

Feeding dynamics of Northwest Atlantic small pelagic fishes

Justin J. Suca¹, Julie W. Pringle^{1,2}, Zofia R. Knorek^{1,3}, Sara L. Hamilton^{1,4}, David E. Richardson⁵, Joel K. Llopiz^{1,*}

¹ Biology Department, Woods Hole Oceanographic Institution, 266 Woods Hole Road, Woods Hole, MA 02543, USA

² Current address: Department of Marine Sciences, University of Connecticut, 1080 Shennecossett Road, Groton, CT 06340, USA

³ Current address: Oregon Institute of Marine Biology, University of Oregon, P.O. Box 5389 Charleston, OR 97420, USA

⁴ Current address: Department of Integrative Biology, Oregon State University, 3029 Cordley Hall, Corvallis, OR 97330, USA

⁵ NOAA National Marine Fisheries Service, Northeast Fisheries Science Center, 28 Tarzwell Drive, Narragansett, RI 02882, USA

*Corresponding author: 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 in detail the diets, along with stable isotope signatures, of five dominant small
5 pelagic species of the northeast US continental shelf ecosystem (Atlantic mackerel *Scomber scombrus*,
6 Atlantic herring *Clupea harengus*, alewife *Alosa pseudoharengus*, blueback herring *Alosa aestivalis*, and
7 Atlantic butterfish *Peprilus triacanthus*). Diet analyses revealed strong seasonal differences in most
8 species. Small 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

22 *Region:* USA, Northeast 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 genera such as *Pseudocalanus* and
62 *Temora*, and fluctuations in the abundance of the large copepod *Calanus finmarchicus*, particularly in the
63 Mid-Atlantic Bight region (Pershing et al., 2005; Kane, 2007; Hare and Kane, 2012; Bi et al., 2014). It is
64 possible that these changes may affect the dynamics of the food web and energy flow in the system—and
65 specifically the food available to zooplanktivorous small pelagics. Changes in zooplankton communities
66 may select for different small pelagic fish species based on their life histories and feeding behaviors,
67 including any differences in feeding apparatuses (such as the distance between gill rakers) or inherent
68 preferences for some prey types over others (Magnuson and Heitz, 1971; Dalpadado et al., 2000; Casini et
69 al., 2004). However, it is uncertain whether small pelagic fishes within a region truly represent different
70 foraging niches, thus questioning the role of bottom-up trophodynamics in population fluctuations of
71 these fishes—a topic noted as needing further research (Peck et al., 2013; Yasue et al., 2013; Chauvelon
72 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}C among primary producers (DeNiro and
126 Epstein, 1978). Nitrogen isotopes can also reflect base-of-the-food-web variability, but within a system

127 can also 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°C freezer to
149 minimize digestion occurring postmortem, and samples were stored at -80°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*), and appendicularians. Appendicularians were always of the genus *Oikopleura* when
168 identifiable, and consist of the organism itself and often a gelatinous ‘house’ within which the organism
169 lives (Allredge and Madin, 1982). Both were enumerated, but numbers rarely matched, likely due to a
170 combination of reasons: appendicularians sometimes lack a house, abandoned houses could be consumed
171 on their own, or houses in a fish’s gut digest more slowly than the organisms (pers. obs.). As such,
172 appendicularian counts were taken to be the maximum of the number of houses or organisms in each fish.
173 Fecal pellets of appendicularians were not counted, as the number of fecal pellets per appendicularian
174 varies. Many fish, particularly butterfish (>90% frequency of occurrence; Table S8), contained
175 unidentifiable prey items that were often soft-bodied. These prey were enumerated but no biomass
176 estimation could be calculated. Infrequently observed prey items, including fish eggs, squid eggs, and
177 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 CCAs 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 ¹³C:¹²C and ¹⁵N:¹⁴N in each
218 sample. We report stable isotope ratios using the conventional delta notation (i.e. δ¹³C and δ¹⁵N; Fry,
219 2006), with the reference standards of Pee Dee belemnite (for δ¹³C) and atmospheric nitrogen (for δ¹⁵N),
220 calculated with the following equation:

$$221 \quad \delta^{13}C \text{ or } \delta^{15}N = \left(\frac{R_{sample}}{R_{standard}} - 1 \right) * 1000$$

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

$$225 \quad \delta^{13}C \text{ corrected} = \delta^{13}C - 4.763 + 4.401 * \ln(\text{C:N})$$

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

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

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

$$237 \text{SEA}_c = \text{SEA} * (n-1) / (n-2)$$

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

252 **3. Results**

253 3.1 Diet composition

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

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

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

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

290 3.2 Hierarchical cluster analysis

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

298 3.3 Canonical correspondence analysis

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

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

314 3.4 Stable isotope analysis

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

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

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

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

341 **4. Discussion**

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

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

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

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

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

515 This work would not have been possible without the samples provided by NOAA’s Northeast Fisheries
516 Science Center, specifically including Jakub Kircun and the many other scientists and crewmembers on
517 the NOAA’s *Henry B. Bigelow* during the spring and fall trawl surveys. We are thankful for the laboratory
518 assistance of Sarah Glancy, Marissa Lerner, Katie Swoap, and Isabelle Stewart. Funding for this work
519 was primarily through a US National Science Foundation (NSF) OCE-RIG [grant number OCE1325451,
520 2015] to JKL, with additional support from NOAA through the Cooperative Institute for the North
521 Atlantic Region (CINAR) under Cooperative Agreement NA14OAR4320158 in the form a CINAR
522 Fellow Award (JKL), a Hendrix College summer research award (ZRK), and an NSF REU-supported
523 Woods Hole Oceanographic Institution Summer Student Fellowship (SLH). Funding agencies had no role
524 in the study design, data collection and analysis, or writing of the manuscript.

525

526 **Contributors**

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

533

534 **Declaration of interest:** none.

535 **References**

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

579 Chouvelon, T., Violamer, L., Dessier, A., Bustamante, P., Mornet, F., Pignon-Mussaud, C.,
580 Dupuy, C., 2015. Small pelagic fish feeding patterns in relation to food resource
581 variability: an isotopic investigation for *Sardina pilchardus* and *Engraulis encrasicolus*
582 from the Bay of Biscay (Northeast Atlantic). Marine Biology, 162, 15-37.

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

619 Hanson, J.M., 2017. Feeding interactions between fishes in a coastal ecosystem in the southern
620 Gulf of St. Lawrence, Atlantic Canada. *Transactions of the American Fisheries Society*,
621 10.1002/tafs.10021.

622 Harbison, G., Biggs, D., Madin, L., 1977. The associations of Amphipoda Hyperidea with
623 gelatinous zooplankton—II. Associations with Cnidaria, Ctenophora and Radiolaria.
624 *Deep Sea Research*, 24, 465-488.

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

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

630 Head, E.J., Pepin, P., 2010. Spatial and inter-decadal variability in plankton abundance and
631 composition in the Northwest Atlantic (1958–2006). *Journal of Plankton Research*, 32,
632 1633-1648.

633 Hirche, H.-J., 1996. Diapause in the marine copepod, *Calanus finmarchicus*—a review. *Ophelia*,
634 44, 129-143.

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

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

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

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

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

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

651 Jansen, T., 2016. First-year survival of North East Atlantic mackerel (*Scomber scombrus*) from
652 1998 to 2012 appears to be driven by availability of *Calanus*, a preferred copepod prey.
653 *Fisheries Oceanography*, 25, 457-469.

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

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

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

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

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

668 Kennedy, J., Skjæraasen, J.E., Nash, R.D., Thorsen, A., Slotte, A., Hansen, T., Kjesbu, O.S.,
669 2009. Do capital breeders like Atlantic herring (*Clupea harengus*) exhibit sensitive

670 periods of nutritional control on ovary development and fecundity regulation? Canadian
671 Journal of Fisheries and Aquatic Sciences, 67, 16-27.

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

712 Naman, S.M., Greene, C.M., Rice, C.A., Chamberlin, J., Conway-Cranos, L., Cordell, J.R.,
713 Hall, J.E., Rhodes, L.D., 2016. Stable isotope-based trophic structure of pelagic fish and
714 jellyfish across natural and anthropogenic landscape gradients in a fjord estuary. *Ecology
715 and Evolution*, 6, 8159-8173.

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

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

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

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

728 Oviatt, C.A., Kremer, P.M., 1977. Predation on the ctenophore, *Mnemiopsis leidyi*, by butterfish,
729 *Peprilus triacanthus*, in Narragansett Bay, Rhode Island. Chesapeake Science, 18, 236-
730 240.

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

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

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

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

743 Pershing, A.J., Greene, C.H., Jossi, J.W., O'Brien, L., Brodziak, J.K., Bailey, B.A., 2005.
744 Interdecadal variability in the Gulf of Maine zooplankton community, with potential
745 impacts on fish recruitment. ICES Journal of Marine Science: Journal du Conseil, 62,
746 1511-1523.

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

796 Wiebe, P.H., Lawson, G.L., Lavery, A.C., Copley, N.J., Horgan, E., Bradley, A., 2013. Improved
797 agreement of net and acoustical methods for surveying euphausiids by mitigating
798 avoidance using a net-based LED strobe light system. *ICES Journal of Marine Science*,
799 70, 650-664.

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

803

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				

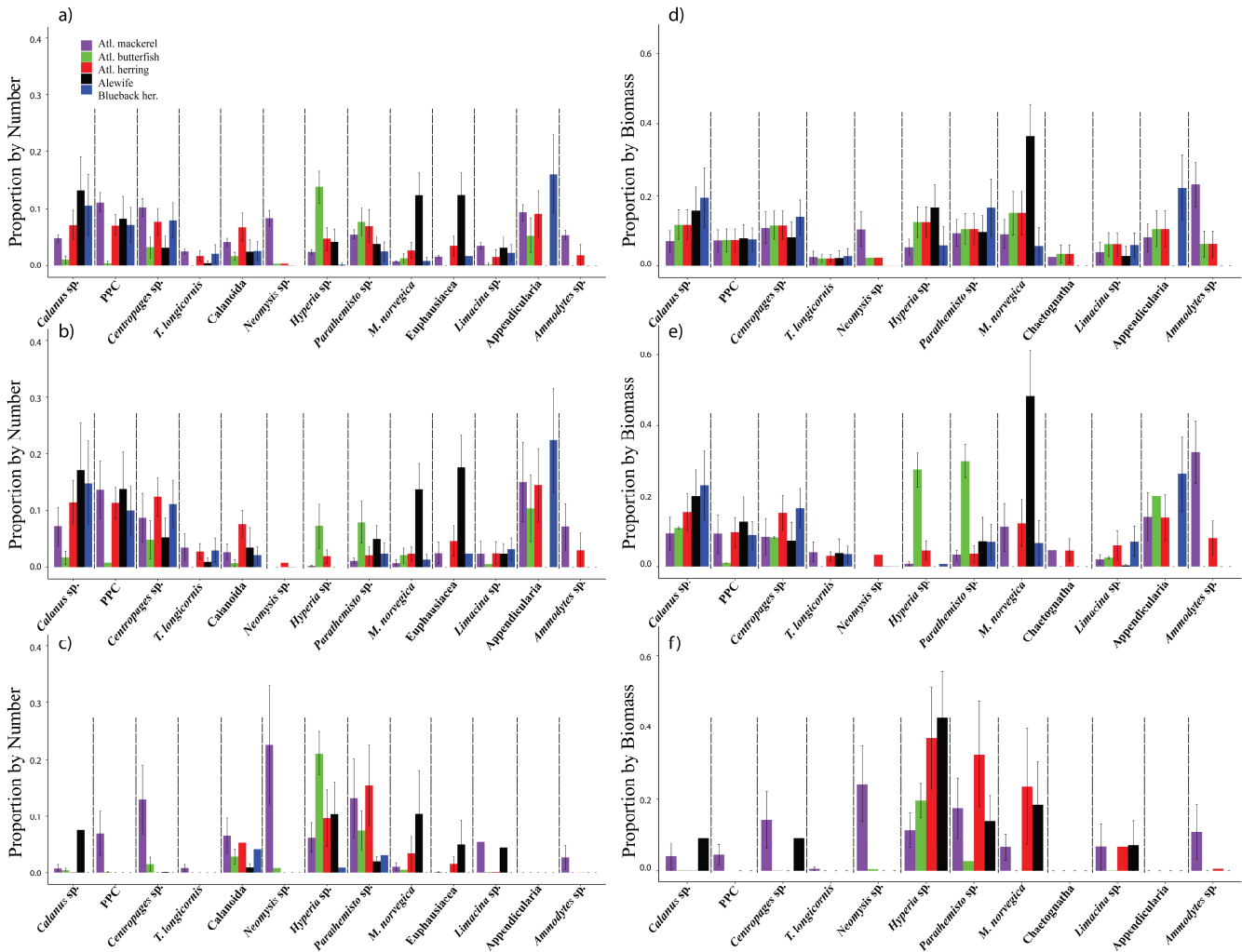


Figure 1. Proportion of Prey in the Diets of Small Pelagic Fishes. Mean proportions of common prey taxa in stomach contents by number (a-c) and biomass (d-f) in total (a, d), the spring (b, e), and the fall, (c, f) of five species of small pelagic fishes. *T. longicornis* = *Temora longicornis*, *M.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

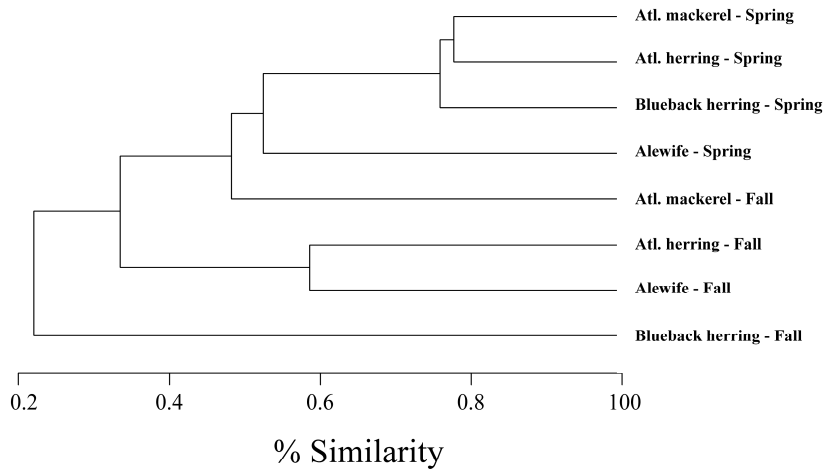


Figure 2. *Hierarchical Cluster Analysis of Diet Similarity.* Dendrogram of a hierarchical cluster analysis indicating diet similarity of small pelagic fishes separated by spring and fall.

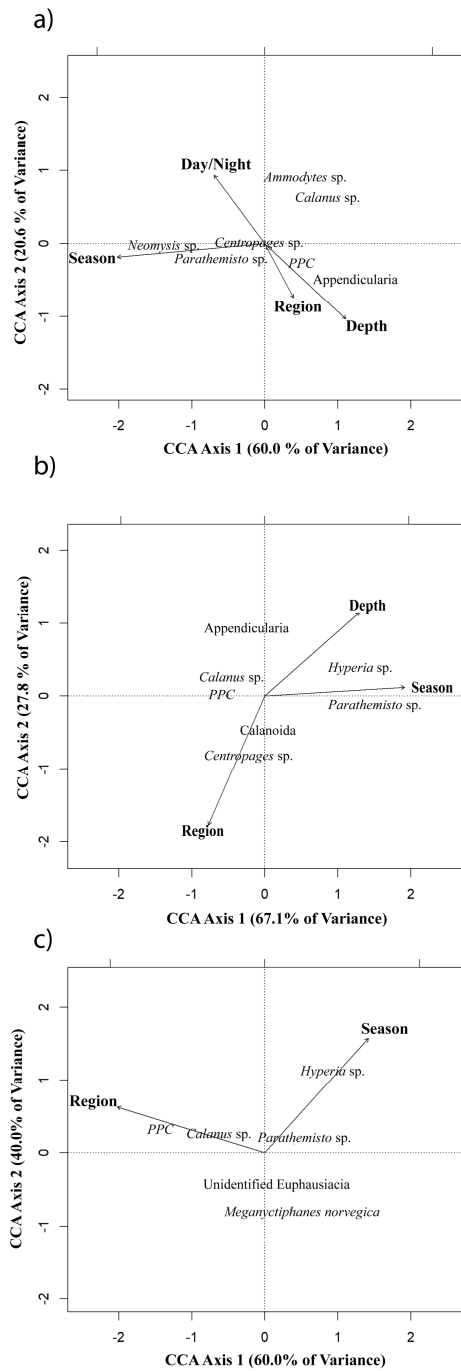


Figure 3. *Canonical Correspondence Analyses.* Ordination biplots from results of canonical correspondence analysis of diets of (a) Atlantic mackerel, (b) Atlantic herring, and (c) alewife with explanatory variables of season, depth, and region. Arrows indicate explanatory variables that significantly 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.

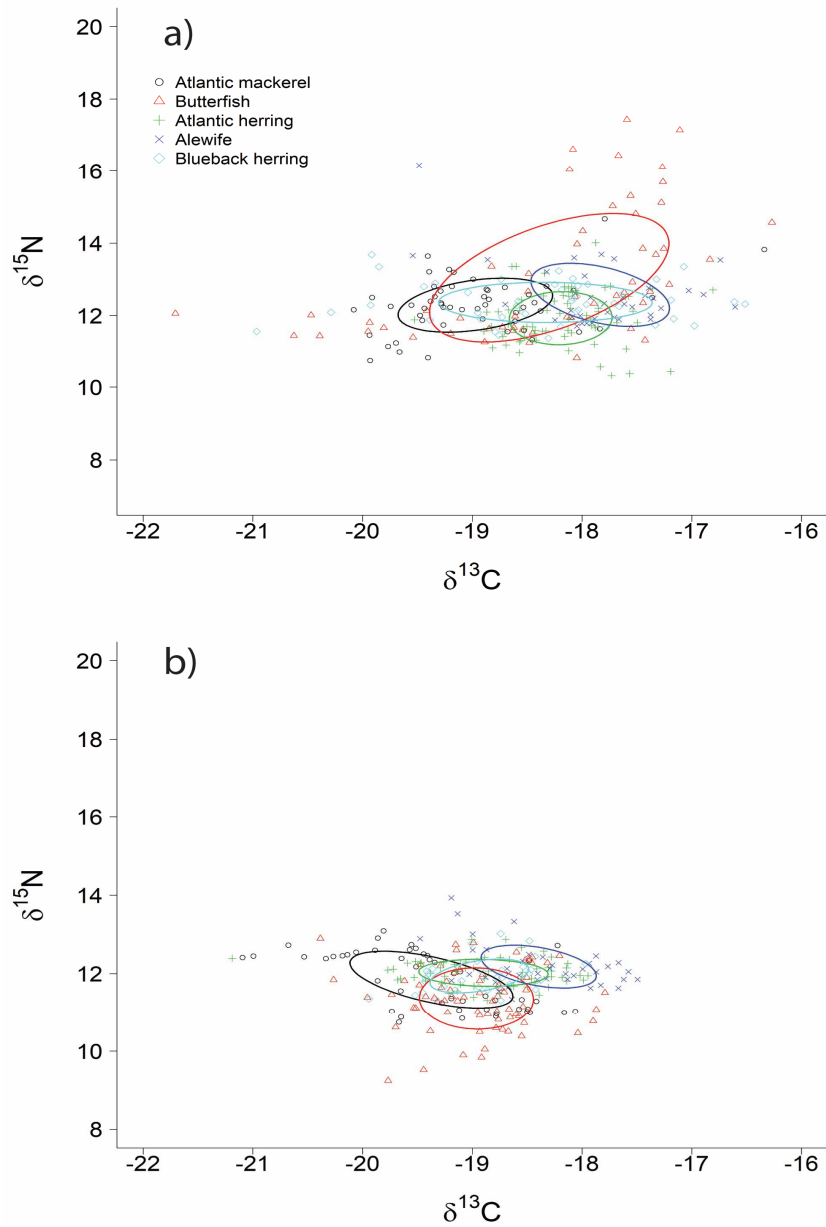


Figure 4. *Stable Isotope Ratios and Standard Ellipses.* Stable isotope ratios ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) of small pelagic fishes in the (a) spring and (b) fall, along with each species' standard ellipse corrected for sample size.

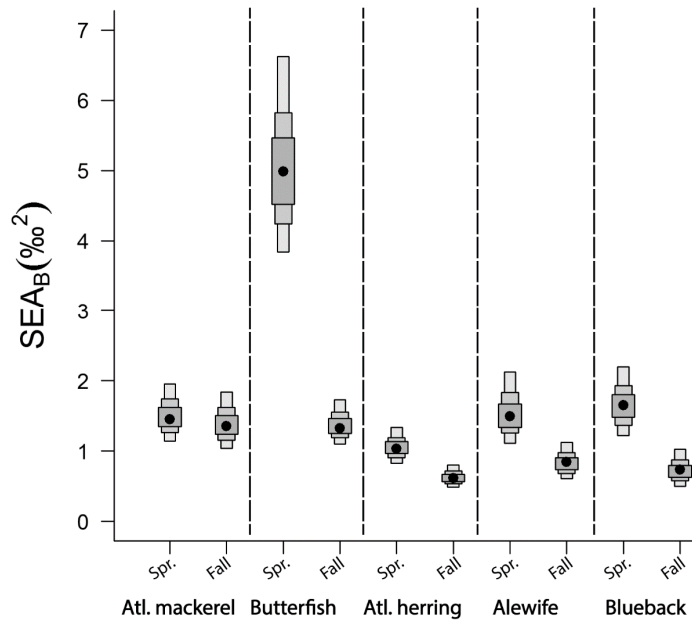


Figure 5. *Bayesian Ellipse Areas.* Density plot of Bayesian standard ellipse areas (SEA_B) for small pelagic fishes in the spring and fall. Black dots represent the mode of posterior distribution of SEA_B values with grey boxes presenting 50%, 75%, and 95% credible intervals.