

1 Effects of warm and cold climate conditions on capelin (*Mallotus villosus*) and Pacific herring
2 (*Clupea pallasii*) in the eastern Bering Sea

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4 Alexander G. Andrews III^{1*}, Wesley W. Strasburger¹, Edward V. Farley Jr.¹, James M. Murphy¹,
5 and Kenneth O. Coyle²

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7 ¹Auke Bay Laboratories, Alaska Fisheries Science Center, National Marine Fisheries Service,
8 National Oceanic and Atmospheric Administration, 17109 Point Lena Loop Road, Juneau, AK
9 99801, USA

10

11 ²School of Fisheries and Ocean Sciences, University of Alaska, Fairbanks, AK 99775-7220,
12 USA

13

14 *Corresponding author: tel: +1 907 789-6655; fax: +1 907 789-6408; email:
15 alex.andrews@noaa.gov

16

17 **Abstract**

18 Climate warming has impacted the southern extent of sea ice in the eastern Bering Sea (EBS)
19 ecosystem leading to many changes in ocean conditions and food webs there. We explore how
20 these changes have affected two key forage fish species, capelin (*Mallotus villosus*) and Pacific
21 herring (*Clupea pallasii*), examining the effects of climate change on this commercially
22 important ecosystem in the EBS. Catch per unit effort (CPUE) data from surface trawls, size,
23 and diet of capelin and Pacific herring were collected during a series of warm and cold years by
24 fisheries oceanographic surveys conducted from mid-August to early October, 2003 through
25 2011. Overall, mean CPUE for both species was higher in the northeastern Bering Sea [NEBS;
26 capelin = 1.23 kg/km² (warm) and 40.01 kg/km² (cold); herring = 141.08 kg/km² (warm) and
27 132.43 kg/km² (cold)] relative to the southeastern Bering Sea [SEBS; capelin = 0.16 kg/km²
28 (warm) and 5.78 kg/km² (cold); herring = 15.77 kg/km² (warm) and 24.45 kg/km² (cold)],
29 irrespective of temperature conditions. Capelin mean CPUE was significantly lower during
30 warm years than during cold years [$p < 0.001$; 0.57 kg/km² (warm), 18.99 kg/km² (cold)]. Pacific
31 herring mean CPUE was less variable between warm and cold years [$p < 0.001$; 63.78 kg/km²
32 (warm), 66.19 kg/km² (cold)], but was still significantly less during warm years than cold.
33 Capelin and herring lengths remained relatively constant between climate periods. Capelin
34 lengths were similar among oceanographic domains [104.0 mm (South Inner domain), 112.5 mm
35 (South Middle domain), 106.9 mm (North Inner domain), and 104.5 mm (North Middle
36 domain)], while herring were larger in domains further offshore [123.1 mm (South Inner
37 domain), 232.4 mm (South Middle domain), 259.9 mm (South Outer domain), 128.9 mm (North
38 Inner domain), and 198.1 mm (North Middle domain)]. Diets for both species were significantly
39 different between climate periods. Large crustacean prey comprised a higher proportion of the

40 diets in most regions during cold years. Age-0 walleye pollock (*Gadus chalcogrammus*)
41 contributed >60% to the diets of Pacific herring in southern Middle Domain and >30% in the
42 northern Middle domain during warm years. A switch to less energetic prey for these forage
43 fishes during warm years may have implications for fitness and future recruitment. The shifts in
44 the distribution and lower biomass of capelin in the EBS during warm years could lead to
45 disruptions in energy pathways in this complex marine ecosystem.

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47 Key words: Capelin, herring, forage fish, Bering Sea, climate change, diet, crustacean
48 zooplankton.

49

50 **1.0 Introduction**

51 Capelin (*Mallosus villosus*) and Pacific herring (*Clupea pallasii*; hereafter referred to as
52 herring) are two important forage fishes for many upper trophic level predators including
53 seabirds, seals, and whales in the eastern Bering Sea (EBS; (Frost and Lowry, 1981; Lowry and
54 Frost, 1981; Springer et al., 1987; Merrick et al., 1997; Brodeur et al., 1999). Although capelin
55 and herring are integral to the EBS food web (Aydin and Mueter, 2007), little information is
56 available on their basic ecology. Recent studies documenting capelin distribution found that
57 most are concentrated in the shallow (< 50m depth) regions of the EBS shelf (Hollowed et al.,
58 2012). Parker-Stetter et al. (2013) found that capelin were distributed in surface waters in
59 shallow regions, but dense schools were also found in the “surface zone” 15 to ~35m within the
60 middle EBS shelf region. Herring are typically found at the surface to a depth of 250m
61 (Mecklenberg et al., 2002), and have higher relative abundance than capelin and other important
62 forage fishes on the EBS shelf (Brodeur et al., 1999). Changes in the abundance and spatial

63 distribution of capelin and herring have been proposed as one of the potential causes of declining
64 northern fur seal (*Callorhinus ursinus*) populations at the Pribilof Islands in the EBS (Sinclair et
65 al., 1994) and Steller sea lion (*Eumetopias jubatus*) populations in the western region of the
66 Aleutian Islands (Merrick et al., 1997).

67 Climate models predict that anthropogenic-forced trends in ocean temperatures will
68 surpass the natural variability during the 21st century (Wang et al., 2010). Ocean warming has
69 been most dramatic in Arctic and sub-Arctic regions (Overpeck et al., 1997), and it is unknown
70 how marine species that are adapted to current ocean temperature patterns will respond to
71 continued warming (e.g. (Mueter and Litzow, 2008). Warming climate may have its largest
72 effect on the (EBS) ecosystems through the extent and duration of seasonal sea ice (Stabeno et
73 al., 2012b). Sea ice extent and duration are believed to determine the balance between benthic
74 and pelagic productivity on the EBS shelf (Hunt et al., 2002), as well as the boundary between
75 Arctic and Subarctic demersal fish communities (Wyllie-Echeverria and Wooster, 1998;
76 Grebmeier et al., 2006; Mueter and Litzow, 2008; Stabeno et al., 2012a; Stevenson and Lauth,
77 2012).

78 The eastern Bering Sea (EBS) has recently experienced anomalously warm (2001 to
79 2005) and cold (2006 to 2009) late summer and fall mean water column temperatures (Eisner et
80 al., 2014). The anomalously warm period (~2°C above average during spring and summer;
81 (Stabeno et al., 2012b)) is comparable to summer sea temperatures projected into the future by
82 climate models (Mueter et al., 2011). These contrasting climate periods provide an opportunity
83 to evaluate the response of the EBS shelf to temperature. For example, shifts in fish distribution
84 and relative abundance (see (Farley et al., 2009; Moss et al., 2009; Farley et al., 2011; Hollowed
85 et al., 2012) as well as fish size and diet (Farley and Trudel, 2009; Coyle et al., 2011; Hunt Jr. et

86 al., 2011; Heintz et al., 2013; Farley Jr. et al., 2015) have already been noted in response to warm
87 and cold climate conditions in the EBS. In addition, zooplankton species composition and
88 biomass also shifted between climate periods where small zooplankton species dominated the
89 biomass in warm years and larger zooplankton species (e.g. *Calanus* spp.) dominated during cold
90 years (Coyle et al., 2011; Eisner et al., 2014). The results from these studies suggest that
91 continued warming on the EBS shelf is likely to have a negative impact on pelagic fishes, via
92 lengthening of energy pathways and reduction of the energy to upper trophic level organisms
93 (Coyle et al., 2011).

94 In this paper, we examine the impact of warm and cold climate conditions on capelin and
95 herring distribution, relative biomass (Catch Per Unit Effort), size, and diet for fish captured on
96 the EBS shelf during 2003 to 2011. We build on capelin distribution described by Hollowed et
97 al. (Hollowed et al., 2012) and Parker-Stetter et al. (Parker-Stetter et al., 2013) by adding new
98 information for surface caught fish during the ‘warm’ years and extend this analysis to the
99 northeastern Bering Sea shelf. We also examine the impact of these climate conditions on
100 capelin diet and size and extend the analysis of distribution, relative abundance, size, and diet to
101 herring. Our analyses include dividing the EBS region into oceanographic domains based on the
102 location of a series of fronts occupying the shelf during spring, summer, and fall (Iverson et al.,
103 1979; Coachman, 1986). Distinct habitats and food webs are contained within each domain
104 (Iverson et al., 1979). Recently, these domains and regions have been further divided into
105 smaller regions based on a combination of biological data and large-scale oceanographic patterns
106 (Ortiz et al., 2012). We discuss the impact of changing climate on ecology of capelin and
107 herring.

108 **2.0 Methods**

109 *2.1 Study Region*

110 The eastern Bering Sea shelf in spring, summer, and fall is characterized by multiple
111 cross-shelf oceanic domains including Inner (<50 m depth), Middle (50–100 m depth), and Outer
112 (100–200 m depth) domains, that progress from a mostly unstratified system, to a two-layered
113 system, and finally to a three-layered system, respectively (Coachman, 1986). Based on EBS
114 Marine Region designations made during the Bering Sea Project (BSP) (Ortiz et al., 2012;
115 Harvey and Sigler, 2013), we grouped stations into six domains (Fig. 1). The Off-shelf and S
116 Outer domains were excluded from some analyses due to low sample size (Table 1). Several
117 nearshore stations occurred just outside BSP region designations; these stations were assigned to
118 the nearest BSP region. The domains were divided into northeastern Bering Sea (NEBS) and
119 southeastern Bering Sea (SEBS) regions at approximately 60°N, based on biophysical
120 differences such as surface salinity, thickness of pycnocline, and bottom temperatures (Stabeno
121 et al., 2012a); Fig. 1). Warm and cold periods were defined by late summer/early fall water
122 temperatures as defined by Eisner et al. (2014; warm = 2002–2005, cold = 2006–2011). They
123 differ somewhat from Stabeno et al. (2012a) in that 2006 is defined here as a cold year, whereas
124 Stabeno et al., considered 2006 water temperatures close to the long-term average.

125 *2.2 Field sampling*

126 Samples were collected during the Bering-Aleutian Salmon International Survey
127 (BASIS), on the EBS shelf by scientists from the Alaska Fisheries Science Center from mid-
128 August to early October 2003-2011 (Appendix A). The geographic area of the survey
129 encompassed stations ranging from 54.0 – 65.5°N and 161.5 – 174.0°W (Fig. 2). A 198-m
130 midwater rope trawl with hexagonal mesh in the wings and body, and a 1.2-cm mesh liner in the
131 codend was used to collect small, pelagic fishes. Buoys were secured to wing tips to keep the

132 headrope at or near the surface (Farley et al., 2005; Moss et al., 2009). Vessels used Noreastern
133 Trawl Systems¹ 5 m alloy doors and trawled at speeds from 180 cm/s to 260 cm/s (3.5 to 5
134 knots). Vertical opening and horizontal net spread ranged from 15 to 20 m and 50 to 60 m,
135 respectively. Contents of the codend were sorted to the lowest taxonomic level possible.
136 Capelin and herring fork lengths were measured to the nearest 1.0 mm at each station. Total
137 catch weights were measured for each species at each station.

138 *2.3 Distributions and catch per unit effort (CPUE)*

139 Catch per unit effort (CPUE) was based on catch weight per area swept (kg/km²)
140 calculated as:

141

$$142 \quad CPUE \text{ (kg/km}^2\text{)}_j = \frac{w_j}{d_j \times h_j}$$

143

144 where w_j is the weight (kg) of fish at a given station j , d is the distance (km) towed from net
145 equilibrium to haulback, and h is the horizontal spread (km) of the net. The Haversine formula
146 (Sinnott, 1984) was used to calculate great circle distance between the beginning and ending
147 coordinates of the trawl. The Shapiro-Wilk test was performed on CPUE to test whether or not
148 the underlying distribution of the data was normal. Tests between mean CPUEs were performed
149 using the Mann-Whitney Rank Sum test ($p < 0.05$); a test used for data that have non-normal
150 distributions. Statistical tests were performed using Minitab 17.1.0.0.

151 Contours of the distribution of both species were created for spatial visualization after
152 first gridding and then interpolating the data using the local polynomial interpolation routine in

¹ Use of trade names does not constitute an endorsement by the National Marine Fisheries Service

153 ESRI ArcMap 10.0. Contours of distribution were created for warm (2002-2005) and cold
154 (2006-2011) climate periods.

155 *2.4 Catch-weighted mean length calculations*

156 Fish fork lengths were measured for a random subsample of 25-100 fish of each species
157 and at each station, when possible. Catch-weighted mean lengths were calculated from length
158 subsamples that were expanded by catch using:

$$159 \quad \text{Catch-weighted mean length} \\ 160 \quad = \frac{\sum_i (\text{mean length}_j \times \text{catch}_j)}{\sum_i \text{catch}_j}$$

161 where mean length each year was calculated from measured lengths at station j , and catch is the
162 number of fish captured at station j . Catch-weighted mean lengths were calculated by climate
163 period and domain represented by the subscript i . Variance was estimated using bootstrap
164 techniques (Efron and Tibshirani, 1998). Due to the skewed and often non-normal distribution
165 of fish length composition within a station, we performed a bootstrap procedure to estimate
166 within station variance in mean length. For each station, observed lengths were resampled with
167 replacement and mean lengths were calculated. This was repeated 1000 times. Standard
168 deviations were calculated based on the within station variance of resampled station means and
169 between station variance of observed station means using variance estimation methods cited
170 above. Upper and lower 95% confidence intervals were calculated and used to determine catch-
171 weighted mean length differences within and between domains for each climate periods.

172 *2.5 Capelin and herring diets*

173 Stomach contents were examined at sea (Moss et al., (2009); Coyle et al., (2011),
174 following standard methods developed by Tikhookeanskiy Nauchno-Issledovatel'skiy Institut
175 Rybnogo Khozyaystva i Okeanografiy (Chuchukalo and Volkov, 1986; Volkov and Kuznetsova,

176 2007; Moss et al., 2009; Coyle et al., 2011). Typically, the contents of 10 stomachs from
177 randomly sampled fish were combined together from each station, and prey composition was
178 recorded as a stomach content index (SCI). The SCI was calculated as prey taxon weight
179 multiplied by 10,000 and divided by predator body weight. Multiplying by a factor of 10,000
180 made these numbers easier to handle, as predator body weight was always much larger than prey
181 taxon weight. In some cases, accurate prey weights could not be measured due to movement of
182 the vessel; Marel Inc., scales were used at sea. In these instances, prey taxon weight was
183 estimated based upon percent volume and the assumption of equal bodily densities of all prey
184 items.

185 Prey categories occurring in less than 10% of all stomachs (for either capelin or herring)
186 were combined into more broad taxonomic classes. If a prey category occurred in less than 10%
187 of all stomachs, within either species, and could not be grouped with other more common prey
188 types, it was assigned to an Other category. The Other category consisted of prey items such as:
189 Balanidae, Bivalvia, Cnidaria, Polychaeta, and Cladocera. Prey composition was summarized as
190 %SCI contribution (individual prey category SCI divided by the sum of SCI) and percent
191 frequency of occurrence (%FO) for each domain and within warm and cold climate periods.
192 Average stomach fullness index ($SFI = \sum SCI$) was calculated for each domain and within warm
193 and cold climate periods. Feeding incidence was defined as the proportion of non-empty
194 stomachs for each domain and climate period.

195 Dietary comparisons were made using PRIMER Version 6, PERMANOVA Version 1.0.1
196 (Clarke and Gorley, 2006). All diet data was fourth root transformed prior to statistical testing to
197 give less weight to the most prevalent prey items prior to calculating similarity measures (Clark
198 and Warwick, 2001). Dietary composition comparisons within species and among domains and

199 climate periods were made using nested mixed PERMANOVA designs operating on Bray-Curtis
200 similarity matrices. Temperature and domain were treated as fixed effects; year was treated as a
201 random nested factor within temperature and BSP region was treated as a random nested location
202 block within domain. Type I sum of squares was used to account for unbalanced sample design
203 (Clarke and Gorley, 2006). The order of these factors in the model was chosen to minimize
204 mean square error (Eisner et al., 2014); all interactions were included from each species,
205 respective model. The Similarity Percentages Routine (SIMPER) was used to identify prey
206 categories that most influenced significant differences in prey composition between domains and
207 climate periods.

208 BSP regions were included in the model only if they had been sampled at least twice
209 during both warm and cold climate periods. The resultant analysis of capelin diet data was
210 constrained to BSP regions 9 and 10 (N Middle), and 3 and 6 (S Middle) within both warm and
211 cold climate periods to meet these restrictions.

212 **3.0 Results**

213 *3.1 Distributions and catch per unit effort (CPUE)*

214 *3.1.1 Capelin*

215 Capelin showed marked changes in their distribution between cold and warm climate
216 periods (Fig. 2). Over the entire EBS, mean CPUE was significantly higher during the cold
217 period (18.99 kg/km²) versus the warm period (0.57 kg/km²) ($p < 0.001$; Tables 2 and 3). In
218 addition, mean CPUE was significantly higher in the NEBS, independent of climate period
219 (Warm periods, $p < 0.001$; Cold periods, $p < 0.001$; Tables 2 and 3). During the cold period,
220 capelin distribution extends into the SEBS and occupies a large portion of both the Inner and
221 Middle domains. During the warm period, capelin were largely absent from the SEBS (0.16

222 kg/km²), and occurred mainly in the NEBS (1.23 kg/km²). The NEBS and SEBS regions were
223 tested separately and displayed the same relationship as the EBS; mean CPUE was significantly
224 higher during the cold period in both regions (NEBS, $p < 0.001$; SEBS, $p < 0.001$; Tables 2 and 3).

225 Within the NEBS and SEBS regions, capelin biomass in surface waters was evenly
226 distributed between Inner and Middle domains independent of climate period, with the exception
227 of the N Inner (31.60 kg/km²) vs. N Middle (58.91 kg/km²) domains during the cold period
228 ($p = 0.002$; Tables 2 and 3). There were no significant differences between: the S Inner vs. S
229 Middle domains ($p = 0.051$) during the warm period, the N Inner vs. N Middle domains ($p = 0.461$)
230 during the warm period, and S Inner vs. S Middle domains during the cold period ($p = 0.187$;
231 Tables 2 and 3). During the cold period, there were several areas of high CPUE; north of St.
232 Lawrence Island, as well as an area that straddles the NEBS and SEBS boundary west of
233 Nunivak Island. The high CPUE area in the central EBS contributed to the higher catches in the
234 N Middle. Mean CPUE by climate period, region, and domain showed that catches were higher
235 in cold years, higher in the north during either climate period, and higher in the N Middle vs. N
236 Inner domains during cold periods.

237 *3.1.2 Herring*

238 Overall, herring catches showed less variation between warm and cold periods.
239 However, there were slight shifts in distribution between warm and cold periods (Fig. 2). Over
240 the entire EBS, mean CPUE was lower during the warm period (63.78 kg/km²) than in the cold
241 period (66.19 kg/km²) (Tables 2 and 3); although these differences were small, they were
242 statistically significant ($p < 0.001$). The results for the SEBS was similar, with mean CPUE
243 during the warm period (15.77 kg/km²) being significantly lower ($p < 0.001$) than during the cold
244 period (24.45 kg/km²). Although not significantly different ($p = 0.277$), the NEBS showed the

245 opposite pattern, where warm period CPUE (141.08 kg/km²) was higher than cold period CPUE
246 (132.43 kg/km²). In addition, herring were more widely distributed in the NEBS during the
247 warm years, and had a more contracted distribution during cold years. In both warm and cold
248 periods, herring catches were substantially larger in the NEBS than the SEBS (NEBS, $p<0.001$;
249 SEBS $p<0.001$), a pattern consistent with capelin catches.

250 There were consistent differences between mean CPUE estimates for herring by region
251 and domain. During both climate periods and in both regions, herring showed a preference for
252 the Inner domain; with the exception of the S Inner and S Middle domains during the cold period
253 where there was no significant difference ($p=0.441$; Tables 2 and 3). In the NEBS, where
254 herring catches were largest, mean CPUE was significantly higher ($p<0.001$) in the N Inner
255 (165.85 kg/km²) domain when compared to the N Middle (100.08 kg/km²) domain during the
256 warm period. (Tables 2 and 3). In the SEBS, during the warm period, mean CPUE was
257 significantly higher ($p=0.005$) in the S Inner (22.33 kg/km²) compared to the S Middle (12.89
258 kg/km²) domain. The same relationship was demonstrated between the N Inner (175.41 kg/km²)
259 and the N Middle (35.85 kg/km²) domains during the cold period ($p<0.001$).

260 *3.2 Catch-weighted mean length calculations*

261 Catch-weighted mean lengths of capelin and herring, within individual domains,
262 remained relatively constant between warm and cold climate periods (Fig. 3). Similarly, when
263 pooled by climate periods, capelin mean lengths for the S Inner (104.0 mm; 9.8 C.I. 95%), S
264 Middle (112.5 mm; 5.10 C.I. 95%), N Inner (106.9 mm; 12.0 C.I. 95%) and N Middle (104.5
265 mm; 10.1 C.I. 95%) domains showed no statistically significant difference (based on 95%
266 confidence intervals). Conversely, when pooled by climate periods, herring, mean lengths for
267 the S Inner (123.1 mm; 41.6 C.I. 95%), S Middle (232.4 mm; 18.0 C.I. 95%), S Outer (259.9

268 mm; 25.2 C.I. %) domains displayed increasing mean lengths from Inner to Outer domains;
269 However, the only significant difference (based on 95% confidence intervals) was between the S
270 Inner and S Middle domains. This pattern of increasing length offshore was also documented in
271 the NEBS. Climate periods were pooled and showed herring mean lengths in the N Inner (128.9
272 mm; 8.8 C.I. 95%) domain to be significantly smaller (based on 95% confidence intervals) than
273 the N Middle (198.1 mm, 6.9 C.I. 95%).

274 *3.3 Diets*

275 A total of 1,564 capelin stomachs from 146 stations and 3,894 herring stomachs from 382
276 stations, divided among climate periods and domains (Table 1) were used for diet analysis.
277 Capelin feeding incidence ranged from 100% in the S Inner domain to 52% in the N Middle
278 domain during warm periods and 95.5% in the N Inner domain to 76.3% in the N Middle domain
279 during cold periods. Note that the capelin diet in the S Inner domain during warm periods was
280 represented by a single station. Herring feeding incidence ranged from 85.7% in the N Inner
281 domain to 72.5% in the N Middle domain during warm periods and 83.8% in the N Middle
282 domain to 57.7% in the S Middle domain during cold periods. Generally, average stomach
283 fullness follows the same pattern as feeding incidence, with higher average fullness following a
284 higher feeding incidence.

285 *3.3.1 Capelin*

286 The proportion of *Calanus* spp. in the diet increased from warm to cold periods in every
287 domain (Fig. 4). The proportion of euphausiids remained relatively static in the N Inner domain
288 from warm to cold periods, but euphausiids were much more prevalent in the N Middle domain
289 diet during warm periods. Conversely, the proportion of euphausiids increased from warm to
290 cold in both southern domains. Larvaceans (*Oikopleura* spp.) were a major prey item in the S

291 Middle domain during the warm period, but not cold. The small copepod *Pseudocalanus* spp.
292 was more prevalent in the southern domains than in the north. *Pseudocalanus* spp. was
293 consumed in a higher proportion during warm years in the south, and in a higher proportion
294 during cold years in the north. Chaetognaths were present in the diet in all domains and climate
295 periods, with the exception of warm years in the S Middle domain. During warm periods in the
296 N Inner domain, the prey category Other represented 43% of the total SCI, this was
297 approximately 16 times higher than the consumption of the Other category in any other domain
298 or climate period.

299 The capelin diet data was constrained to the N Middle domain (regions 9 and 10) and the
300 S Middle domain (regions 3 and 6) to meet data requirements to be included in the
301 PERMANOVA model. Within the full model for this reduced data set, temperature was the only
302 significant factor ($p=0.013$), and there were no significant interactions. SIMPER analysis
303 indicated that increased consumption of the euphausiid *Thysanoessa raschii* during warm climate
304 periods was the primary driver in this difference, followed by increased consumption of *Calanus*
305 spp., chaetognaths, and *Pseudocalanus* spp. during cold climate periods (Table 4). It should be
306 noted that SIMPER analysis was performed by temperature, as this was the only significant
307 factor in the full PERMANOVA model. Results from the SIMPER analysis therefore discount
308 any variation from north to south. This is particularly evident in the indicated increase in
309 *Pseudocalanus* spp. When samples were pooled across the north-south boundary, the increase in
310 the proportion of *Pseudocalanus* spp. in the north during cold years outweighed the increase in
311 *Pseudocalanus* spp. consumption during warm years in the south. This was mostly due to
312 sample size during warm years. The contrasting changes in the relative consumption of this
313 small calanoid copepod can be seen in Fig. 4.

314 3.3.2 Herring

315 The proportion of *Calanus* spp. consumed by Pacific herring in the northern Bering Sea
316 increased notably from warm to cold, in both the Middle and Inner domains, but not in the south
317 (Fig. 4). Consumption of these large calanoid copepods was lower, but less variable in the S
318 Middle domain from warm to cold periods, and relatively stable in the S Inner domain. The
319 proportion of euphausiids consumed, particularly *T. raschii*, was much higher in the SEBS
320 during cold years in both the Middle and Inner domains. An opposite pattern was observed in
321 the N Middle domain, with a larger proportion of euphausiids being consumed during warm
322 periods. Fish became an important prey item during warm periods, and was present in every
323 domain (Fig. 4). Particularly, age-0 walleye pollock was consumed in high proportions in every
324 domain, with the exception of the N Inner domain during warm climate periods. The hyperiid
325 amphipod *Themisto libellula* became an important prey item during cold climate periods in the N
326 Middle domain, and was consumed in the S Middle domain during cold climate periods, but not
327 to the same extent as in the north.

328 No data restrictions were necessary to meet the conditions of our PERMANOVA design
329 for herring. All fixed and nested random factors were significant ($p \leq 0.001$), and the interaction
330 between temperature and domain, as well as the interaction between temperature and nested
331 random BSP region, were significant ($p \leq 0.001$) (Table 5). Pairwise tests were performed on the
332 interaction between temperature and domain, both for pairs of levels within temperature and for
333 pairs of levels within domain. Within the S Middle and N Inner domains, there were significant
334 differences ($p \leq 0.05$) in dietary composition between warm and cold climate periods. No other
335 within-domain and across-climate period tests were significant. Within the warm climate period,
336 pairwise comparisons of diets for herring between the S Inner and S Middle domains were

337 significantly different ($p \leq 0.05$). The S Inner and N Inner domains were significantly different
338 ($p \leq 0.05$) during warm climate periods. Remaining warm climate period pairwise comparisons
339 were not significantly different. Within the cold climate period, there were no statistically
340 significant differences between the different domains.

341 SIMPER analysis indicated that a higher proportion of age-0 walleye pollock during
342 warm conditions, and of the euphausiid *Thysanoessa raschii* during cold conditions, was the
343 primary source of dietary differences between warm and cold periods in the S Middle domain
344 (Table 6). In the N Inner domain, small calanoid copepods such as *Pseudocalanus* spp. and
345 *Centropages abdominalis*, the Other category, and fish increased in prevalence during warm
346 conditions, while larvaceans and *Calanus* spp. contributed the most to the significant difference
347 in dietary composition between warm and cold climate periods. Within the warm climate period,
348 fish, the large calanoid copepod *Epilabidocera amphitrites*, and mysids were consumed in higher
349 proportion in the S Inner Domain, while age-0 walleye pollock and *Thysanoessa raschii* were
350 consumed in higher proportion in the S Middle Domain. These same categories, with the
351 addition of *Pseudocalanus* spp. and *Centropages abdominalis*, contributed most to the
352 differences in dietary composition between the S Inner and N Inner domains within warm
353 climate periods. Small copepods, and the Other category were consumed in higher proportions
354 in the NEBS, while fish, age-0 walleye pollock and mysids represented a larger portion of the
355 diet in the S Inner Domain during warm conditions.

356 **4.0 Discussion**

357 *4.1 Distributions and CPUE*

358 This study provides evidence that capelin and herring distributions and CPUEs responded
359 differently to changing climate in the EBS. Shifts in distribution of marine biota can have far

360 reaching effects, ranging from modifications of species assemblages and interactions (Perry et
361 al., 2005; Graham and Harrod, 2009) to alteration of food webs and energy flow pathways
362 (Coyle et al., 2011; Hunt Jr. et al., 2011). Understanding how these two abundant and
363 widespread forage fishes respond to climate change will aid in our understanding of the effects
364 of climate change on this commercially and ecologically important North Pacific ecosystem.

365 Our observations are consistent with previous studies on shifts in capelin distribution and
366 CPUE during warm and cold climate states (Ciannelli and Bailey, 2005; Rose, 2005; Carscadden
367 et al., 2013). During warm years, capelin CPUE was greatly reduced throughout the EBS, and
368 was coupled with a contraction of the distribution into the NEBS. During cold years, capelin
369 distribution expanded into the SEBS and CPUE was higher overall. Changes in temperature of
370 as little as 1°C were associated with changes in capelin distribution over hundreds of kilometers,
371 and larger changes in temperature may lead to much larger shifts in distributions (Rose, 2005).
372 On the Scotian Shelf, anomalously cool temperatures were associated with higher CPUE of
373 capelin (Carscadden et al., 2001). An analysis of a long-term data set (1972-2001) from the
374 EBS found that capelin are distributed further south into Bristol Bay during cold periods, but
375 become sparse in the survey region and are distributed further north during warm years
376 (Ciannelli and Bailey, 2005). Our study spanned nine years, and although we cannot rule out
377 other reasons for changes in distribution and catch, climate change is the most parsimonious
378 explanation. Other studies have found large shifts in capelin distribution in response to
379 temperature change within as little as a year (Frank et al., 1996).

380 Higher mean CPUE of capelin on the southern shelf match the intrusion of the cold pool
381 into the SEBS as mapped for a similar time period (Coyle et al., 2011; Hollowed et al., 2012).
382 Capelin were confined north of the cold pool during a species interaction study where Pacific

383 cod, a capelin predator, was separated from capelin by the cold pool during a cold period
384 (Ciannelli and Bailey, 2005). Although predator avoidance may have a role in shaping capelin
385 distribution (Ciannelli and Bailey, 2005), a more recent study found that ocean conditions also
386 play a significant role (Hollowed et al., 2012). Overall, our study found higher capelin catches in
387 the NEBS versus the SEBS regardless of climate, indicating NEBS is a potential core area for
388 capelin distribution.

389 Capelin distributions from the Bering-Aleutian Islands Salmon International Survey trawl
390 catches are consistent with findings from a companion acoustic survey that took place during
391 cold years, but differ from bottom trawl findings (Hollowed et al., 2012; Parker-Stetter et al.,
392 2013). Our results do not indicate a preference between the inner and middle domains with one
393 notable exception. During cold years, significantly higher catches occurred in the N Middle
394 versus the N Inner domain. Hollowed et al. (2012) found that capelin occur equally in the Inner
395 and Middle domains during warm and cold years, but were more likely to be distributed over the
396 Middle domain during warm years. This conclusion was reached based on catches from a
397 bottom trawl. Parker-Stetter et al. (2013) used the surface trawl data (a subset of the data used in
398 this study) and midwater target identification trawls collected during cold years along with
399 acoustics to document fish distribution throughout the water column. Capelin occurred
400 predominantly in the upper water column (15 to ~35 m depths) with the highest densities
401 observed in the Middle domain in the SEBS (Parker-Stetter et al., 2013). Our results are
402 consistent with those of Parker-Stetter et al., (2013) during a cold year when we account for the
403 different definitions of the NEBS and SEBS used by each study. We believe that sampling gear
404 bias likely accounts for the different conclusions of Hollowed et al., (2012) versus Parker-Stetter
405 et al., (2013) and this study. We hypothesize that the Hollowed et al., (2012) capelin catches in

406 the Inner domain were inflated (biased) because most of the capelin were in the surface waters
407 and the bottom trawl spends a higher proportion of the tow time in the upper water column when
408 fished in the Inner domain than in the Middle domain where the water is much deeper.

409 The difference in capelin distribution between bottom versus surface trawl surveys is
410 attributable to variability in their vertical distribution across shelf habitats. While timing of the
411 two surveys were different (bottom trawl: May to July; surface trawl and acoustic surveys:
412 August – October), we attribute the differences in distribution and abundance to vertical
413 distribution because capelin in the inner shelf regions were typically found throughout the water
414 column, but capelin in middle and outer shelf regions were predominately found in surface
415 regions not effectively sampled by the bottom trawl (Parker-Stetter et al., 2013). Mean surface
416 trawl CPUEs are as much as two orders of magnitude larger than bottom trawl CPUEs, providing
417 additional evidence that surface trawl surveys are providing an accurate snapshot of capelin
418 distribution.

419 Unlike capelin, herring maintained a broad distribution across all regions and CPUE
420 remained stable between climate states. There is evidence for changes in herring distributions
421 due to the climate effects in other regions (Alheit and Hagen, 1997; Nagasawa, 2001; Attrill and
422 Power, 2002). However, herring live longer than capelin (herring – up to 12 years; capelin – up
423 to 5 years)(Naumenko, 1996), and therefore changes in catches between warm and cold periods
424 are undoubtedly confounded by multiple age classes encountered during a single annual survey
425 (Wespestad and Barton, 1979; Hay et al., 2008).

426 Herring catches tended to be higher in the Inner domains, irrespective of climate
427 conditions. One exception to this pattern was the S Inner versus S Middle domains where
428 catches were not significantly different during the cold period. The lack of significant difference

429 between these domains during the cold period is likely due to the presence of several areas of
430 higher CPUE within the S Middle domain. These areas of concentrated catch are likely related
431 to movement of adults from nearshore spawning areas to offshore overwintering grounds (Tojo
432 et al., 2007). They may have been present in these areas during warm years and were deeper in
433 the water column where they were not caught by the surface trawl. Alternatively, ice edge
434 thermal dynamics may affect the migration route of herring in the EBS (Tojo et al., 2007), which
435 would partly explain the presence of areas of higher catches of herring in the SEBS during cold
436 years. In general, the higher catches in the N Inner and S Inner domains paired with the mean
437 lengths (i.e. smaller herring captured in the inner domains) indicate that the Inner domain is an
438 important nursery area for herring in the EBS, particularly in the NEBS. Mean lengths in the
439 NEBS were below 150 mm, indicating fish of 0 to 1 year of age (Wespestad and Barton, 1979;
440 Hay et al., 2008).

441 Predation on capelin by herring is plausible, given the spatial overlap of these forage fish
442 species. Direct interactions between capelin and herring have been explored in the Barents Sea,
443 (Huse and Toresen, 2000; Hamre, 2003). Although predation on capelin larvae by herring was
444 confirmed in the Barents Sea, rates of predation were too low to influence capelin recruitment
445 (Huse and Toresen, 2000). Our diet results indicate very low predation on capelin by herring,
446 suggesting that herring predation is not influencing capelin distribution, at least during the late
447 summer and early fall.

448 *4.2 Catch-weighted mean length calculations*

449 Capelin and herring lengths were significantly different between climate periods within
450 domains. These results are counter to other investigations of the effect of climate on fish lengths
451 in the EBS. Typically, juvenile fishes are longer during warm than cold years (Andrews et al.,

452 2009; Farley and Trudel, 2009; Moss et al., 2009; Coyle et al., 2011; Farley Jr. et al., 2015). A
453 study in the EBS in warm (2004-2005) and cold (2006-2007) periods determined that juvenile
454 pink salmon (*Oncorhynchus gorbuscha*) were significantly longer during warm periods
455 (Andrews et al., 2009). Annual averages of growth rate potential of juvenile sockeye salmon (*O.*
456 *nerka*) were found to be higher in years with warmer sea surface temperatures (Farley and
457 Trudel, 2009). The higher growth rate potential for juvenile sockeye salmon suggests that
458 temperature and perhaps prey availability are more favorable for sockeye salmon during warm
459 years. Lengths of age-0 walleye pollock were also found to be longer in 2004, 2005, and 2006
460 than in 2007 (Moss et al., 2009). Although other studies have found temperature effects on
461 growth and size of pelagic fishes of the eastern Bering Sea, capelin and herring size differences
462 in our data are more likely influenced by strong recruitment and age class strength, as both
463 species are represented by multiple age classes in our catches. However, since most spawning
464 capelin are 2 to 3 years old (Pahlke, 1985), while spawning herring may be up to 10 years old
465 and more (Hay, 1985), we suspect the effect of age class strength to be more pronounced in our
466 capelin catch data.

467 Herring lengths displayed a pattern of increasing size from the Inner, to Middle, and
468 Outer domains of the NEBS and SEBS, while capelin lengths showed no difference among
469 domains. Herring spawn in nearshore waters in spring and early summer, migrate to summer
470 feeding grounds, and eventually move to offshore overwintering grounds (Hay, 1985). Herring
471 overwinter northwest of the Pribilof Islands in the EBS, but have other potential overwintering
472 grounds southeast of the Pribilof Islands (Tojo et al., 2007). Our surveys confirm this migratory
473 behavior, and we caught larger, older fish offshore (Wespestad and Barton, 1979; Nagasawa,
474 2001).

475 Capelin lengths were similar in the Inner and Middle domains. Two year old capelin
476 usually migrate from nursery-spawning areas to feeding areas (Carscadden et al., 2013). We
477 captured capelin of similar size and age in both the Inner and Middle domains. Capelin feed and
478 migrate along oceanographic fronts (Vilhjálmsón, 2002; Rose, 2005) and may be using the
479 Inner and Middle domains equally, but concentrate along the front delineating the two regions
480 (Iverson et al., 1979).

481 *4.3 Diets*

482 Previous studies on EBS forage and small pelagic fish species have demonstrated a
483 difference in dietary composition between warm and cold climate periods; most notably a lack of
484 large, lipid-rich crustacean prey in stomachs during warm periods (Moss et al., 2009; Coyle et
485 al., 2011; Farley Jr. et al., 2015). This same pattern was present in the diet of herring and capelin,
486 further demonstrating temperature-related contraction and expansion of pelagic energy pathways
487 in the EBS. These shifts in diet and condition (Andrews et al., 2009; Heintz et al., 2013)
488 ultimately change overwinter survival and subsequent recruitment success (Calvert Siddon et al.,
489 2013).

490 While the proportion of large crustacean prey consumed by capelin typically increased in
491 the diet in every domain from warm to cold climate periods (~25% to ~80% in the S Middle
492 domain), there was one exception. The proportion of large crustacean prey in the N Middle
493 domain remained relatively stable from warm to cold. This was due to a much larger proportion
494 of *T. raschii* and other *Thysanoessa* spp. in the diet during warm conditions (Fig. 4). During
495 cold years, sea ice extends into the SEBS, and can persist long enough to produce a strong ice
496 edge bloom of algae (Sigler et al., 2014). *Thysanoessa* spp. has been observed feeding on ice-
497 associated algae (Lessard et al., 2010). The biomass of these euphausiids is expected to increase

498 during cold conditions with greater sea ice cover in the S Middle domain (Eisner et al., 2014).
499 However, in the N Middle domain, sea ice has always persisted until at least April, and
500 combined with nutrient-rich Anadyr waters, potentially provides a stabilizing effect for N Middle
501 domain euphausiids. Lastly, during warm conditions, the capelin in the N Middle domain had a
502 more favorable diet than those in the S Middle domain.

503 Another observation of interest for capelin was the proportion of the Other diet category
504 in the N Inner domain during warm years. This category was created to lump prey categories
505 that occurred very infrequently, and could not be lumped into other broad taxonomic categories.
506 Its prevalence (~16x any other combination of climate and domain) during warm conditions in
507 the N Inner domain suggests that capelin broadened their diet to compensate for a poor foraging
508 environment; with little of the demonstrated preferred prey items in cold conditions and in other
509 locations. The transition from cold to warm may have greater ecological impact, via
510 zooplankton community composition, distribution and abundance (i.e. prey fields) in the N Inner
511 domain. While the N Middle domain may be a refugium for *Thysanoessa* spp., the Inner domain
512 does not appear to be as stable.

513 Large, lipid-rich crustacean prey also occurred in herring diets during cold conditions.
514 Additionally, the increase of *Thysanoessa* spp. consumed by capelin during warm conditions in
515 the N Middle domain was observed in herring diets, supporting the idea of a refugium for ice-
516 edge associated euphausiids in the N Middle domain. The most significant difference in diet of
517 herring relative to capelin was the large proportion of age-0 walleye pollock. Age-0 walleye
518 pollock contributed >60% of the stomach content index during warm conditions in the S Middle
519 domain and >30% in the N Middle domain. This is likely a reflection of the larger mean length
520 of herring as they move offshore. The larger herring in the Middle domain are likely more able

521 to exploit age-0 walleye pollock as a prey resource. Use of age-0 walleye pollock as prey was
522 observed for larger walleye pollock, juvenile Pacific salmon, and age-0 Pacific cod during this
523 same time period (Moss et al., 2009; Coyle et al., 2011; Farley Jr. et al., 2015). Predation by
524 herring and other predators on age-0 walleye pollock during warm periods may also be
525 contributing to poor recruitment of pollock in the EBS (Bailey and Houde, 1989). In addition,
526 during warm periods age-0 walleye pollock have lower energy densities compared to age-0
527 walleye pollock during cold conditions (Heintz et al., 2013), further affecting predator condition.

528 The Arctic hyperiid amphipod *T. libellula* is absent during warm conditions, but
529 becomes an important component of herring diet (>30% SCI) during cold conditions in the N
530 Middle domain, is probably due to temperature influences on the distribution of *T. libellula*
531 (Pinchuk et al., 2013). During cold conditions, *T. libellula* follows the cold pool throughout the
532 Middle domain, and has been observed in the diets of other pelagic fishes during cold conditions
533 (Pinchuk et al., 2013; Farley Jr. et al., 2015). The changes in dietary composition observed in this
534 study reflect the changes in the distribution and abundance of the prey field over this same time
535 period (Eisner et al., 2014). Selectivity analysis would have allowed us to say more about how
536 these forage fish species react to changes in the prey field due to climate change. However, we
537 were not able to investigate dietary selectivity due to our methodology. Selectivity analysis
538 requires prey item counts, as well as an adequate representation of the prey field. We have
539 neither.

540 Results from cold conditions in this study resemble those from other diet studies in sub-
541 Arctic regions (Ajiad and Pushaeva, 1991; Coyle and Paul, 1992; Huse and Toresen, 2000;
542 O'Driscoll et al., 2001; Wilson et al., 2006; Hedeholm et al., 2012; Dalpadado and Mowbray,
543 2013). The similarities between these regions are striking, with circumpolar diet composition

544 sharing a majority of prey genera, and in some cases, the same species. The Bering Sea is
545 unique in having a vast, shallow continental shelf. During warm conditions, water column depth
546 on the shelf may limit the ability of large crustacean zooplankters to mediate physiological
547 demands by seeking colder temperatures at depth (Coyle et al., 2011). Animals living over
548 deeper waters can manage temperature stress by vertical migration, but the Middle domain in the
549 EBS is only 50-100 m deep.

550 **4.0 Conclusion**

551 The distributional shift in capelin and changes in the diets of both species provide strong
552 evidence of ecosystem changes in response to climate change in the EBS. Changes in
553 distribution and abundance of key prey species can directly affect the predators that feed on them
554 (Rose, 2005). The EBS is a particularly rich and productive marine ecosystem that supports not
555 only highly valuable commercial fisheries, but also a diverse and abundant suite of marine
556 mammals and birds. Many of these top level predators prey directly on capelin and herring
557 (Frost and Lowry, 1981; Springer et al., 1987; Merrick et al., 1997; Yang et al., 2005), and the
558 response of these upper trophic level organisms to reductions in prey is unknown. The observed
559 shifts in the dietary composition of capelin and herring add to a growing list of fishes (e.g.
560 juvenile salmonids, age-0 walleye pollock, age-0 Pacific cod) affected by shifts in zooplankton
561 communities due to changing climate, most notably, the reduction of large, lipid-rich crustacean
562 prey during warm years and, a switch from large crustaceans to age-0 walleye pollock in the case
563 of herring. Reductions in energy content of prey has been linked to reduced energy content of
564 predators (Heintz et al., 2013), leading to decreased overwinter survival and ultimately lower
565 recruitment for some species. These capelin and herring findings provide key insights into
566 significant ecosystem changes resulting from warming climate. As a final note, capelin have

567 been identified as a climate “canary” (Rose, 2005) and continuous monitoring of their
568 populations in the eastern Bering Sea could be a sentinel for ecosystem changes, particularly at
569 higher trophic levels (piscivorous fish, seabirds and marine mammals).

570

571 **Acknowledgements**

572 We thank the officers and crew of the NOAA ship *Oscar Dyson* as well as the captains and
573 crews of the following fishing vessels: F/V *Sea Storm*, F/V *Northwest Explorer*, F/V *Epic*
574 *Explorer*, and F/V *Bristol Explorer*. We also thank the many scientists that assisted with
575 processing and sampling the catch. This project would not have been possible without the
576 expertise of Natalia Kuznetsova (TINRO) and Mary Auburn-Cook for performing on board diet
577 analyses. We greatly appreciate Peter Hulson (AFSC), Franz Mueter (UAF) and Kathy Mier
578 (AFSC) for their guidance and assistance with some of the statistical analyses. In addition, we
579 would like to thank Ellen Yasumiishi, the AFSC editorial staff, three anonymous reviewers, and
580 Jeff Napp (guest editor), whose valuable comments and constructive criticism greatly improved
581 the quality of this manuscript. This is BEST-BSIERP Bering Sea Project publication number
582 170 and NPRB publication number 555. The findings and conclusions in this paper are those of
583 the authors and do not necessarily represent the views of the National Marine Fisheries Service.
584

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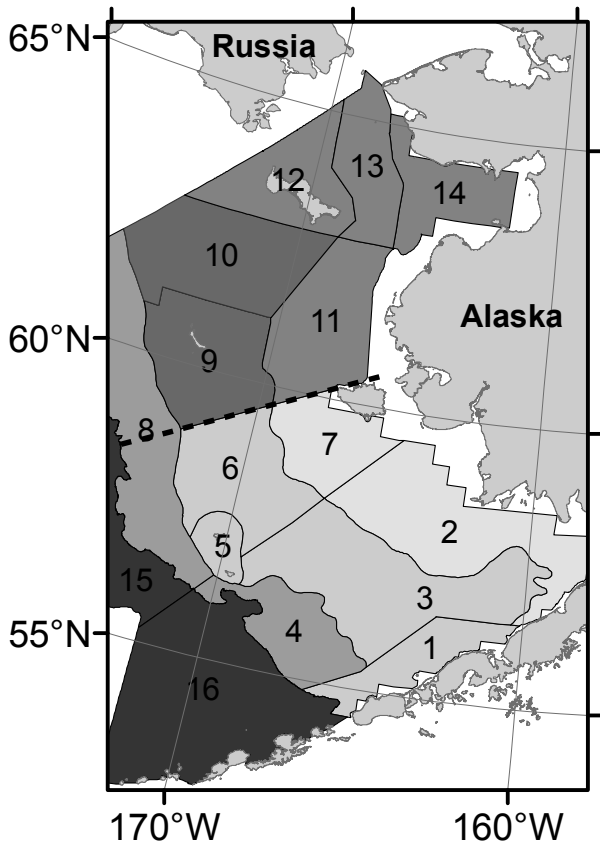
Figures:

Figure 1. Eastern Bering Sea study area with individual Bering Sea Project (BSP) regions (numbered) consolidated into domains (shaded) for this study. Stations were grouped into six domains: N Inner (regions 11, 12, 13, and 14), N Middle (regions 9 and 10), S Inner (regions 2 and 7), S Middle (regions 1, 3, 5, and 6), S Outer (regions 4 and 8), and Off-shelf (regions 15 and 16). The dashed line represents delineation between northeastern Bering Sea (NEBS) and southeastern Bering Sea (SEBS).

Figure 2. Capelin and herring catch per unit effort (CPUE; kg/km²) during warm (2003-2005) and cold (2006-2011) climate periods. Local polynomial data interpolation was used to generate shaded contours for visualization of distributions. Circles represent mean CPUE at each station trawled. (A) Capelin during warm climate period, (B) Capelin during cold climate period, (C) Herring during warm climate period, and (D) Herring during cold climate period.

Figure 3. Catch-weighted mean lengths (mm) for capelin and herring by climate period and domain in the northeastern Bering Sea (NEBS) and the southeastern Bering Sea (SEBS). Error bars represent 95% confidence intervals. Samples sizes are given as the number of stations where lengths were measured.

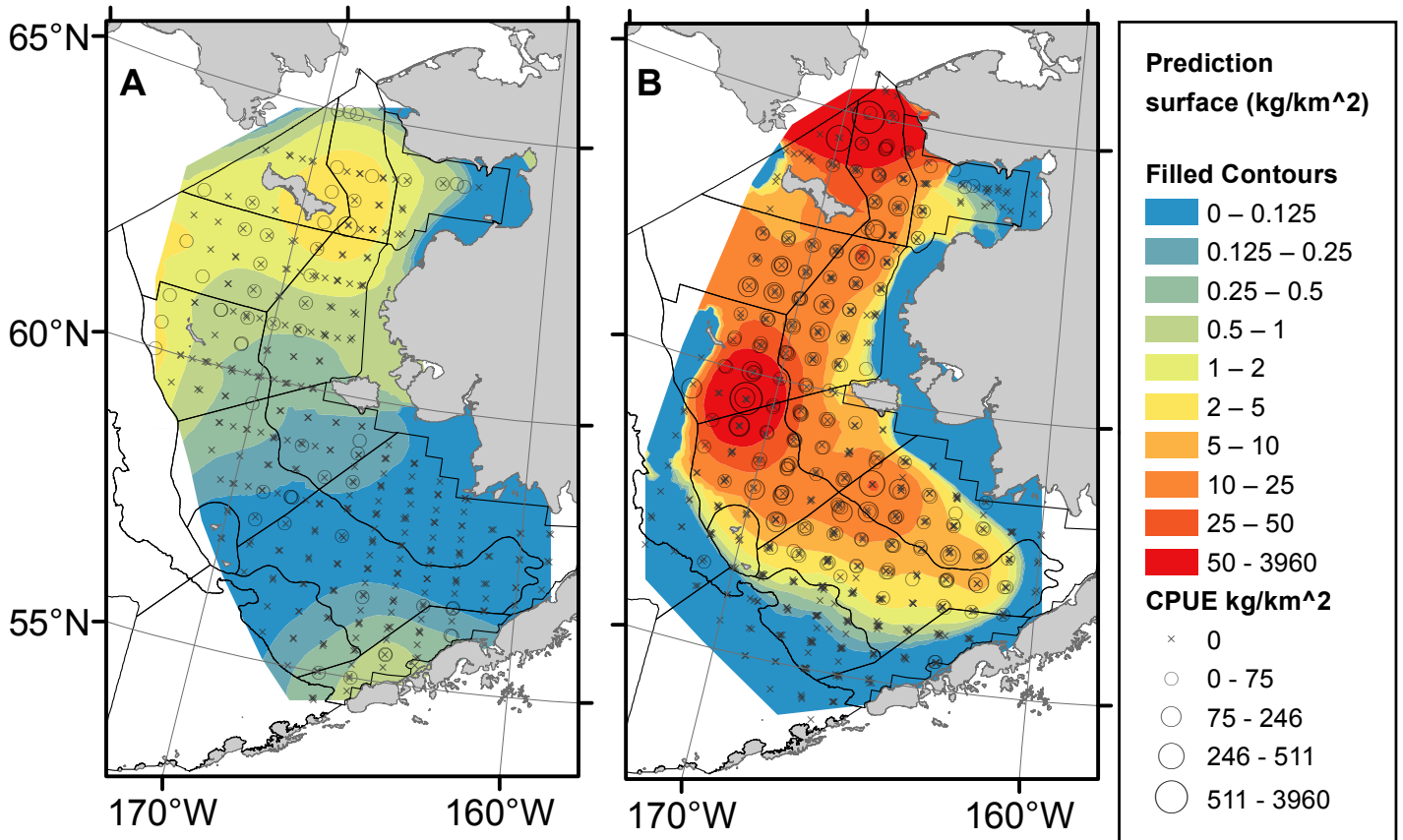
Figure 4. Percent stomach content index (SCI) for prey categories in the diet of capelin (top four bar plots) and herring (bottom four bar plots) within each domain, and during both warm and cold climate periods. Note: Warm climate diet in the southern Inner (S Inner) domain was based on data from a single station.



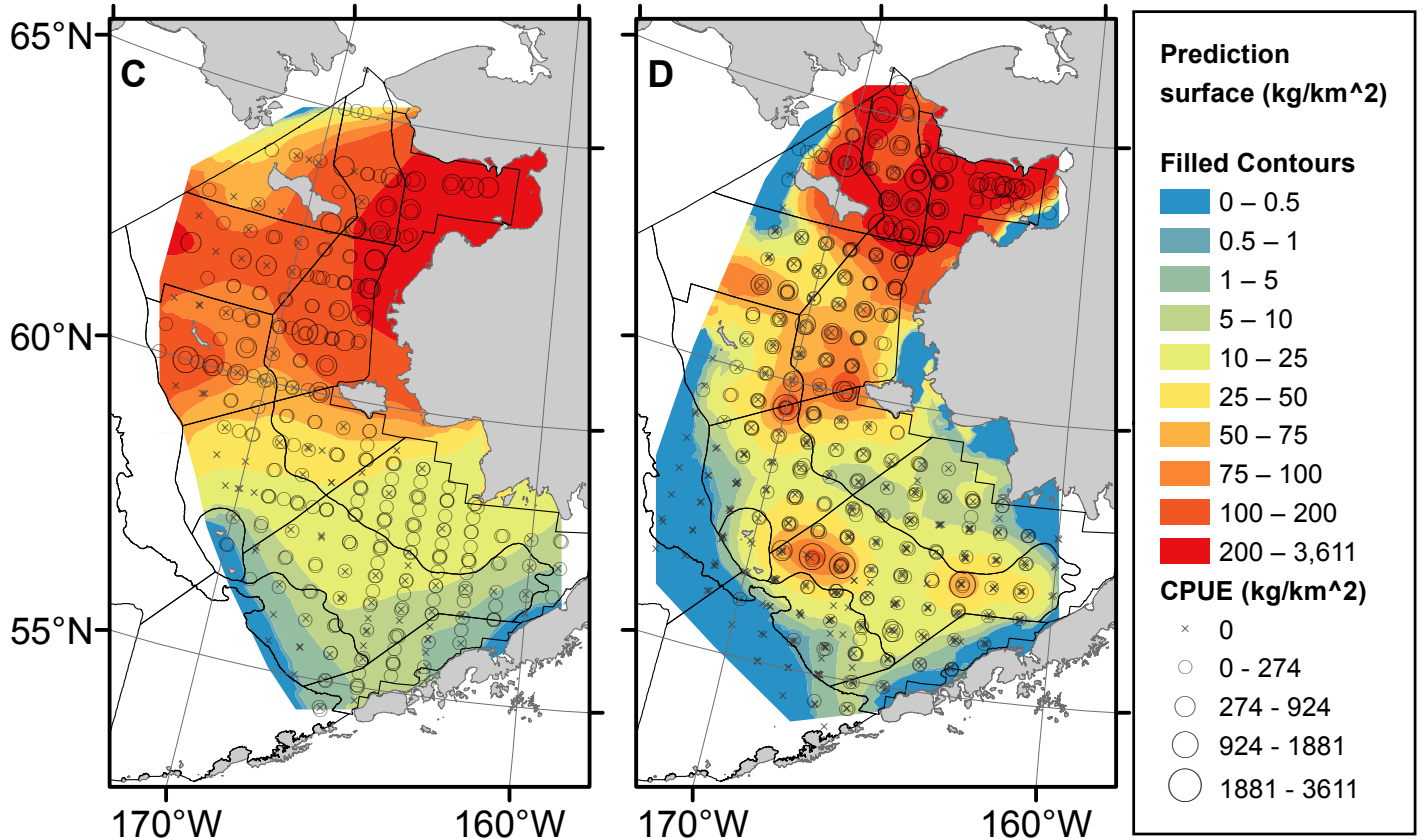
Domains

- South Inner
- South Middle
- South Outer
- South Off-Shelf
- North Inner
- North Middle

Capelin



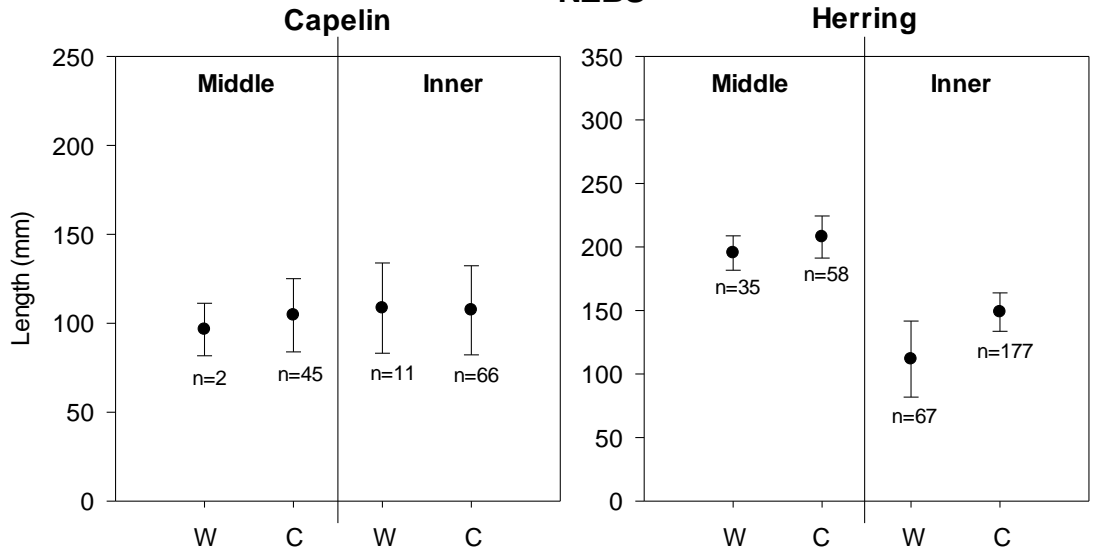
Herring



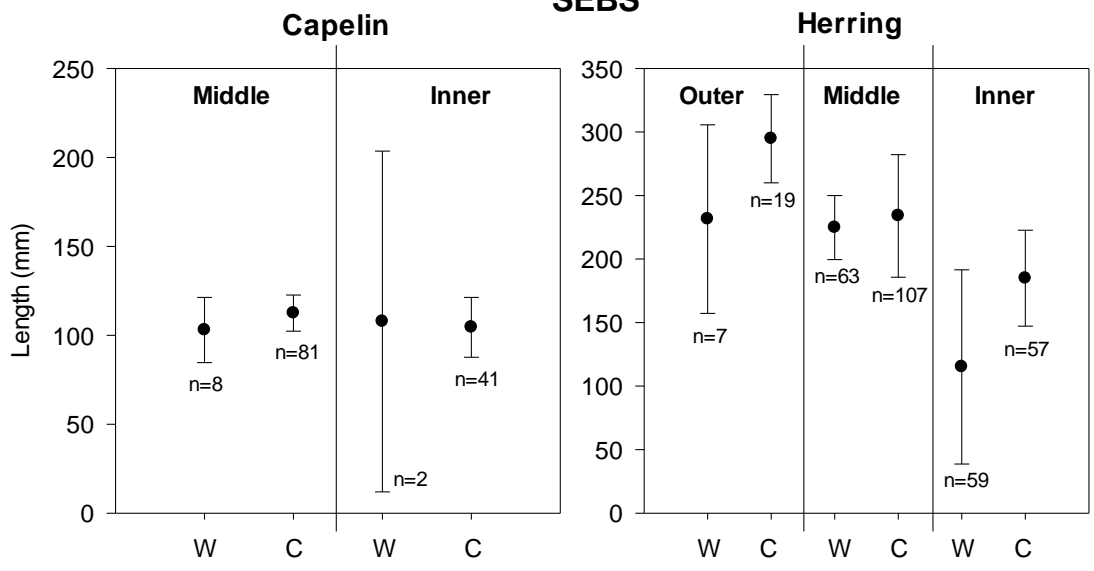
Warm (2003-2005)

Cold (2006-2011)

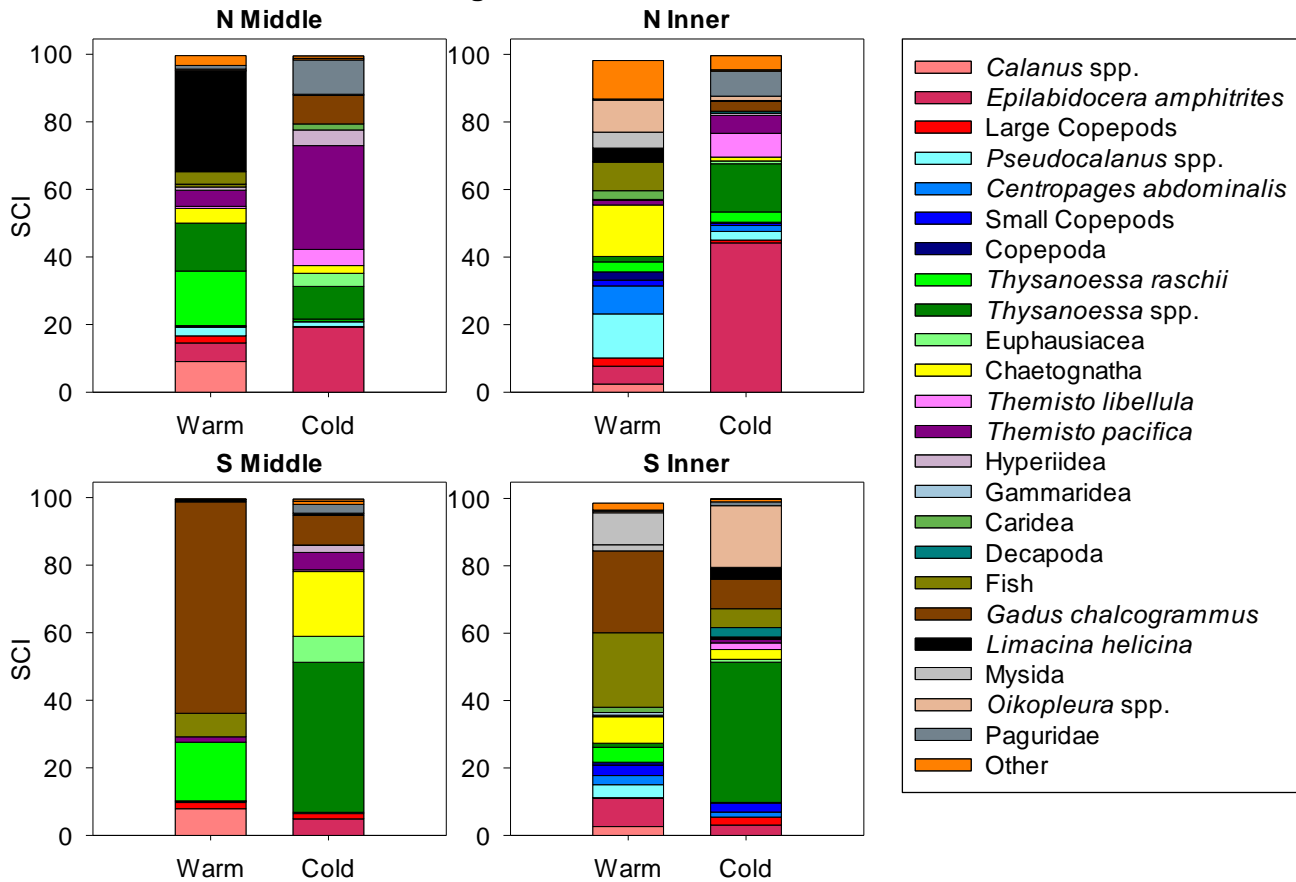
NEBS



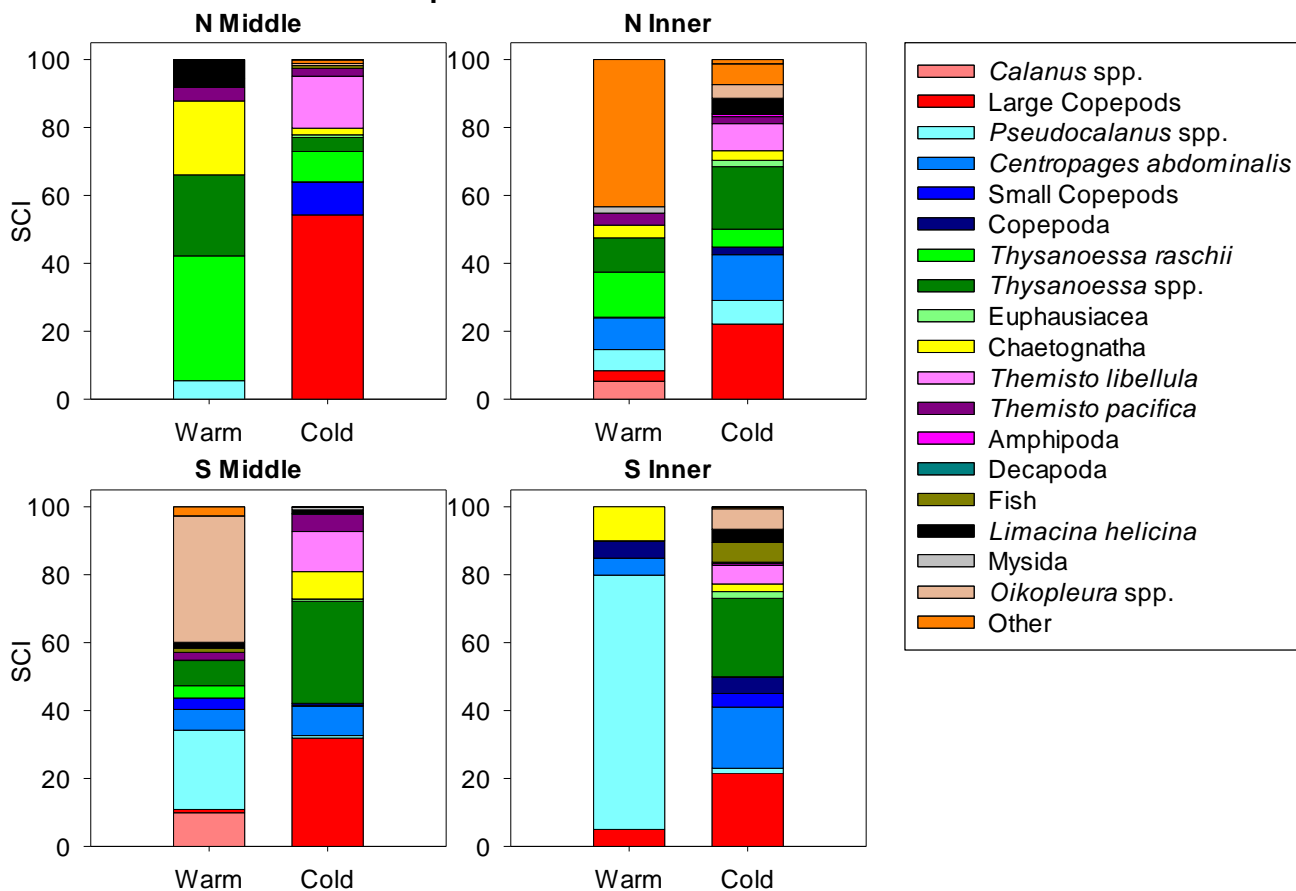
SEBS



Herring Diets



Capelin Diets



1 Table 1. Sample effort by species, climate period, and domain. Total Stations is number of
 2 locations occupied, present is the number of stations with catch for that species, lengths is the
 3 number of stations where lengths were recorded (total number of fish that were lengthed), diet is
 4 the number of stations where diets were examined (total number of fish stomachs that were
 5 examined).

6

	Total Stations	Capelin			Pacific herring		
		Present	Lengths	Diet	Present	Lengths	Diet
Cold Southern Inner	111	40	38 (2405)	26 (365)	58	57 (1145)	36 (321)
Cold Southern Middle	253	76	76 (3244)	39 (394)	109	107 (1676)	47 (382)
Cold Southern Outer	98	1	0	0	22	19 (147)	0
Cold Northern Inner	191	64	64 (2429)	30 (288)	167	167 (8549)	112 (1158)
Cold Northern Middle	85	45	44 (1857)	28 (290)	56	56 (2105)	32 (292)
Warm Southern Inner	94	5	2 (37)	1 (15)	79	57 (2794)	52 (526)
Warm Southern Middle	134	18	8 (131)	11 (102)	88	62 (1380)	29 (281)
Warm Southern Outer	25	0	0	0	15	7 (52)	0
Warm Northern Inner	96	19	11 (438)	6 (60)	84	63 (5205)	51 (698)
Warm Northern Middle	59	15	2 (2)	5 (50)	42	34 (2865)	23 (236)

7

8 Table 2. Mean CPUE (kg/km²; standard error) for capelin and herring by climate period for the
 9 eastern Bering Sea (EBS), the northeastern Bering Sea (NEBS), and the southeastern Bering Sea
 10 (SEBS); as well as, the northern Inner (N Inner), northern Middle (N Middle), southern Inner (S
 11 Inner), and southern Middle (S Middle) domains.

12

	Capelin CPUE (kg/km ²)		Herring CPUE (kg/km ²)	
	Warm	Cold	Warm	Cold
EBS	0.57 (0.23)	18.99 (7.89)	63.78 (8.00)	66.19 (9.39)
NEBS	1.23 (0.59)	40.01 (20.28)	141.08 (18.90)	132.43 (21.23)
SEBS	0.16 (0.06)	5.78 (1.32)	15.77 (2.61)	24.45 (6.74)
N Inner	1.60 (0.95)	31.60 (21.00)	165.85 (25.37)	175.41 (29.95)
N Middle	0.64 (0.29)	58.91 (46.11)	100.08 (26.86)	35.85 (8.54)
S Inner	0.09 (0.07)	9.78 (4.12)	22.33 (5.40)	18.39 (6.27)
S Middle	0.24 (0.11)	5.75 (1.40)	12.89 (2.96)	33.92 (11.40)

13

14 Table 3. Mann-Whitney Rank Sum test results for differences in mean CPUE (kg/km²) between
 15 climate periods for each domain, and within climate periods but between domains.

16

	Capelin	Herring
	<i>p</i> -value	<i>p</i> -value
Warm vs. Cold		
EBS	<0.001	<0.001
NEBS	<0.001	0.277
SEBS	<0.001	<0.001
Warm Periods		
NEBS vs. SEBS	<0.001	<0.001
S Inner vs. S Middle	0.051	0.005
N Inner vs. N Middle	0.461	0.018
Cold Periods		
NEBS vs. SEBS	<0.001	<0.001
S Inner vs. S Middle	0.187	0.441
N Inner vs. N Middle	0.002	<0.001

17

18 Table 4. SIMPER results highlighting prey items that contributed most to significant differences
19 identified by PERMANOVA tests for capelin diet. The first two columns report the average
20 prey abundance in each climate period being analyzed, while the last two columns provide the
21 relative contribution of each prey item, and the sum contribution of prey driving significant
22 differences.

23

SIMPER	Capelin Diet			
Species	Warm	Cold	% Contribution	Cumulative %
<i>Thysanoessa raschii</i>	1.4	0.7	18.9	18.9
<i>Calanus</i> spp.	0.0	1.5	17.8	36.7
Chaetognatha	0.3	0.9	10.0	46.7
<i>Pseudocalanus</i> spp.	0.2	0.6	7.3	54.0
Other	0.7	0.0	6.2	60.2

24

25 Table 5. PERMANOVA results, *t*-values and *p*-values (* indicates statistically significant
 26 difference) for pairwise tests for each level of climate period and domain within the interaction
 27 for herring diet (Climate X Domain).
 28

Pacific Herring PERMANOVA		
Warm vs. Cold	<i>t</i>-value	<i>p</i>-value
S Inner	1.2	0.16
S Middle	1.6	0.012*
N Inner	1.6	0.0006*
N Middle	1.1	0.37
Warm Periods		
S Inner vs. S Middle	1.7	0.043*
S Inner vs. N Inner	1.4	0.0399*
S Middle vs. N Middle	1.1	0.37
N Inner vs. N Middle	1.4	0.0503
Cold Periods		
S Inner vs. S Middle	1.3	0.086
S Inner vs. N Inner	1.1	0.29
S Middle vs. N Middle	1.1	0.21
N Inner vs. N Middle	1.0	0.56

29

30 Table 6. SIMPER results highlighting prey items that contributed most to significant differences
 31 identified within PERMANOVA tests within Pacific herring. The first two columns report the
 32 average abundance in each climate period being analyzed, while the last two columns provide
 33 the relative contribution of each prey item, and the sum contribution of prey driving significant
 34 differences.

35

Herring Diet S Middle				
SIMPER	Warm	Cold	% Contribution	Cumulative %
<i>Gadus chalcogrammus</i>	2.0	0.1	30.5	30.5
<i>Thysanoessa raschii</i>	0.8	1.1	17.6	48.1
Fish	0.6	0.4	11.6	59.7
<i>Themisto libellula</i>	0.0	0.4	5.0	64.7
Herring Diet N Inner				
	Warm	Cold	% Contribution	Cumulative %
<i>Pseudocalanus</i> spp.	1.1	0.3	9.1	9.1
Other	1.0	0.3	8.5	17.6
Larvaceans	0.5	0.7	7.7	25.3
Chaetognatha	0.6	0.6	7.6	32.9
<i>Centropages abdominalis</i>	0.9	0.2	7.6	40.5
<i>Calanus</i> spp.	0.2	0.7	5.9	46.4
Fish	0.5	0.4	5.7	52.1
<i>Epilabidocera amphitrites</i>	0.6	0.2	5.3	57.4
Copepoda	0.3	0.3	5.2	62.6
Herring Diet Warm Period S Inner vs. S Middle				
	S Inner	S Middle	% Contribution	Cumulative %
<i>Gadus chalcogrammus</i>	0.8	2.0	21.2	21.2
Fish	1.2	0.6	13.9	35.1
<i>Epilabidocera amphitrites</i>	0.9	0.0	9.0	44.1
<i>Thysanoessa raschii</i>	0.1	0.8	8.1	52.2
Mysida	0.7	0.1	8.0	60.2
Herring Diet Warm Period S Inner vs. N Inner				
	S Inner	N Inner	% Contribution	Cumulative %
Fish	1.2	0.5	10.6	10.6
<i>Pseudocalanus</i> spp.	0.5	1.1	8.6	19.2
<i>Gadus chalcogrammus</i>	0.8	0.0	8.2	27.4
Other	0.3	1.0	8.2	35.6
<i>Centropages abdominalis</i>	0.4	0.9	7.4	43.0
<i>Epilabidocera amphitrites</i>	0.9	0.6	7.4	50.4
Mysida	0.7	0.4	6.9	57.3
Chaetognatha	0.4	0.6	6.3	63.6

36

37 Appendix A. Vessels, date range, climate conditions, and bounding coordinates (decimal degrees) for data collections cruises
 38 involved in this study.

39

Vessel	Survey Start Date	Survey End Date	Climate Conditions	Latitude Range	Longitude Range
<i>F/V Sea Storm</i>	21-Aug-03	08-Oct-03	Warm	54.52N : 65.55N	172.53W : 160.97W
<i>F/V Sea Storm</i>	14-Aug-04	30-Sep-04	Warm	54.53N : 64.12N	174.04W : 158.99W
<i>F/V Sea Storm</i>	14-Aug-05	06-Oct-05	Warm	54.49N : 64.13N	174.01W : 159.04W
<i>F/V Sea Storm</i>	16-Aug-06	20-Sep-06	Cold	54.49N : 64.10N	173.02W : 163.04W
<i>F/V Northwest Explorer</i>	21-Aug-06	04-Sep-06	Cold	54.52N : 59.00N	167.02W : 159.98W
<i>FSV Oscar Dyson</i>	05-Sep-07	26-Sep-07	Cold	57.97N : 65.55N	172.07W : 164.05W
<i>F/V Sea Storm</i>	15-Aug-07	08-Oct-07	Cold	54.50N : 64.03N	172.01W : 159.98W
<i>FSV Oscar Dyson</i>	11-Sep-08	27-Sep-08	Cold	55.48N : 59.54N	169.03W : 161.00W
<i>FSV Oscar Dyson</i>	03-Sep-09	27-Sep-09	Cold	54.48N : 60.01N	173.07W : 160.98W
<i>F/V Epic Explorer</i>	30-Aug-09	13-Sep-09	Cold	60.50N : 64.49N	172.03W : 163.07W
<i>FSV Oscar Dyson</i>	18-Aug-10	24-Sep-10	Cold	54.45N : 59.47N	169.06W : 161.00W
<i>F/V Epic Explorer</i>	05-Sep-10	05-Oct-10	Cold	57.01N : 65.47N	172.03W : 162.72W
<i>FSV Oscar Dyson</i>	23-Aug-11	15-Sep-11	Cold	54.51N : 58.52N	169.06W : 161.93W
<i>F/V Bristol Explorer</i>	21-Aug-11	19-Sep-11	Cold	56.51N : 65.49N	171.07W : 161.55W

40