6.6	2.9	0.3	7.0	6.0	7.1	-
Appendicularia	8.1	14.1	0	10.5	20.0	0	10.5	13.9	0	0	0	0	22.1	26.2	-
<i>Ammodytes</i> sp.	23.1	32.4	10.8	6.3	0	0	6.3	8.1	0.6	0	0	0	0	0	-

**Table S4.** Overall numerical percentages of the dominant prey items of five species of Northeast US continental shelf small pelagic fishes by season.

Prey taxon	Atlantic mackerel			Atlantic butterfish			Atlantic herring			Alewife			Blueback herring		
	Tot.	Spr.	Fall	Tot.	Spr.	Fall	Tot.	Spr.	Fall	Tot.	Spr.	Fall	Tot.	Spr.	Fall
Polychaeta	0	0.1	0	2.5	5.7	0.8	0	1.6	0	0.5	0.5	0	0.3	0.3	0
Cladocera	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Calanus</i> sp.	1	1.7	0	0.5	0.6	0.5	10.4	17.6	0.7	11.3	11.7	1	6.5	6.6	0
<i>Pseudo-/Para-/Clausocalanus</i>	33.3	53.8	4.2	0.9	1.6	0.5	17.4	7.3	0	52.7	54.9	0	32.7	32.9	0
<i>Centropages</i> sp.	30.8	28.2	34.6	5.9	15.2	0.8	22.5	10.5	0	24.4	25.4	0.2	25.3	25.5	0
<i>T. longicornis</i>	2.6	3.9	0.8	0	0	0	7.2	10.4	0	2.8	2.9	0	16.3	16.4	0
Calanoida	6.2	1.5	12.9	3.4	3.1	3.6	10.3	0	4.7	0.2	0.2	0.7	1	1	0.7
<i>Candacia</i> sp.	0	0	0	1.2	0	1.9	0	0	0.1	0.2	0	5.6	0	0	0
<i>Caligus</i> sp.	0	0.1	0	0.1	0	0.1	0	0.3	0	0	0	0	0	0	0
<i>Mysis mixta</i>	0	0	0	0.3	0	0.5	0	0	0	0	0	0	0	0	0
<i>Mysis bigelowi</i>	0	0	0	0	0	0	0	0.2	0	0	0	0	0	0	0
<i>Neomysis</i> sp.	7.4	0	17.8	1.7	0	2.6	0.2	22	0	0	0	0	0	0	0
Mysidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cumacea	0	0	0	0	0	0	1.6	0	0	1.6	1.6	0	0	0	0
<i>Gammaria</i> sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Gammarus</i> sp.	0	0	0	0.1	0	0.2	0	0	0	0	0	0	0	0	0
Ampithoidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Aoridae	0	0	0	0.1	0.2	0	0	0.7	0	0	0	0	0	0	0
Haustoriidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Melitidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Corophiidae	0	0	0	0	0	0	0	0	0	0.1	0.1	0	0	0	0
<i>Hyperia</i> sp.	0.2	0	0.5	15.2	4.3	21.2	0.8	0.7	44.2	0.4	0	9.9	0	0	0.2
<i>Parathemisto</i> sp.	2.2	0.8	4.2	11.9	12.9	11.3	1	0	29.3	0.3	0.1	3.9	0.2	0.2	0.5
Lycaeidae	0	0	0	0.1	0	0.2	0	0	0	0	0	0	0	0	0
Phronimidae	0	0	0	0	0	0	0	0.2	0	0	0	0	0	0	0
Pronoidea	0	0	0	0.8	0	1.2	0	0	0	0	0	0	0	0	0
Hyperoidea	0	0	0	1.7	1.8	1.7	0.1	0	5.3	0	0	0.6	0	0	0
<i>Euphausia</i> sp.	10.1	0	24.4	0	0	0	0	0.1	1.9	0.1	0.1	1.6	0	0	0.2
<i>M. norvegica</i>	0	0	0	0	0	0	0.1	0	1.9	0.4	0.3	2.1	0	0	0
<i>Nematoscelis</i> sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Thysanopoda</i> sp.	0	0	0	0.1	0.2	0	0	0	0.5	0.1	0	2.2	0	0	0
<i>Thysanoessa</i> sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Euphausiacea	0.2	0.1	0.2	0.5	1.2	0.1	0.1	0	4.3	0.8	0.2	14.4	0	0	0
Ostracoda	0	0	0	0	0	0	0.9	0.2	0	1.5	1.6	0	0.1	0.1	0
Isopoda	0	0	0	0	0	0	0	0	0	0	0	0.2	0	0	0
Crustacean larvae	0	0	0	0.8	1.6	0.3	0.2	0	0	0	0	0	0	0	0.3
Chaetognatha	0.8	1.3	0	0.1	0.2	0.1	4.2	0	0.1	0.1	0.1	1	1.8	1.8	0
<i>Limacina</i> sp.	0.2	0.4	0	0	0	0	0.7	0.9	0	0	0	0	0	0	0
<i>Clione</i> sp.	0	0.1	0	0.1	0.2	0	0	0	0	0	0	0	0	0	0
Salpida	0	0	0	0	0	0	0	0	0	0	0	0	0.1	0	93.3
Appendicularia	4.3	7.3	0	13.7	38.5	0	21.8	0.1	0	0	0	0	14.9	15	0
<i>Ammodytes</i> sp.	0.3	0.6	0	0	0	0	0.1	4.2	0.2	0	0	0	0	0	0
Fish Larva	0	0	0	0	0	0	0	0	0.6	0	0	0	0	0	0
Fish Remains	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Other	0	0	0	0.1	0	0.2	0	0	0.5	0	0	0.2	0	0	0
Unknown	0.1	0.1	0.1	1	0.4	1.4	0.3	0.1	0	0	0	0	0	0	0
Total prey	187,570	90,728	278,298	482	1191	1,673	86,587	775	87362	30,185	3120	33,305	122,319	596	122,915

**Table S5.** Overall biomass (dry weight) percentage of the dominant prey items for five species of Northeast US continental shelf small pelagic fishes by season. Values were calculated for prey taxa with known length-to-weight relationships (Table S1).

Prey taxon	Atlantic mackerel			Atlantic butterfish			Atlantic herring			Alewife			Blueback herring		
	Tot.	Spr.	Fall	Tot.	Spr.	Fall	Tot.	Spr.	Fall	Tot.	Spr.	Fall	Tot.	Spr.	Fall
<i>Calanus</i> sp.	1.6	3.3	0	0.5	1.2	0.4	20.4	22.3	0.2	22.2	24.8	0.6	25.9	25.9	-
<i>Pseudo-/Para-/Clausocalanus</i>	7.7	14.5	0.9	0.2	0.5	0.1	5.4	6	0	14.3	16	0	17.9	17.9	-
<i>Centropages</i> sp	13.7	15	12.5	1.8	7.8	0.2	12.7	13.9	0	12.2	13.6	0	25.5	25.5	-
<i>T. longicornis</i>	0.8	1.5	0.2	0	0	0	2.9	3.1	0	1	1.1	0	11.6	11.6	-
<i>Neomysis</i> sp.	33.1	0	66.2	5.1	0	6.5	1.1	1.2	0	0.1	0.1	0	0	0	-
<i>Hyperia</i> sp.	1.3	0.2	2.4	58.7	27.4	67.2	6.2	2.2	48.2	2.6	0	24.5	0.3	0.2	-
<i>Parathemisto</i> sp.	8.9	3.9	14	32.5	59	25.3	5.4	3.8	22.6	1.4	0.7	6.9	2.2	2.2	-
<i>M. norvegica</i>	1.6	0.3	2.8	0	0	0	6.8	5	25.8	45.8	43.5	65.3	5.3	5.3	-
Chaetognatha	1.9	3.8	0	0	0	0	7.7	8.4	0	0	0	0	0	0	-
<i>Limacina</i> sp.	1.6	2.9	0.3	0.4	0.5	0.4	11	12	0.1	0.4	0.1	2.6	8.3	8.3	-
Appendicularia	0.4	0.7	0	0.8	3.7	0	2.5	2.7	0	0	0	0	3.1	3.1	-
<i>Ammodytes</i> sp.	27.3	53.8	0.7	0	0	0	17.9	19.3	3	0	0	0	0	0	-

**Table S6.** Mean numerical percentage by station of the dominant prey items for five species of Northeast US continental shelf small pelagic fishes by cruise.

Prey Taxon	Atlantic mackerel				Atlantic butterfish				Atlantic herring				Alewife				Blueback herring			
	Spr. 2013	Spr. 2014	Fall 2014	Fall 2015	Spr. 2013	Spr. 2014	Fall 2014	Fall 2015	Spr. 2013	Spr. 2014	Fall 2014	Fall 2015	Spr. 2013	Spr. 2014	Fall 2014	Fall 2015	Spr. 2013	Spr. 2014	Fall 2014	Fall 2015
Polychaeta	0	2.5	0	0.1	6.9	0	1	0.5	0	0	0	0	-	0.1	0	0	-	0.2	0	0
Cladocera	0	0	0	0	0	0	0	0	0	0	0	0	-	0	0	0	-	0	0	0
<i>Calanus</i> sp.	11.2	4.4	1.9	0.1	0	3.5	0.3	1.2	14.3	9.3	0.1	0	-	17	15.3	0	-	14.8	0	0
<i>Pseudo-/Para-/Clausocalanus</i>	12.1	14.8	13	2.4	1.5	0	0.2	0.5	5	15.7	0	0	-	13.8	0	0	-	10	0	0
<i>Centropages</i> sp.	15	4.5	2.9	20.9	9.3	0	2.1	0.5	10.8	13.4	0	0	-	5.2	0	0.3	-	11.1	0	0
<i>T. longicornis</i>	4	3.2	1.2	0.8	0	0	0	0	1.3	3.9	0	0	-	0.9	0	0	-	3	0	0
Calanoida	5.3	0.9	2.5	9.9	1.3	0	3.3	1.9	9	6.7	9.3	0	-	3.5	1	1.1	-	2.1	5.6	0
<i>Candacia</i> sp	0	0	0	0.5	0	0	2.2	1.6	0	0	0	1.4	-	0	0	16.2	-	0	0	0
<i>Caligus</i> sp	2.1	1.7	0	0	0	0	0.7	0	0	0	0	0	-	0	0	0	-	0.2	0	0
<i>Mysis mixta</i>	0	0	0	0	0	0	0	0.2	0	0	0	0	-	0	0	0	-	0	0	0
<i>Mysis bigelowi</i>	0	0	0	0	0	0	0	0	0	0	0	0	-	0	0	0	-	0	0	0
<i>Neomysis</i> sp.	0	0	14.1	29.2	0	0	0	3.5	1.8	0	0	0	-	0	0	0	-	0	0	0
Mysidae	0	0	0	0	0	0	0	0	0	0	0	0	-	0.1	0	0	-	0.2	0	0
Cumacea	0	0	0	0	0	0	0	0	0	1.2	0	0	-	2.6	0	0	-	0	0	0
<i>Gammaria</i> sp.	0	0.9	0	0	0	0	0	0	0	0	0	0	-	0	0	0	-	0	0	0
<i>Gammarus</i> sp.	0	0.1	0	1.9	0	0	1.4	0	0	0	0	0	-	1.6	0	0	-	0.5	0	0
Ampithoidae	0	0	0	0	0	0	0	0	0	0.3	0	0	-	0	0	0	-	0	0	0
Aoridae	0	0	0	0	0.1	0	0	0	0	0	0	0	-	0.2	0	0	-	0	0	0
Haustoriidae	0	0	0	0	0	0	0	0	0	0	0	0	-	0	0	0	-	0	0	0
Melitidae	0	0.1	0	0	0	0	0	0	0	0	0	0	-	0	0	0	-	0	0	0
Corophiidae	0	0.6	0	0	0	0	0	0	0	0	0	0	-	4	0	0	-	0	0	0
<i>Hyperia</i> sp.	0.5	0	9.5	3.8	1.2	13.7	21.6	20.1	4.3	0.1	12.1	6.2	-	0	4.8	16.1	-	0	1.4	0
<i>Parathemisto</i>	0.5	1.4	28.6	1.2	11.4	4.3	1.6	22.8	4.9	0	17.7	12.5	-	5	2.7	1.5	-	2.3	4.2	0.1
Lycaeidae	0	0	0	0	0	0	0.8	0	0	0	0	0	-	0	0	0	-	0	0	0
Phronimidae	0	0	0.1	0	0	0	0	0	0	0	0	0	-	0	0	0	-	0	0	0
Pronoidae	0	0	0	0	0	0	0	1.5	0	0	0	0	-	0	0	0	-	0	0	0

Hyperiidea	0	0	0.6	0	2.7	6.7	0.6	1.4	0	0	11.8	0	-	0	0.3	0.3	-	0	0	0
<i>Euphausia</i> sp.	0	3.1	1.2	10	0	0	0	0	0	1.2	1.9	2.6	-	4	1.6	0	-	0.6	0	0.1
<i>M. norvegica</i>	0	4.3	0.4	0.1	0	0	0	0	4.2	4.9	1.9	1.3	-	17.5	9.9	0	-	2.5	0	0
<i>Nematoscelis</i>	0	0	0	0	0	0	0	0	0	0	0	0	-	0	0	0	-	0	0	0
<i>Thysanopoda</i>	0	2.1	0.1	0	0.1	0	0	0	0	1.7	0.6	0	-	0	1.8	0	-	0.2	0	0
<i>Thysanoessa</i> sp.	0	0	0	0	0	0	0	0	0	0.3	0	0	-	1.9	0	0	-	0	0	0
Euphausiacea	0	1.1	2.6	0.1	2.8	1.3	0.9	0	1.4	2.9	5	1.3	-	13.8	21.1	0	-	1.3	0	0
Ostracoda	0	0	0	0	0	0	0	0	0	7.9	0	0	-	0.7	0	0	-	2.5	0	0
Isopoda	0	0	0	0	0	0	0	0	0	0	0	0	-	0	0	0.1	-	0	0	0
Crustacean	0	0	3.4	0	0.5	2.8	0.8	0	0.3	0	0	0	-	5.6	0	0	-	0	4.2	0
Chaetognatha	8.8	0	0	0	0	0	0	0	2	0	0	0	-	0	0	0	-	0	0	0
<i>Limacina</i> sp.	0	3.9	12.7	0	0	1.1	0.2	0	0.1	4.2	0.2	0	-	2.4	8.8	0.1	-	3.2	0	0
<i>Clione</i> sp.	2.1	0.1	0	0	0.2	0	0	0	0	0	0	0	-	0	0	0	-	0	0	0
Salpida	0	0	0	0	0	0	0	0	0	0	0	0	-	0	0	0	-	0	0	99.8
Appendicularia	0	25.3	0	0	20	0	0	0	31.6	2.5	0	0	-	0	0	0	-	22.3	0	0
<i>Ammodytes</i> sp.	4.9	8.6	0	4.9	0	0	0	0	0	5.2	0	0	-	0	0	0	-	0	0	0
Fish Larva	0.1	0	0	0	0	0	0	0	0	0	0	0	-	0	0	0	-	0.6	0	0
Fish Remains	4.5	0	0.2	0	0	0	1.2	0	0	0	4	0	-	0	0.1	0.1	-	0	0	0
Other	3.1	1.5	0.1	13.8	0.2	0	0.3	14.1	0.3	0.1	0	0	-	0	0	0	-	0	0	0
Unknown	25.8	14.8	4.8	0.4	41.8	66.7	60.7	30.1	8.4	18.3	35.4	74.7	-	0	32.6	64.1	-	22.4	84.7	0
Total	50331	123438	19804	52127	409	56	219	629	23365	33997	693	41	-	30079	1976	916	-	101740	28	560

**Table S7.** Mean biomass (dry weight) percentage by station of the dominant prey items for five species of Northeast US continental shelf small pelagic fishes by cruise. Values were calculated for prey taxa with known length-to-weight relationships (Table S1).

Prey Taxon	Atlantic mackerel				Atlantic butterfish				Atlantic herring				Alewife				Blueback herring			
	Spr. 2013	Spr. 2014	Fall 2014	Fall 2015	Spr. 2013	Spr. 2014	Fall 2014	Fall 2015	Spr. 2013	Spr. 2014	Fall 2014	Fall 2015	Spr. 2013	Spr. 2014	Fall 2014	Fall 2015	Spr. 2013	Spr. 2014	Fall 2014	Fall 2015
<i>Calanus</i> sp.	19	4.6	8.9	0.1	0	27.2	0.2	1	15.1	15.8	0.1	0	-	19.9	20	0	-	23.1	-	-
<i>Pseudo-/Para-/Clausocalanus</i>	10.9	8.6	8.3	1.4	1.7	0	0	0	2.4	15.4	0	0	-	12.8	0	0	-	8.9	-	-
<i>Centropages</i> sp.	7.2	2.8	0.2	0.8	0	0	0	0	1.7	3.9	0	0	-	3.9	0	0	-	3.5	-	-
<i>T. longicornis</i>	17.4	3.9	1.8	23.6	13.8	0	0.5	0.1	9.6	19.7	0	0	-	7.4	0	16.7	-	16.6	-	-
<i>Neomysis</i> sp.	0	0	14.3	32	0	0	0	5	7.4	0	0	0	-	0.1	0	0	-	0.1	-	-
<i>Hyperia</i> sp.	1.7	0.3	18.8	5.5	13.5	48.3	96.9	64.5	5	4.4	35.3	39.7	-	0	14.1	66.4	-	0.7	-	-
<i>Parathemisto</i> sp.	1.3	4.3	27.4	9.9	37.7	18.3	1.9	29.3	7.9	0.1	33	31.8	-	7.2	13.5	13.9	-	7.1	-	-
<i>M. norvegica</i>	0	16.8	5.5	7.3	0	0	0	0	10	14.2	20.3	28.6	-	48.4	37.7	2.4	-	6.7	-	-
Chaetognatha	14.2	0	0	0	0	0	0	0	10.6	0	0	0	-	0	0	0	-	0	-	-
<i>Limacina</i> sp.	0.1	2.9	14.9	0.2	0	6.2	0.5	0	0.4	10.6	10.5	0	-	0.3	14.6	0.6	-	7.1	-	-
Appendicularia	0	21.3	0	0	33.3	0	0	0	30	1.4	0	0	-	0	0	0	-	26.3	-	-
<i>Ammodytes</i> sp.	28.2	34.6	0	19.3	0	0	0	0	0	14.4	0.9	0	-	0	0	0	-	0	-	-



**Table S8.** Frequency of occurrence (% of non-empty fish with the prey type present) of prey items extracted from five species of Northeast US shelf small pelagic fishes.

Prey taxon	Atlantic mackerel			Atlantic butterfish			Atlantic herring			Alewife			Blueback herring		
	Tot.	Spr.	Fall	Tot.	Spr.	Fall	Tot.	Spr.	Fall	Tot.	Spr.	Fall	Tot.	Spr.	Fall
Polychaeta	2.9	3.8	2	6.2	3.6	9.5	0.8	1.7	0	3.7	7.9	0	1.5	2.4	0
Cladocera	1	1.9	0	0	0	1.4	0	0	0	1.2	2.6	0	1.5	2.4	0
<i>Calanus</i> sp.	22.5	30.8	14	4.7	3.6	6.8	21.1	40	3.2	9.9	13.2	7	13.6	22	0
<i>Pseudo-/Para-/Clausocalanus</i>	33.3	40.4	26	2.3	1.8	4.1	24.4	50	0	12.3	26.3	0	16.7	26.8	0
<i>Centropages</i> sp.	40.2	40.4	40	4.7	3.6	6.8	21.1	43.3	0	12.3	21.1	4.7	24.2	39	0
<i>T. longicornis</i>	14.7	15.4	14	0	0	1.4	11.4	23.3	0	6.2	13.2	0	7.6	12.2	0
Calanoida	17.6	15.4	20	9.3	3.6	14.9	13.8	26.7	1.6	7.4	5.3	9.3	10.6	12.2	8
<i>Candacia</i> sp	2	0	4	6.2	0	12.2	0.8	0	1.6	1.2	0	2.3	0	0	0
<i>Caligus</i> sp	5.9	11.5	0	0.8	0	2.7	0	0	0	0	0	0	3	4.9	0
<i>Mysis mixta</i>	0	0	0	0.8	0	2.7	0	0	0	0	0	0	0	0	0
<i>Mysis bigelowi</i>	1	0	2	0	0	1.4	0	0	0	0	0	0	0	0	0
<i>Neomysis</i> sp.	17.6	1.9	34	0.8	0	2.7	0.8	1.7	0	1.2	2.6	0	1.5	2.4	0
Mysidae	0	0	0	0	0	1.4	0	0	0	3.7	7.9	0	1.5	2.4	0
Cumacea	1	1.9	0	0	0	1.4	2.4	5	0	8.6	18.4	0	0	0	0
<i>Gammaria</i> sp.	2.9	5.8	0	0	0	1.4	2.4	5	0	1.2	2.6	0	0	0	0
<i>Gammarus</i> sp.	3.9	5.8	2	1.6	0	4.1	0.8	1.7	0	3.7	7.9	0	1.5	2.4	0
Ampithoidae	0	0	0	0	0	1.4	0.8	1.7	0	0	0	0	0	0	0
Aoridae	0	0	0	0.8	1.8	1.4	0	0	0	1.2	2.6	0	0	0	0
Haustoriidae	0	0	0	0	0	1.4	0.8	1.7	0	0	0	0	0	0	0
Melitidae	1	1.9	0	0	0	1.4	0	0	0	1.2	2.6	0	0	0	0
Corophiidae	2	3.8	0	0	0	1.4	0	0	0	6.2	13.2	0	0	0	0
<i>Hyperia</i> sp.	22.5	13.5	32	35.7	12.5	54.1	17.1	20	14.3	18.5	0	34.9	3	2.4	4
<i>Parathemisto</i> sp.	23.5	25	22	11.6	12.5	12.2	14.6	13.3	15.9	28.4	31.6	25.6	16.7	22	8
Lycaeidae	0	0	0	1.6	0	4.1	0	0	0	0	0	0	0	0	0
Phronimidae	2.9	0	6	0	0	1.4	0	0	0	0	0	0	0	0	0
Pronoidea	0	0	0	2.3	0	5.4	0.8	1.7	0	1.2	2.6	0	0	0	0
Hyperidea	2.9	3.8	2	7.8	8.9	8.1	4.9	3.3	6.3	4.9	0	9.3	1.5	2.4	0
<i>Euphausia</i> sp.	12.7	3.8	22	0	0	1.4	4.1	3.3	4.8	13.6	18.4	9.3	6.1	7.3	4
<i>M. norvegica</i>	13.7	9.6	18	0	0	1.4	7.3	8.3	6.3	19.8	31.6	9.3	3	4.9	0
<i>Nematoscelis</i> sp.	0	0	0	0	0	1.4	0	0	0	0	0	0	1.5	2.4	0
<i>Thysanopoda</i> sp.	2.9	1.9	4	0.8	1.8	1.4	2.4	3.3	1.6	1.2	0	2.3	1.5	2.4	0
<i>Thysanoessa</i> sp.	0	0	0	0	0	1.4	0.8	1.7	0	6.2	13.2	0	1.5	2.4	0
Euphausiacea	12.7	7.7	18	4.7	8.9	2.7	8.9	13.3	4.8	29.6	44.7	16.3	9.1	14.6	0
Ostracoda	2.9	1.9	4	0	0	1.4	11.4	23.3	0	6.2	13.2	0	6.1	9.8	0
Isopoda	1	0	2	0	0	1.4	0.8	1.7	0	2.5	0	4.7	0	0	0
Crustacean larvae	8.8	3.8	14	4.7	7.1	4.1	5.7	11.7	0	1.2	2.6	0	4.5	2.4	8
Chaetognatha	1	1.9	0	0	0	1.4	3.3	6.7	0	1.2	2.6	0	0	0	0
<i>Limacina</i> sp.	17.6	11.5	24	1.6	1.8	2.7	7.3	13.3	1.6	6.2	7.9	4.7	13.6	22	0
<i>Clione</i> sp.	3.9	7.7	0	0.8	1.8	1.4	0	0	0	0	0	0	0	0	0
Salpida	0	0	0	0	0	1.4	0	0	0	0	0	0	3	0	8
Appendicularia	8.8	17.3	0	3.1	7.1	1.4	8.9	18.3	0	0	0	0	13.6	22	0
<i>Ammodytes</i> sp.	15.7	23.1	8	0	0	1.4	4.1	6.7	1.6	0	0	0	0	0	0
Fish Larva	2.9	5.8	0	0	0	1.4	0	0	0	1.2	2.6	0	3	4.9	0
Fish Remains	6.9	1.9	12	0.8	0	2.7	3.3	0	6.3	6.2	7.9	4.7	0	0	0
Other	18.6	13.5	24	8.5	3.6	13.5	8.9	18.3	0	0	0	0	0	0	0
Unknown	43.1	44.2	42	90.7	85.7	94.6	51.2	35	66.7	37	2.6	67.4	77.3	68.3	92

**Table S9.** Standard ellipse areas corrected for sample size (%<sup>2</sup>) for each species by season as calculated using  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values to represent their isotopic niche.

	Spring	Fall	Total
Atlantic mackerel	1.53	1.41	1.77
Atlantic butterfish	5.13	1.40	3.58
Atlantic herring	1.07	0.64	1.14
Alewife	1.57	0.82	1.44
Blueback herring	1.69	0.75	1.45
Sand lance	2.19	1.13	2.02

**Table S10.** Percentage overlap in standard ellipse area corrected for sample size (SEA<sub>c</sub>) for  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  of small pelagic fish species in the spring. Values represent the percentage of niche area of row-heading species overlapped by the species in the column headings.

	Atl. mackerel	Atl. butterfish	Atl. herring	Alewife	Blueback herring	Sand lance
Atl. mackerel		65.2	0.1	0.0	40.0	0.5
Atl. butterfish	11.4		7.5	1.6	28.2	8.0
Atlantic herring	0.1	69.5		0.1	14.2	40.4
Alewife	0.0	17.0	0.1		73.4	0.1
Blueback herring	20.6	82.5	4.5	20.3		0.1
Sand lance	0.2	22.9	12.6	0.1	0.1	

**Table S11.** Percentage overlap in standard ellipse area corrected for sample size (SEA<sub>c</sub>) for  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  of small pelagic fish species in the fall. Values represent the percentage of niche area of row-heading species overlapped by the species in the column headings.

	Atl. mackerel	Atl. butterfish	Atl. herring	Alewife	Blueback herring	Sand lance
Atl. mackerel		46.1	22.0	0.1	26.6	26.5
Atl. butterfish	46.3		25.7	7.7	33.4	45.1
Atlantic herring	48.6	56.7		35.6	86.5	85.5
Alewife	0.1	12.7	26.6		33.8	54.0
Blueback herring	50.2	62.7	73.7	38.5		84.4
Sand lance	33.0	56..0	48.2	40.8	55.8	

*Supplementary figure captions*

**Figure S1.** Locations of small pelagic fish used in this study for stomach contents: a) Atlantic mackerel, b) Atlantic butterfish, c) Atlantic herring, d) alewife, e) blueback herring, and f) sand lance. Symbols indicate year and colors indicate season. Relative size of symbol indicates number of fish analyzed from a station, ranging from one to six. GOM=Gulf of Maine, MAB=Mid-Atlantic Bight, GSC= Great South Channel.

**Figure S2.** Relationships of (a)  $\delta^{13}\text{C}$  and (b)  $\delta^{15}\text{N}$  with latitude. Trendlines indicate significant correlations ( $p<0.01$ ).

**Figure S3.** Relationships of  $\delta^{15}\text{N}$  with depth. Trendlines indicate significant correlations ( $p<0.01$ ).

Figure S1.

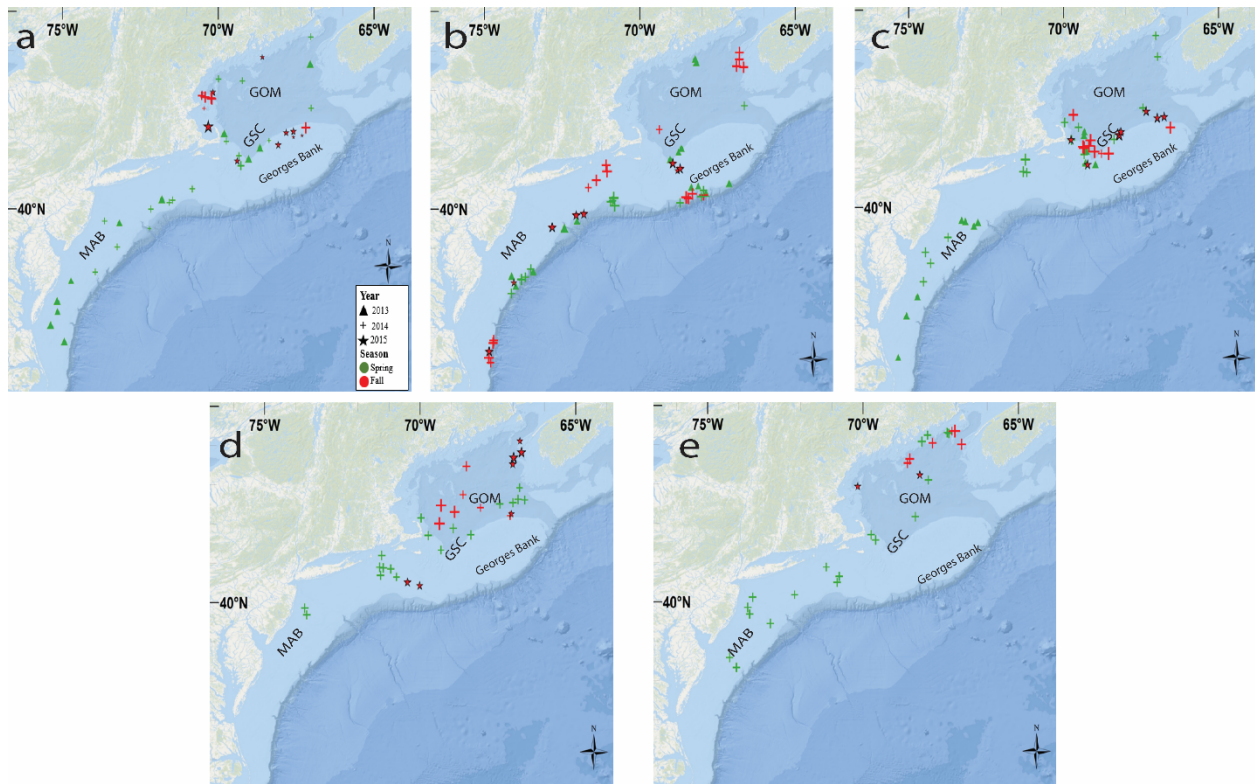


Figure S2.

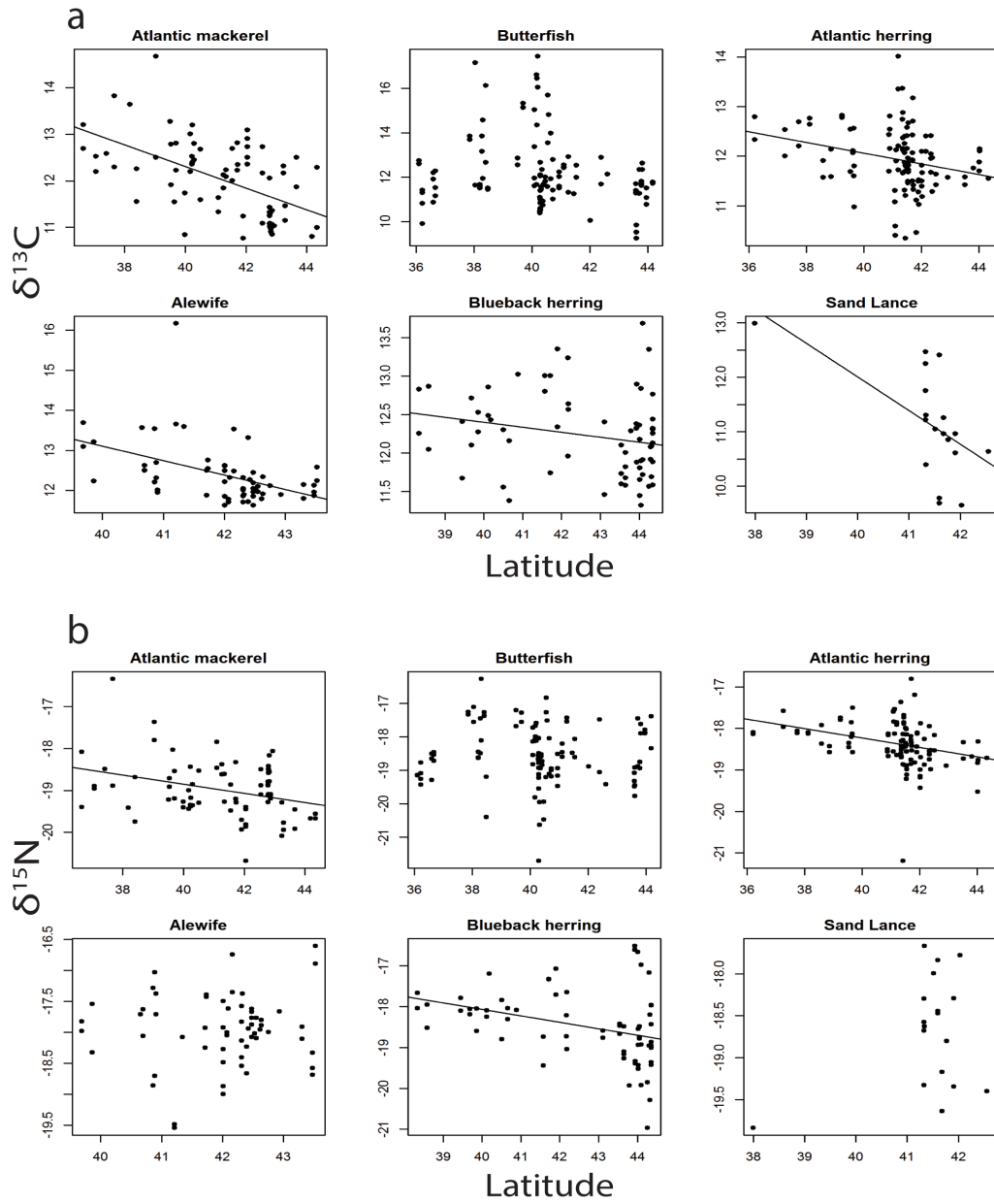
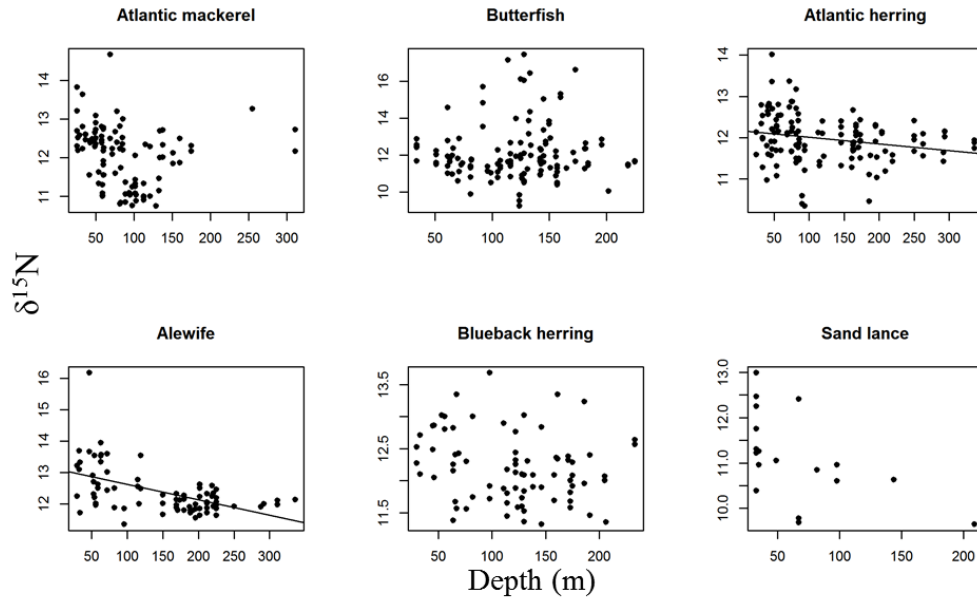


Figure S3.





**Supplement References:**

- Clutter, R. I., and Theilacker, G. H. 1971. Ecological efficiency of a pelagic mysid shrimp, estimates from growth, energy budget, and mortality studies. *Fishery Bulletin*, 69: 93-115.
- Coston-Clements, L., Waggett, R. J., and Tester, P. A. 2009. Chaetognaths of the United States South Atlantic Bight: Distribution, abundance and potential interactions with newly spawned larval fish. *Journal of Experimental Marine Biology and Ecology*, 373: 111-123.
- Harvey, H. R., Pleuthner, R. L., Lessard, E. J., Bernhardt, M. J., and Shaw, C. T. 2012. Physical and biochemical properties of the euphausiids *Thysanoessa inermis*, *Thysanoessa raschii*, and *Thysanoessa longipes* in the eastern Bering Sea. *Deep Sea Research Part II: Topical Studies in Oceanography*, 65: 173-183.
- Hopcroft, R. R., Roff, J. C., and Bouman, H. A. 1998. Zooplankton growth rates: the larvaceans Appendicularia, Fritillaria and Oikopleura in tropical waters. *Journal of Plankton Research*, 20: 539-555.
- Pepin, P. 1995. An analysis of the length-weight relationship of larval fish: limitations of the general allometric model. *Fishery Bulletin*, 93: 419-426.
- Robertson, A. 1968. Continuous plankton recorder: a method for studying the biomass of calanoid copepods. *Bulletins of Marine Ecology*, Vol. 6, Part 7, Issue 1 (223 pp).