

1 **Title**

2

3 Multispecies Biomass Dynamics Models Reveal Effects of Ocean Temperature on  
4 Predation of Juvenile Pollock in the Eastern Bering Sea

5

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12

13 **Author's contribution**

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- 15 • Have made substantial contributions to conception and design, acquisition, analysis  
16 and interpretation of data.
- 17 • Been involved in drafting the manuscript.
- 18 • Given final approval of the version to be published and take public responsibility  
19 for appropriate portions of the content.
- 20 • Agreed to be accountable for all aspects of the work in ensuring that questions  
21 related to the accuracy or integrity of any part of the work are appropriately  
22 investigated and resolved.

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- 25 • Have made substantial contributions to conception and design and acquisition of  
26 data.
- 27 • Been involved in revising the manuscript critically for important intellectual  
28 content.

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- 35       • Have made substantial contributions to conception and design.
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41       related to the accuracy or integrity of any part of the work are appropriately  
42       investigated and resolved.

43

#### 44   **Statement of conflict of interests**

45   None of the coauthors has any conflict of interests.

46

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55

#### 56   **Abstract**

57 Walleye pollock (*Gadus chalcogrammus*) supports one of the largest commercial fisheries  
58 in the world. Juvenile pollock are important forage fish in the EBS ecosystem, often  
59 representing the largest fraction in the diets of major Bering Sea piscivores. Large  
60 variability in the eastern Bering Sea (EBS) pollock stock biomass in recent years has been  
61 attributed primarily to fluctuations in recruitment. It has been hypothesized that predation  
62 rates on forage fishes increase when the cold pool (a body of cold water  $< 2^{\circ}\text{C}$ ) is extensive  
63 and covers much of the middle continental shelf, which tends to concentrate larger  
64 predatory fishes in the outer shelf and slope regions. In contrast, young pollock appear to  
65 tolerate colder temperatures than older fish and can stay in the cold pool, thereby reducing  
66 predation. We used a multispecies modeling approach to examine the effects of the cold  
67 pool size on predation of juvenile pollock. We found that predation on age-1 pollock by  
68 age-3+ pollock decreased, and predation on age-1 and age-2 pollock by arrowtooth  
69 flounder increased with increasing bottom temperature, which was used as a proxy for the  
70 cold pool size. These results suggest that the cold pool creates spatial separation between  
71 juvenile pollock and arrowtooth flounder, but not between adult and juvenile pollock. The  
72 model developed in this study could be used to examine effects of other covariates on  
73 interspecific interactions, help explain observed changes in fish communities, and  
74 understand implications of climate change on ecosystems and their productivity.

75

76 **Keywords:** Multispecies model, Bering Sea, biomass dynamics model, predator-prey  
77 interaction, ocean temperature

78

## 79 **Introduction**

80 Walleye pollock (*Gadus chalcogrammus*) is the most abundant and commercially important  
81 groundfish species in the Bering Sea. Pollock represent 56% of exploitable groundfish  
82 biomass in the Bering Sea and Aleutian Islands fisheries management area (NPFMC,  
83 2015), and commercial catches of pollock averaged 75% of the total groundfish catch by  
84 weight from this area over 1990 to 2016 (NPFMC, 2016). Commercial fisheries for pollock  
85 represent over 40% of the global whitefish production. However, the eastern Bering Sea

86 (EBS) pollock stock declined more than 60% from a high of 12.2 million t in 2003 (age 3+  
87 biomass) to a low of 4.6 million t in 2008, before increasing again in recent years through  
88 2016 (Ianelli et al., 2016). This decrease in biomass was also reflected in reduced harvests.  
89 In 2009 and 2010, annual EBS pollock catch dropped to 0.81 million tons, roughly a 40%  
90 reduction from the average catch (1.28 million tons) over the previous 9 years (Ianelli et al.,  
91 2009). Changes in stock biomass are primarily due to the effect of year-class variability and  
92 the sharp decline after 2003 has been attributed to poor recruitment between 2001 and 2005  
93 (Coyle et al., 2011; Ianelli et al., 2009). The recent rebound was associated with strong year  
94 classes in 2008 and 2012 (Ianelli et al. 2016). Mechanisms controlling pollock recruitment  
95 are complex and poorly understood, but likely involve both physical and biological factors,  
96 as well as interactions among them (Duffy-Anderson et al., 2016; Hunt et al., 2011; Jurado-  
97 Molina and Livingston, 2002a; Mueter et al., 2006; Sigler et al., 2016) .

98  
99 Juvenile pollock are important forage fish in the EBS ecosystem, often representing the  
100 largest fraction in the diets of major Bering Sea piscivores, including arrowtooth flounder  
101 (*Atheresthes stomias*), flathead sole (*Hippoglossoides elassodon*), and adult walleye  
102 pollock (Aydin et al., 2007; Coyle et al., 2011). Cannibalism by adult pollock has been  
103 estimated to cause 40% of juvenile pollock mortality (Aydin et al., 2007) and plays an  
104 important role in determining pollock year-class strength (Wespestad and Quinn, 1996).  
105 Arrowtooth flounder are a major predator of both juvenile and adult pollock, raising  
106 concerns about the effects of a nearly four-fold increase in total biomass of arrowtooth  
107 flounder over 1976-2009 in the eastern Bering Sea (Spies et al., 2016) on future pollock  
108 recruitment.

109  
110 In addition to the direct effects of currents on the transport of eggs and larvae and of water  
111 temperature on individual growth and development, physical oceanographic conditions also  
112 affect pollock recruitment indirectly via trophic interactions. These include effects on food  
113 production (bottom-up) and on predation intensity (top-down), the latter of which is in part  
114 regulated by the degree of spatial overlap between predators and prey (Yamamura, 2004). It

115 has been hypothesized that warm spring conditions and early sea ice retreat on the EBS  
116 shelf reduces the availability of large zooplankton prey for age-0 pollock, resulting in weak  
117 age-1 recruitment in the following year (Coyle et al., 2011; Hunt et al., 2011). Low  
118 abundance of large zooplankton in warm years may reduce pollock recruitment further as  
119 fish predators shift to age-0 pollock as an alternative prey (Coyle et al., 2011; Moss et al.,  
120 2009). On the other hand, stronger northward advection during warm years transports  
121 juvenile pollock inshore and away from adults (Smart et al., 2012). For example, large-  
122 scale surveys using a midwater rope trawl in late summer and early autumn found age-0  
123 walleye pollock to be abundant and widely distributed from Bristol Bay to offshore and  
124 northern areas during warm years (2004–2005) and less abundant with a distribution that  
125 was more restricted to the southeastern Bering Sea in cool years (2006–2007. See Figure 1  
126 in Moss et al., 2009). The resulting spatial separation between juveniles and adults may  
127 reduce cannibalism and enhance recruitment the following year (Mueter et al., 2006;  
128 Wespestad et al., 2000).

129  
130 The presence of the so-called “cold pool” is one of the important physical features of the  
131 EBS shelf. The cold pool is a body of cold bottom water generally  $< 2^{\circ}\text{C}$ , which persists on  
132 the middle shelf at depths of 50 to 100 m throughout summer. The cold pool forms when  
133 sea ice freezes in the winter, and the size of the cold pool in summer depends on the extent  
134 of sea ice during the previous winter. Many subarctic fish species avoid the cold pool (  
135 Mueter and Litzow, 2008; Zador et al., 2011) and are therefore excluded from much of the  
136 shelf when the cold pool is extensive, concentrating fish in the outer shelf and slope regions  
137 (Spencer, 2008; Figure 1a). It has been hypothesized that an extensive cold pool increases  
138 encounter rates between prey and predators and results in higher predation rates on forage  
139 fishes (Hunsicker et al., 2013; Wespestad et al., 2000; Wyllie-Echeverria and Ohtani,  
140 1999). On the other hand, there is some evidence that young pollock, in particular age-1  
141 fish, can tolerate cold temperatures better than older fish and thus are able to seek refuge in  
142 the cold pool to avoid predation (Bailey, 1989; Francis and Bailey, 1983; Sogard and Olla,  
143 1993; Wyllie-Echeverria and Wooster, 1998). If that were the case, then predation on

144 juvenile pollock is expected to be lower in cold years with an extensive cold pool (Figure  
145 1b). Either way, these studies suggest that the extent of the cold pool can affect recruitment  
146 of pollock by modulating interactions between juvenile pollock and its predators on the  
147 Bering Sea shelf.

148

149 In this study we use a multispecies modeling approach to examine the effects of variability  
150 in the cold pool on predation of juvenile pollock. Our objectives are to quantify 1) the  
151 magnitude of predation among six EBS groundfish species using a multispecies biomass  
152 dynamics model fitted to survey biomass data and 2) the effect of changing bottom  
153 temperature on the predation rates on juvenile pollock by their fish predators. In particular,  
154 we are interested in finding out which predatory interactions (prey-predator combinations)  
155 involving juvenile pollock are more strongly affected by changes in bottom temperatures  
156 associated with a variable cold pool.

157

## 158 **Methods**

### 159 Overview

160 We quantified predation on juvenile pollock by modeling the biomass dynamics of six EBS  
161 groundfish species – walleye pollock, arrowtooth flounder, Pacific cod (*Gadus*  
162 *macrocephalus*), yellowfin sole (*Limanda aspera*), northern rock sole (*Lepidopsetta*  
163 *polyxystra*), and flathead sole – and predatory interactions among them (Figure 2). We  
164 aggregated all flatfish species except arrowtooth flounder into a ‘small-mouth flatfish’  
165 group because of similar decadal trends in stock biomass (Figure 3) and similar trophic  
166 roles in the ecosystem. Walleye pollock was divided into four age classes (age 0, 1, 2, and  
167 3+) to explicitly model cannibalism of juveniles (age 0, 1, and 2) by adult and subadult  
168 pollock (age 3+, referred to as “adult pollock” hereafter for simplicity). As a result, seven  
169 species-age groups were modeled (arrowtooth flounder, Pacific cod, small-mouth flatfish,  
170 and four age groups of pollock). Model details are provided in Uchiyama et al. (2016) and  
171 Appendix 1.

172

173 To test for the effects of variability in the cold pool on predation, in this study we modified  
174 the model of Uchiyama et al. (2016) to include temperature-dependent predation rates as  
175 described below. The model was fit to survey biomass data and estimated prey biomass  
176 consumed by predators. We used mean bottom water temperature in the model as a proxy  
177 for the cold pool extent. Multiple alternative models, including different combinations of  
178 temperature-dependence for one or more predator-prey interactions, were considered to  
179 identify predator-prey interactions that show strong temperature dependence, and to  
180 quantify the effect of bottom temperature on predation rates.

181

#### 182 Data

183 Survey biomass estimates of the study species, commercial catch statistics, and estimated  
184 biomass lost to predation used in this study are summarized in Appendix 2 and described in  
185 detail in Uchiyama et al. (2016). In addition, an annual index of summer bottom  
186 temperature ( $T_B$ ) was used as an environmental factor that affects the predator-prey  
187 interactions in the model (see the descriptions in “Models” section below). The index was  
188 estimated by fitting a spatial Generalized Additive Model (GAM) to observed bottom  
189 temperatures during the EBS summer trawl survey. Bottom temperature data were obtained  
190 from NOAA (<https://www.afsc.noaa.gov/RACE/groundfish/ebs.htm>) and were modeled  
191 using a spatial smoother (thin-plate regression spline, Wood, 2017), while including year  
192 and smooth functions of depth and day of sampling as covariates in the model to account  
193 for differences in mean temperature conditions among years, as well as for differences in  
194 sample locations and in the timing of the survey among years. Predicted temperatures along  
195 the 70 m depth contour on July 1<sup>st</sup> of each year were used to index interannual temperature  
196 variability on the middle shelf.

197

#### 198 Apportionment of pollock predation into age classes

199 Estimated biomass lost to predation reported in the Alaska Fisheries Science Center’s  
200 groundfish food habits reports (Lang et al., 2005; Lang et al., 2003, 1991; Livingston and  
201 DeReynier, 1996; Livingston et al., 1993) represent aggregated biomass of all prey age

202 classes. To estimate predation on pollock by age class from available diet data, Uchiyama  
203 et al. (2016) apportioned pollock prey biomass into age classes (ages 0, 1, 2, and 3+)  
204 according to their proportion in the estimated total pollock biomass, assuming constant  
205 predation mortality across all age classes for simplicity. To more accurately estimate  
206 predation on each age class, in this study we reapportioned reported predation estimates to  
207 pollock age classes 0 through 3+ based on the body lengths of pollock prey.

208

209 The length distribution of pollock prey consumed by their predators was obtained from the  
210 Alaska Fisheries Science Center (Kerim Aydin, NMFS, personal communication) and data  
211 were subdivided into four sampling quarters (January – March, April – June, July –  
212 September, October – December). Based on visual examination of the prey body length  
213 distributions (Figure 4), we assumed that pollock prey in each quarter consisted of four  
214 groups of individuals with varying body lengths, and that the body lengths of individual  
215 prey in each group followed a Gaussian distribution. We assumed the group with the  
216 smallest mean body length in the first sampling quarter consisted of age-1 fish because the  
217 mean body length of this group was larger than that of the smallest group in the second  
218 quarter, and because pollock spawning peaks in early April in the EBS (Wespestad et al.,  
219 2000). For the second, third, and fourth sampling quarters, we assumed the smallest group  
220 was age-0. The means of the length frequency distributions of these groups approximately  
221 corresponded to the body lengths of Bering Sea walleye pollock at age (47, 156, 246, and  
222 320 mm for age 0, 1, 2, and 3, respectively) calculated from the life history parameters  
223 reported in Kooka (2012).

224

225 The mean body length of each age class and its variance were estimated using the R  
226 package ‘mixtools’ (Benaglia et al., 2009). Based on the quarter-specific age class body  
227 length distributions, the probability that prey of a given size in a given quarter belongs to a  
228 particular age class was calculated. Individual pollock prey were then assigned to one of  
229 four age classes (0, 1, 2, and 3+) by their body length, based on the probability calculated  
230 above. Body weights of individual prey were estimated from their body length and the



231 length-weight relationship for the Bering Sea shelf stock of walleye pollock reported in  
 232 Kooka (2012). Individual prey weights were summed by prey age class, predator, and  
 233 sampling year. The proportion by weight of each prey age class in the diet of a particular  
 234 predator was calculated for each sampling year by dividing the total weight of the prey in  
 235 each age class for a particular predator and sampling year by the total weight of prey in all  
 236 age classes. The biomass of each pollock age class lost to predation was then calculated by  
 237 multiplying total pollock biomass lost to predation by the age class proportions calculated  
 238 above.

239

#### 240 Models

241 Previously, we developed two alternative multispecies models for focal EBS groundfish  
 242 species – a biomass dynamics model and a delay difference model (Uchiyama et al. 2016).  
 243 Although each model has advantages and disadvantages, we selected the multispecies  
 244 biomass dynamics model as the preferred model, because it produces more stable and  
 245 realistic predictions in simulations than the multispecies delay difference model. Therefore,  
 246 in this study, biomass dynamics of adult walleye pollock (age 3+), arrowtooth flounder (age  
 247 1+), Pacific cod (age 1+), and a small-mouth flatfish group (age 1+) were modeled using  
 248 the multispecies biomass dynamics model described in Uchiyama et al. (2016), modified to  
 249 include temperature-dependent predation rates, as well as new estimates of the age  
 250 composition of pollock prey as described above. Biomass of juvenile pollock (ages 0, 1, 2)  
 251 was modeled with age structure to account for the effect of predation on recruitment  
 252 through multiple juvenile age classes as described in Uchiyama et al. (2016).

253

254 The size of the cold pool is negatively proportional to mean bottom temperature, hence  
 255 mean bottom temperature provides a measure of habitable space for the prey and predator  
 256 species on the EBS shelf. To examine the effects of bottom temperature on juvenile pollock  
 257 predation we modeled predation rates (see Appendix 1) in the biomass dynamics model as a  
 258 linear function of the GAM-estimated summer bottom temperature anomalies ( $T_{B,y}$ ):

$$259 \quad d_{mz} = \bar{d}_{mz} + e_{mz}T_{B,y} \quad (1)$$

260 where  $d_{mz}$  is the predation rate for predator  $z$  and prey juvenile age class  $m = \{P0, P1, P2\}$ ,  
 261  $\bar{d}_{mz}$  is the mean predation rate at  $T_B = 0$ , and  $e_{mz}$  is the slope parameter for the linear  
 262 relationship between predation rate and temperature for predator  $z$  and prey juvenile age  
 263 class  $m = \{P0, P1, P2\}$ . A linear relationship was assumed between predation rate and  
 264 bottom temperature because we expect the overlap of prey and predator distributions, based  
 265 on the areas occupied, to change linearly with the area of suitable habitat (Spencer et al.  
 266 2016). Thus, the per-capita predation rate of predator  $z$  on juvenile age class  $a$  increases  
 267 with bottom temperature if  $e_{mz} > 0$  and decreases if  $e_{mz} < 0$ . Parameters  $\bar{d}_{mz}$  for juvenile  
 268 pollock and  $d_{mz}$  for all other species groups were constrained to be positive in estimation.  
 269 To assess our assumption of a linear response of predation rates to temperature variability,  
 270 we modified the best approximating model selected in this study to allow for curvilinear  
 271 (quadratic) responses to bottom temperature by adding an extra parameter in each of the  
 272 predation functions found to be affected by bottom temperature, re-fitted the model, and  
 273 compared the fit to the linear model. Model parameters were estimated by maximizing the  
 274 likelihood function described in Appendix 1.

275

#### 276 Model selection

277 To identify the predator-prey interactions that are most strongly affected by bottom  
 278 temperature, we fit a series of nested models with different numbers and combinations of  
 279 the slope parameters  $e_{mz}$ , ranging from the ‘null’ model without temperature-dependent  
 280 predation to the full model with temperature-dependent rates for all 12 predation terms on  
 281 juvenile pollock (total of 4096 models). The nested models were then ranked by the Akaike  
 282 Information Criterion corrected for small sample size ( $AIC_C$ ) following Burnham and  
 283 Anderson (2002):

$$284 \quad AIC_C = -2 \ln(L) + 2k + \frac{2k(k+1)}{n-k-1}, \quad (2)$$

285 where  $L$  = likelihood,  $k$  = number of parameters (52 to 64, depending on the model. See  
 286 Appendix 2), and  $n$  = number of observations (577, number of data points used to fit the  
 287 model.). The model with the smallest  $AIC_C$  value was considered to be the “best”

288 approximating model describing the data. However, for drawing inferences and estimating  
 289 parameters we considered a broader set of models to account for model uncertainty. To  
 290 incorporate model selection uncertainty, we first selected a subset of models that had good  
 291 support in the data. The candidate models were chosen based on differences in  $AIC_C$  values  
 292 ( $\Delta AIC_C$ ), calculated by subtracting the  $AIC_C$  value of the best model from that of each of  
 293 the other models. All models with  $\Delta AIC_C < 4$  were considered to have good support  
 294 (Burnham and Anderson, 2002) and were included in further analyses.  
 295 To weight models based on their relative support, Akaike weights ( $w_i$ ) were calculated for  
 296 each model  $i$  using the following equation:

$$297 \quad w_i = \frac{\exp\left(-\frac{1}{2}\Delta_i\right)}{\sum_{i=1}^R \exp\left(-\frac{1}{2}\Delta_i\right)}, \quad (3)$$

298 where  $\Delta_i = AIC_{C,i} - AIC_{C,minimum}$ , and  
 299  $R =$  number of models compared.

300 The relative importance of each slope parameter (i.e., the importance of the temperature  
 301 effect on a given predator-prey interaction) was computed as the sum of the Akaike weights  
 302 over only those candidate models that included the respective slope parameter. To reduce  
 303 bias related to model selection uncertainty, parameter estimates were averaged over the  
 304 candidate models following Burnham and Anderson (2002):

$$305 \quad \hat{\theta}_j = \sum_{i=1}^R w_i \hat{\theta}_{j,i}, \quad (4)$$

306 where  $\hat{\theta}_j =$  model-averaged estimate of  $j^{th}$  parameter, and  
 307  $\hat{\theta}_{j,i} =$  estimator of the  $j^{th}$  parameter in model  $i$ .

308 Model-averaged predictions for biomass and biomass lost to predation were computed  
 309 similarly:

$$310 \quad \hat{B}_y = \sum_{i=1}^R w_i \hat{B}_{y,i}, \quad (5)$$

311 where  $\hat{B}_y$  = model-averaged prediction of biomass or biomass lost to predation in year  $y$ ,  
 312 and  
 313  $\hat{B}_{y,i}$  = the model-averaged estimated biomass or biomass lost to predation in year  $y$   
 314 for model  $i$ .

315 To illustrate the effects of bottom temperature on biomasses and predator-prey interactions  
 316 among the species studied, biomass estimates of all species were projected forward from  
 317 the predicted biomass in 2009 to the next year at various bottom temperatures between 1.1  
 318 and 3.8°C. The range of bottom temperatures for the projection encompasses the lowest and  
 319 the highest index of the GAM-estimated bottom temperatures used in model fitting (1.13  
 320 and 3.72 °C, respectively). Biomass lost to predation was predicted under different bottom  
 321 temperatures for comparison. To illustrate the effect of changing the amount of predation  
 322 on future biomass levels, we further projected biomasses of all species for three more years  
 323 to allow all juvenile pollock age classes to enter the adult population under a constant  
 324 bottom temperature of 2.24 °C, which is the average temperature between 1982 and 2009.  
 325 Projected biomass estimates were subjected to fishing mortality rates fixed at the average  
 326 value between 1982 and 2009 for each species. Projections were made with all candidate  
 327 models with their respective maximum likelihood parameters, and the results were  
 328 averaged according to eq. (5). For comparison, projections were also made with the model  
 329 that assumes no temperature effect on predation.

330

### 331 **Results**

332 We found strong support for the importance of temperature-dependent interactions between  
 333 several predator-prey pairs. A total of 17 models were retained for multi-model inference  
 334 based on Akaike weights. Variation in biomass predictions among the 17 models was small  
 335 (Figure 5). Among the 17 models retained, the best and second best models had nearly  
 336 identical AIC<sub>c</sub> values (5180.78 and 5180.92, respectively). The third and subsequent  
 337 models had much less support, as indicated by much lower Akaike weights (Table 1). The  
 338 best model included the slope parameters  $e_{PIP}$ ,  $e_{PIA}$ , and  $e_{P2A}$ , which represent the

339 temperature effects on the predation of age-1 pollock by adult pollock and by arrowtooth  
340 flounder, and of age-2 pollock by arrowtooth flounder. Two of the slope parameters,  $e_{PIP}$   
341 and  $e_{PIA}$  were also included in the second best model, while the third best model only  
342 included  $e_{PIA}$ . The parameter  $e_{PIA}$  was included in all of the 17 candidate models, and was  
343 the most important parameter based on the sum of the Akaike weights. Estimates of the  $e_{PIA}$   
344 parameter were consistently positive for all 17 models, but varied substantially in  
345 magnitude. The parameter  $e_{PIP}$  was the second most important parameter (relative  
346 importance = 0.69), was included in 9 of the 17 models, and was consistently estimated to  
347 be negative. The third most important parameter ( $e_{P2A}$ , relative importance = 0.35) was  
348 included in only 6 out of 17 models and was consistently positive. The model-averaged  
349 parameter estimates for  $e_{PIP}$ ,  $e_{PIA}$ , and  $e_{P2A}$  were -2.11, 26.62, and 0.33, respectively,  
350 indicating that predation on age-1 pollock by adult pollock decreases with increasing  
351 bottom temperature, while predation on age-1 and age-2 pollock by arrowtooth flounder  
352 increases with temperature. The model with a quadratic function on these three predation  
353 terms fitted the biomass data only slightly better than the model with linear predation terms,  
354 and the addition of extra parameters resulted in an increase in the  $AIC_C$  value by 5.59,  
355 which is greater than those of all 17 selected models.

356

357 Due to substantial model selection uncertainty, five other slope parameters ( $e_{P0P}$ ,  $e_{P0F}$ ,  $e_{PIC}$ ,  
358  $e_{PIF}$ ,  $e_{P2C}$ ) were also retained by some of the candidate models, but were of marginal  
359 importance in explaining the data. Two parameters, ( $e_{P0F}$ ,  $e_{PIF}$ ) were consistently estimated  
360 to be positive, and one parameter ( $e_{PIC}$ ) was consistently negative, but the importance of  
361 these parameters was relatively low (between 0.10 and 0.21). The two remaining  
362 parameters ( $e_{P0P}$ ,  $e_{P2C}$ ) had even lower importance (0.09 and 0.08, respectively), and their  
363 estimates were neither consistently positive nor negative. Four slope parameters ( $e_{P0A}$ ,  $e_{P0C}$ ,  
364  $e_{P2P}$ ,  $e_{P2F}$ ) did not occur in any of the 17 candidate models.

365

366 Model-averaged predictions suggest that large portions of the age-0 and age-1 pollock  
367 biomass were lost to predation between 1982 and 2009, but predation by any of the

368 predators in the model was relatively small for age-2 pollock, adult pollock, arrowtooth  
369 flounder, Pacific cod, and small-mouth flatfishes (Table 2). Adult pollock was the largest  
370 source of predation mortality for age-0 and age-1 pollock with 53.5% and 48.2%,  
371 respectively, of the estimated biomass lost to predation on average. Arrowtooth flounder  
372 was the largest source of predation mortality for age-2 pollock (1.94% on average), and  
373 also consumed a large portion (8.86%) of age-1 pollock biomass on average.

374

375 Model-averaged biomass projections simulated under a range of possible bottom  
376 temperatures showed little variation in the amount of predation on age-0 pollock (Figure  
377 6a). In contrast, bottom temperatures had much larger effects on age-1 pollock predation.  
378 The predicted proportion of age-1 pollock biomass consumed by all predators combined  
379 increased from 34.3% at 1.1 °C to 84.8% at 3.8 °C. This increase was due to a large  
380 increase in predation by arrowtooth flounder with increasing bottom temperatures, even  
381 though predation by adult pollock decreased slightly with temperature (Figure 6b).  
382 Predation on age-2 pollock was also predicted to increase with bottom temperature, from  
383 8.8% at 1.1 °C to 12.1% at 3.8 °C, and was similarly due to an increase in predation by  
384 arrowtooth flounder (Figure 6c).

385

386 The model without the effects of bottom temperature predicted higher predation on age-0  
387 pollock and lower predation on age-2 pollock at all temperatures compared to the model-  
388 averaged projections from the 17 best models (Figure 6a, 6c). The model-averaged  
389 prediction of total age-1 pollock predation was lower than the prediction from the model  
390 without temperature effects below 2.0 °C and was higher than predicted at higher  
391 temperatures (Figure 6b).

392

393 After a one-time temperature anomaly in predicting temperature-dependent predation,  
394 biomass estimates were projected for three more years at the average bottom temperature.  
395 As a result of increased predation on juvenile pollock with increasing temperature in the  
396 first year of the projection, the projected pollock biomass estimate (juvenile and adult

397 combined) after three years was 45.6% lower with a bottom temperature of 3.8 °C in the  
398 first year compared to that projected with a bottom temperature of 1.1 °C (Figure 7).  
399 Predicted biomass of all other species also decreased with bottom temperature, but not as  
400 much as pollock. In comparison to the biomass projection by the model without  
401 temperature effects (Figure 7), the model-averaged biomass projections were lower at all  
402 temperatures for all species. The difference between the model-averaged projections with  
403 temperature effects and the projection with no temperature effect was particularly large for  
404 pollock biomass. The model-averaged projected pollock biomass was largest at 1.1 °C at  
405 13.5 million tons, while the projection by the model without a temperature effect was 20.4  
406 million tons.

407

#### 408 **Discussion**

409 In this study, we quantified the magnitude of predation among six EBS groundfish species  
410 using a multispecies biomass dynamics model. We also quantified the effect of changing  
411 bottom temperatures on the predation rates on three juvenile pollock age classes by their  
412 major fish predators. We identified three predator-prey interactions involving juvenile  
413 pollock that are strongly affected by changes in bottom temperature. The model without an  
414 effect of bottom temperature on predation resulted in higher estimates of predation on age-0  
415 pollock, but tended to result in lower estimates of predation on age-1 and age-2 pollock  
416 compared to the model with temperature effects. The net result was that biomasses of all  
417 species were predicted to be higher in the model that lacks bottom-temperature effects on  
418 predation.

419

420 Our results suggest that changes in the extent of the cold pool on the EBS shelf affect  
421 predator-prey interactions among commercially important fishes. In particular, warmer  
422 temperatures are associated with enhanced predation by arrowtooth flounder on age-1  
423 pollock and, to a lesser extent, on age-2 pollock. These results are consistent with the  
424 hypothesis that an extensive cold pool provides a refuge for juvenile pollock from their  
425 predators (Figure 1b). Arrowtooth flounder have been shown to avoid the cold pool

426 (Mueter and Litzow, 2008; Spencer, 2008; Zador et al., 2011), while age-1 pollock can  
427 tolerate a wider range of water temperatures and are often found within the cold pool  
428 (Bailey, 1989; Duffy-Anderson et al., 2003; Hollowed et al., 2012). The overlap between  
429 the distribution of juvenile pollock and arrowtooth flounder increases in warm years, when  
430 arrowtooth flounder are more widely distributed on the shelf (Ciannelli et al., 2012;  
431 Spencer, 2008), and may explain the estimated increase in predation on age-1 pollock and,  
432 to some extent, age-2 pollock by arrowtooth flounder at higher bottom temperatures. This  
433 increase in predation, in turn, provides a mechanism explaining the negative correlation  
434 between pollock recruitment and the magnitude of the spatial overlap between arrowtooth  
435 flounder and juvenile pollock (Hunsicker et al., 2013).

436  
437 Our results also suggest that warmer temperatures are associated with reduced predation on  
438 age-1 pollock by adult pollock, consistent with the hypothesis that both predator (adult  
439 pollock) and prey (age-1 pollock) are excluded from the cold pool (Figure 1a). This result  
440 appears to contradict the finding above, which indicates that age-1 pollock are not excluded  
441 from the cold pool. The apparent negative effect of bottom temperature on age-1 predation  
442 by adult pollock may be explained by several factors: the response of adult pollock to  
443 temperature, competitive interactions between adult pollock and arrowtooth flounder, and  
444 differences in vertical distribution between cold and warm years. First, the different  
445 responses to water temperature by the two predators may be attributed to differences in  
446 their tolerance to cold temperature. While arrowtooth flounder generally avoid  
447 temperatures  $< 2$  °C and are excluded from much of the shelf when the cold pool is  
448 extensive, adult walleye pollock seem to have a higher tolerance for cold water and are  
449 often found in temperatures as low as 0 °C (Kotwicky et al., 2005; Swartzman et al., 1995).  
450 If this is the case, predation on juveniles by adult pollock may not be affected much by cold  
451 temperatures, as the distributions of both the prey and the predator are not strongly affected  
452 by the presence of the cold pool. Second, although changes in temperature alone may not  
453 have noticeable effects on age-1 predation by adult pollock, increasing arrowtooth flounder  
454 predation on juvenile pollock at higher temperatures may be associated with reduced



455 predation by adult pollock through competition with arrowtooth flounder for juvenile  
456 pollock prey. Finally, changes in vertical stratification with temperature may result in a  
457 reduced vertical overlap between juvenile and older pollock at warmer temperatures,  
458 potentially reducing cannibalism (e.g., Bailey, 1989).

459

460 Our results imply that increasing abundances of arrowtooth flounder, in combination with  
461 anticipated decreases in ice extent and duration, will reduce pollock recruitment in the  
462 future through both bottom-up and top-down processes. Decreases in ice extent and  
463 enhanced summer temperatures reduce the overwinter survival and subsequent recruitment  
464 of young-of-year pollock due to reduced prey availability (Heintz et al., 2013; Hunt et al.,  
465 2011). Yasumiishi et al. (2015) also found that ocean conditions associated with increased  
466 summer sea surface temperature negatively affect recruitment of age-0 pollock to age 1.  
467 This study suggests that recruitment may be further reduced in years following a warm year  
468 because of increased predation mortality on age-1 and age-2 pollock. Therefore, anticipated  
469 declines in the future recruitment and abundance of walleye pollock in a warming climate  
470 may be even more pronounced than previously predicted (Mueter et al., 2011). While  
471 Mueter et al. (2011) included scenarios with increasing arrowtooth flounder abundances in  
472 projections, the effect of increasing temperatures on predation was not considered. Spencer  
473 et al. (2016) extended the model used by Mueter et al. (2011) and Ianelli et al. (2011) to  
474 include both the effect of sea surface temperature (SST) on pollock recruitment and  
475 spatially-resolved predation mortality by arrowtooth flounder. They projected EBS pollock  
476 biomass through 2050 using SST and cold pool area projections from nine global climate  
477 models and predicted that pollock biomass decreases largely due to the effect of an  
478 increasing trend in SST on pollock recruitment. They predicted a further decrease in  
479 pollock biomass under a scenario in which the arrowtooth flounder distribution in the EBS  
480 shifts towards the northwest middle shelf, where high densities of juvenile pollock are  
481 found, by simulating the distribution of arrowtooth flounder under smaller cold pool sizes.  
482 Their findings offer a possible mechanism for the increased arrowtooth flounder predation  
483 on juvenile pollock with increasing bottom temperatures found in this study. By comparing

484 biomass projections with and without bottom temperature effects on predation, the current  
485 study shows that not taking into account the effect of temperature on predator-prey  
486 interactions may lead to underestimating predation mortality of young pollock in the EBS,  
487 which in turn leads to overestimation of future biomasses. This finding is in agreement with  
488 Spencer et al. (2016).

489

490 We identified some caveats in our approach. Although our results suggest that bottom  
491 temperature affects predator-prey interactions among the EBS groundfish species, many of  
492 the estimated effects were highly uncertain and weak, hence it is possible that these may  
493 not be ecologically important relationships. A large number (17) of models had some  
494 support based on Akaike weights, indicating substantial model selection uncertainty.

495 However, the three most important parameters  $e_{P1P}$ ,  $e_{P1A}$ , and  $e_{P2A}$ , appeared in many of the  
496 candidate models, and were consistently estimated to be negative, positive, and positive,  
497 respectively. The models ranked first and second had Akaike weights nearly twice as large  
498 as that of the third model, indicating that these models are almost twice as likely to be the  
499 best approximating model describing the available biomass data compared to the third  
500 model. Both the first and second models contained the parameters  $e_{P1P}$  and  $e_{P1A}$ , while the  
501 third model only contained  $e_{P1A}$ . A simplification in our approach was that estimated  
502 temperature effects on predation rates were assumed to be linear. We hypothesized that the  
503 cold pool size affects the size of the available habitat on the EBS shelf for both predators  
504 and prey, but the effects differ among species because of different thermal preferences.  
505 Therefore, changes in the cold pool modify the spatial overlap and the encounter rates  
506 between predators and their prey. However, temperature may also affect predation rates  
507 through fishes' physiological responses. In the laboratory, food consumption by juvenile  
508 pollock increases with temperature from 2 to 12°C, but decreases at 16°C (Kooka et al.,  
509 2007). If prey availability is not limiting and temperature has a similar effect on older  
510 pollock, predation rates by pollock are expected to increase to some optimal temperature  
511 and then decrease. Quadratic relationships were also found between feed conversion ratio  
512 (feed intake divided by weight gain) and temperature in immature Atlantic cod (*Gadus*

513 *morhua*; Björnsson et al., 2001), which decreased with temperature up to 12°C and 8°C for  
514 smaller and larger cod, respectively, indicating that less feed is required to attain the same  
515 amount of growth at higher temperatures. Although temperature may induce non-linear  
516 physiological responses that affect predation rates, in this study we used bottom  
517 temperature as a proxy for the cold pool size, i.e., as an indicator of habitat size, rather than  
518 an indicator of the fishes' thermal environment. We assumed that fish can move relatively  
519 freely to avoid or minimize adverse physiological effects of unfavorable thermal  
520 conditions, based on the observations that many of the EBS groundfish species change their  
521 distributions with changing water temperature (e.g., Mueter and Litzow, 2008). The overall  
522 effect of water temperature on predation rates is likely a combination of both physiological  
523 and distributional changes, hence the actual forms of the functional responses of predation  
524 rates to temperature are unknown and may vary among predator-prey combinations. In this  
525 study, inclusion of quadratic functions in predation terms resulted in an AIC<sub>C</sub> value greater  
526 than all of the 17 selected models with linear functions in predation terms, indicating that  
527 the available data do not support a more complex functional form than a linear relationship  
528 between predation rates and temperature. It is also worth noting that, in the aforementioned  
529 feeding studies, the observed inflection points for physiological responses occurred at much  
530 higher temperatures (8°C - 12°C) than the range of bottom temperature used for biomass  
531 projections in this study (1.1°C – 3.8°C). This suggests that the use of a linear relationship  
532 was reasonable over the observed range of temperatures in the EBS during the study period  
533 (1.13 °C – 3.72 °C). Nonetheless, the linear relationships estimated in this study may not  
534 hold outside the observed range of bottom temperature, and our simulation results at the  
535 extreme ends of the temperature range should be interpreted with caution. Regardless of the  
536 exact functional form of predator response to temperature, the direction of the effect of  
537 bottom temperature on pollock cannibalism found in this study was the opposite of the  
538 physiological effect of temperature on predation rate; i.e., the rate of cannibalism decreased  
539 with increasing bottom temperature. The positive effect of warmer temperature on  
540 predation rate expected by the positive relationship below 12 °C would have been offset by  
541 the negative effect of the cold pool.

542

543 Increasing awareness of long-term cumulative impacts of fishing and climate-driven  
544 changes on marine ecosystems have led to calls for more holistic approaches to fishery  
545 management (Link, 2002; Marasco et al., 2007; Myers and Worm, 2003; Pauly et al., 2002;  
546 Pikitch et al., 2004). Fisheries in the EBS within the U.S. Exclusive Economic Zone are  
547 managed under the auspices of the North Pacific Fishery Management Council, whose  
548 policy for groundfish fisheries calls for the adoption of ecosystem-based fishery  
549 management principles. Accordingly, a number of multispecies models have been  
550 developed for this region to work towards incorporating trophic interactions into  
551 management decisions (e.g., Livingston and Jurado-Molina, 2000; Jurado-Molina and  
552 Livingston, 2002b; Jurado-Molina et al., 2005; Holsman et al., 2016). The model in this  
553 study was developed as a simpler alternative to a fully age-structured, multispecies model,  
554 such as the CEATTLE model (Holsman et al., 2016).

555

556 Results from the current study are complementary to, and broadly agree with, those from  
557 the CEATTLE model. Holsman et al. (2016) incorporated temperature-dependent von  
558 Bertalanffy (VB) weight-at-age functions and temperature-specific bioenergetics-based  
559 predation interactions in a multispecies statistical catch-at-age model of walleye pollock,  
560 Pacific cod, and arrowtooth flounder. They observed that the temperature-dependent VB  
561 growth function causes moderate changes (5 – 15%) in predicted spawning, survey, and  
562 total biomass of the three species, while variations in predation mortality from temperature-  
563 dependent changes in predator rations were relatively small (1 – 7%). This is in contrast to  
564 our finding that water temperature has strong effects on juvenile pollock predation,  
565 particularly by arrowtooth flounder. While the statistical catch-at-age model of Holsman et  
566 al. (2016) is in many respects more realistic compared to our biomass dynamics model  
567 (e.g., age structure, VB growth function, physiology-based predator rations, etc.), predator  
568 rations were predicted deterministically and not calibrated with observed diet data.  
569 Although predator rations are temperature-dependent in their model, these rations are  
570 determined by the energetic requirement of the predators and not by the availability of the

571 prey to the predators, which may also be influenced by variability in the environment as  
572 suggested by our findings. By fitting our models to observed diet data, we were able to test  
573 hypotheses about factors affecting predation on juvenile pollock. The CEATTLE model is  
574 currently being extended to include possible bottom-up effects on age-0 mortality,  
575 presumably linked to availability of suitable zooplankton prey (K. Holsman, NOAA,  
576 Seattle, pers. comm.). However, a multispecies model that includes effects of temperature  
577 on zooplankton prey, growth, predator ration, and predator-prey overlap for multiple life  
578 stages has yet to be developed and the combined effects of these processes remain  
579 uncertain. Continuing efforts on integrating temperature, and possibly other environmental  
580 variables, in multispecies models and collecting diet data to test the modeled predator-prey  
581 relationships are necessary in reducing the uncertainty in predictions.

582

583 The model developed in this study expands the current portfolio of multispecies modeling  
584 options and specifically can be used to examine the effects of environmental or other  
585 covariates on predator-prey interactions. The model helps explain observed changes in the  
586 EBS fish community and broadly agrees with other studies suggesting that warmer  
587 temperatures on the EBS shelf are associated with increased predation by arrowtooth  
588 flounder on juvenile walleye pollock, although the effects on cannibalism were minimal.  
589 The model can be used to improve our understanding of the implications of climate change  
590 on the EBS ecosystem and its productivity and we are currently extending the model to  
591 project future changes in the biomass of these groundfish species under different future  
592 climate change scenarios.

593

#### 594 **Data Availability Statement**

595 The data that support the findings of this study are available from the corresponding author  
596 upon reasonable request.

597

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791 **Tables**

792 Table 1. Estimated model parameters, differences in the Akaike Information Criterion from  
 793 the best model ( $\Delta AIC_C$ ), and Akaike weights ( $w_i$ ) of 17 candidate models with good support  
 794 ( $\Delta AIC_C < 4$ ). The parameter  $e_{mz}$  represents the effect of bottom temperature on the  
 795 predation of prey juvenile age class  $m = \{P0, P1, P2\}$  by predator  $z$ .

Rank	$e_{P0P}$	$e_{P0F}$	$e_{PIP}$	$e_{PIA}$	$e_{PIC}$	$e_{PIF}$	$e_{P2A}$	$e_{P2C}$	$\Delta AIC_c$	$w_i$
1	0	0	-5.48	57.44	0	0	1.29	0	0.00	0.1661
2	0	0	-1.09	25.98	0	0	0	0	0.14	0.1552
3	0	0	0	6.06	0	0	0	0	1.24	0.0893
4	0	289.01	-3.96	32.55	0	0	0	0	1.76	0.0690
5	0	0	-2.87	8.59	0	179.63	0	0	1.76	0.0690
6	0	0	-1.31	23.06	0	159.41	0.51	0	2.18	0.0559
7	0	0	-4.45	19.12	-2.48	0	0	0	2.30	0.0526
8	-0.35	0	-0.79	50.69	0	0	0	0	2.40	0.0500
9	0	0	-1.32	62.95	0	0	1.42	0.02	2.43	0.0492
10	4.94	0	0	4.12	0	0	0	0	2.68	0.0436
11	0	0	0	2.65	0	119.72	0.12	0	3.26	0.0326
12	0	135.46	0	5.14	0	0	0	0	3.30	0.0320
13	0	0	0	6.86	0	79.34	0	0	3.30	0.0320
14	0	0	0	1.70	-25.51	0	0	0	3.46	0.0295
15	0	0	0	17.17	0	0	0	-3.05	3.68	0.0264
16	0	0	0	2.52	-82.80	0	0.11	0	3.88	0.0239
17	0	0	-6.19	22.12	-20.48	179.16	0.49	0	3.90	0.0237
Model-averaged	0.20	24.28	-2.11	26.62	-3.34	32.00	0.33	-0.079		
Relative importance	0.09	0.10	0.69	1	0.13	0.21	0.35	0.08		

796

797 Table 2. Model-averaged percentage of prey biomass consumed by each predator averaged  
 798 over 1982 – 2009.

	Predator				Total
	Pollock	Arrowtooth	Cod	Flatfish	
Age-0 pollock	53.52%	0.04%	0.01%	0.07%	53.64%
Age-1 pollock	48.21%	8.86%	0.74%	5.77%	63.69%
Age-2 pollock	0.76%	1.94%	0.34%	0.00%	3.04%
Prey Adult pollock		0.14%	1.08%		1.22%
Arrowtooth	0.00%		0.08%		0.08%
Cod	0.02%				0.02%
Flatfish	0.01%	0.21%	0.32%		0.54%

799

800

801 **Figure legends**

802 Figure 1. Schematic diagrams showing alternative hypotheses on how the cold pool may  
 803 affect predation on juvenile pollock. The cold pool (a) excludes young pollock from the  
 804 shelf, exposing them to predators on the slope; or (b) protects young pollock from predators  
 805 if they can tolerate the cold temperature.

806

807 Figure 2. Predator-prey relationships among EBS fish species modeled in this study.

808 Arrows represent the directions of predator  $\longrightarrow$  prey.

809

810 Figure 3. Composition of small-mouth flatfish species as absolute biomass (1000 tons) and  
 811 as proportion of total biomass.

812

813 Figure 4. Body length distributions of walleye pollock prey from the stomachs of eastern  
 814 Bering Sea walleye pollock, Pacific cod, arrowtooth flounder, and yellowfin sole (1981 –

815 2012). The superimposed lines show the Gaussian probability density functions estimated  
816 from the data.

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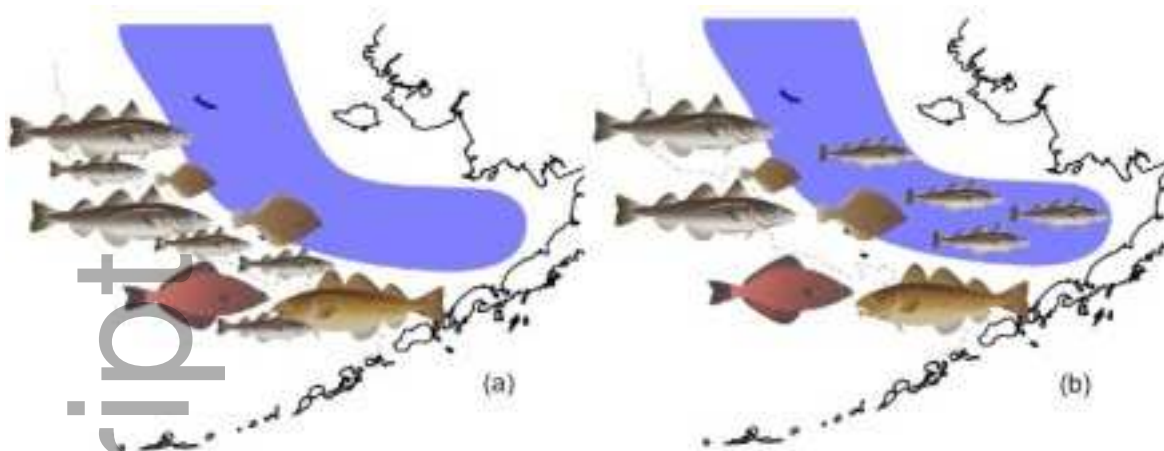
818 Figure 5. Predicted biomass from 17 candidate models (dotted lines) and model-averaged  
819 predictions (solid lines) for (a) age-1 pollock, (b) age-2 pollock, (c) age 3+ pollock, (d)  
820 arrowtooth flounder, (e) Pacific cod, and (f) small-mouth flatfish. Open circles and asterisk  
821 (only for pollock) are biomass estimates from bottom trawl and EIT surveys, respectively,  
822 to which models were fitted. For pollock, the survey estimates were divided by the  
823 catchability estimates of each respective survey for presentation. For other species,  
824 catchability was assumed to be 1.

825

826 Figure 6. Predicted proportion of prey biomass consumed by a given predator for (a) age-0,  
827 (b) age-1, and (c) age-2 pollock at different bottom temperatures. The predictions of  
828 predation were calculated from the biomass estimates of prey and predators in 2009 for  
829 each of the 17 candidate models, then averaged over the models. The vertical bar on the  
830 right side of each panel shows the prediction from the model which includes no temperature  
831 effect on predation. Panel (d) shows the 95% prediction interval for the predicted  
832 proportion of age-1 pollock biomass consumed by arrowtooth flounder, based on  
833 unconditional (model-averaged) standard errors of the predicted values.

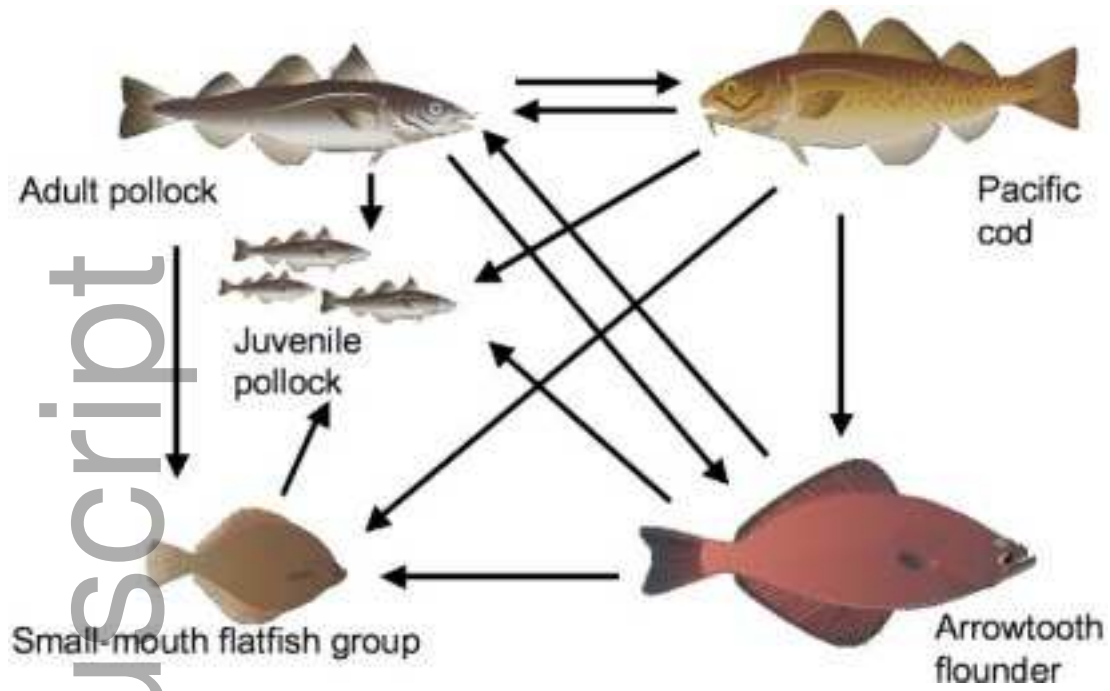
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835 Figure 7. The 4<sup>th</sup> year biomass projections vs. bottom temperature in the first year, showing  
836 the effects of a one-time bottom temperature anomaly on biomass levels. Biomasses were  
837 projected from the 2009 estimates by varying bottom temperature in year 1 of the  
838 projection (2010) and keeping the bottom temperature constant at the average ( $= 2.24$  °C) in  
839 three subsequent years (year 2 to 4). Biomasses were projected to the 4<sup>th</sup> year, in which the  
840 year 1 cohort becomes part of the adult pollock biomass to predict an effect of temperature  
841 on future biomass. The vertical bar on the right side shows the prediction from the model  
842 that includes no temperature effect on predation.



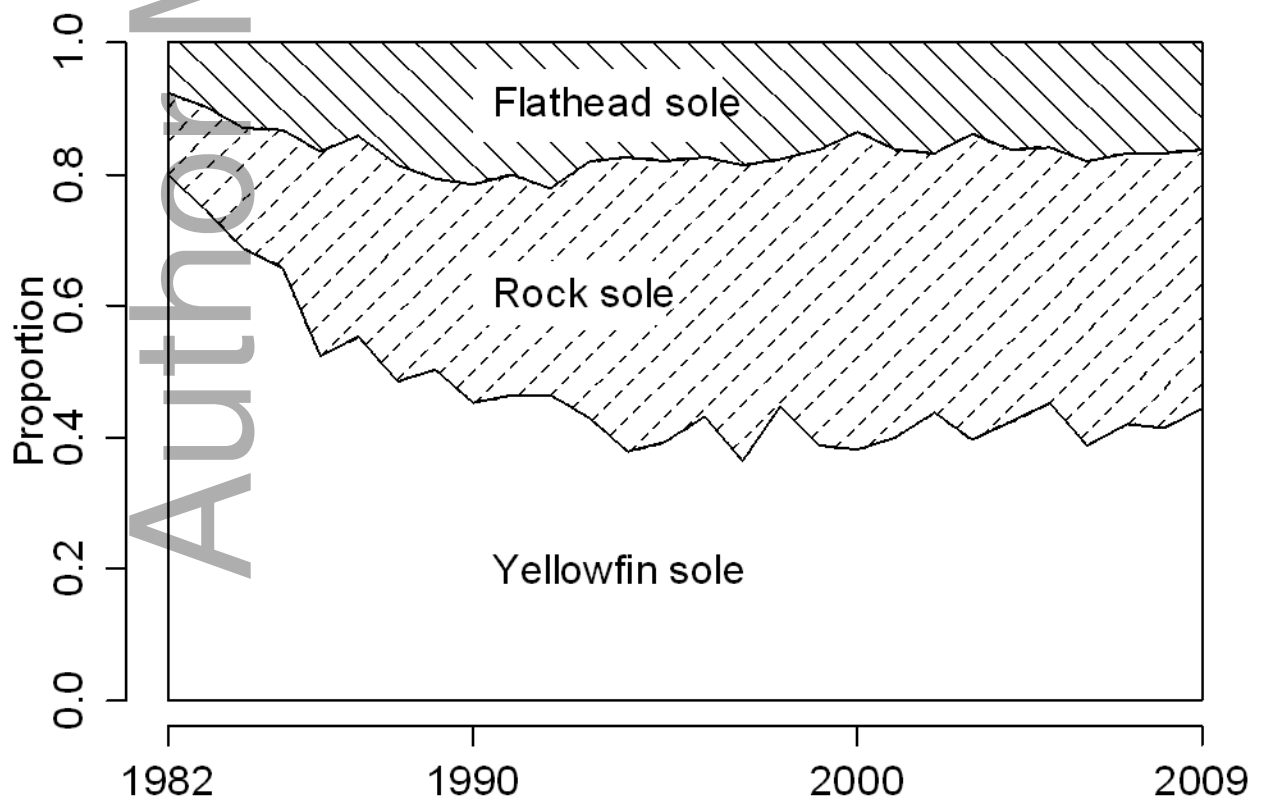
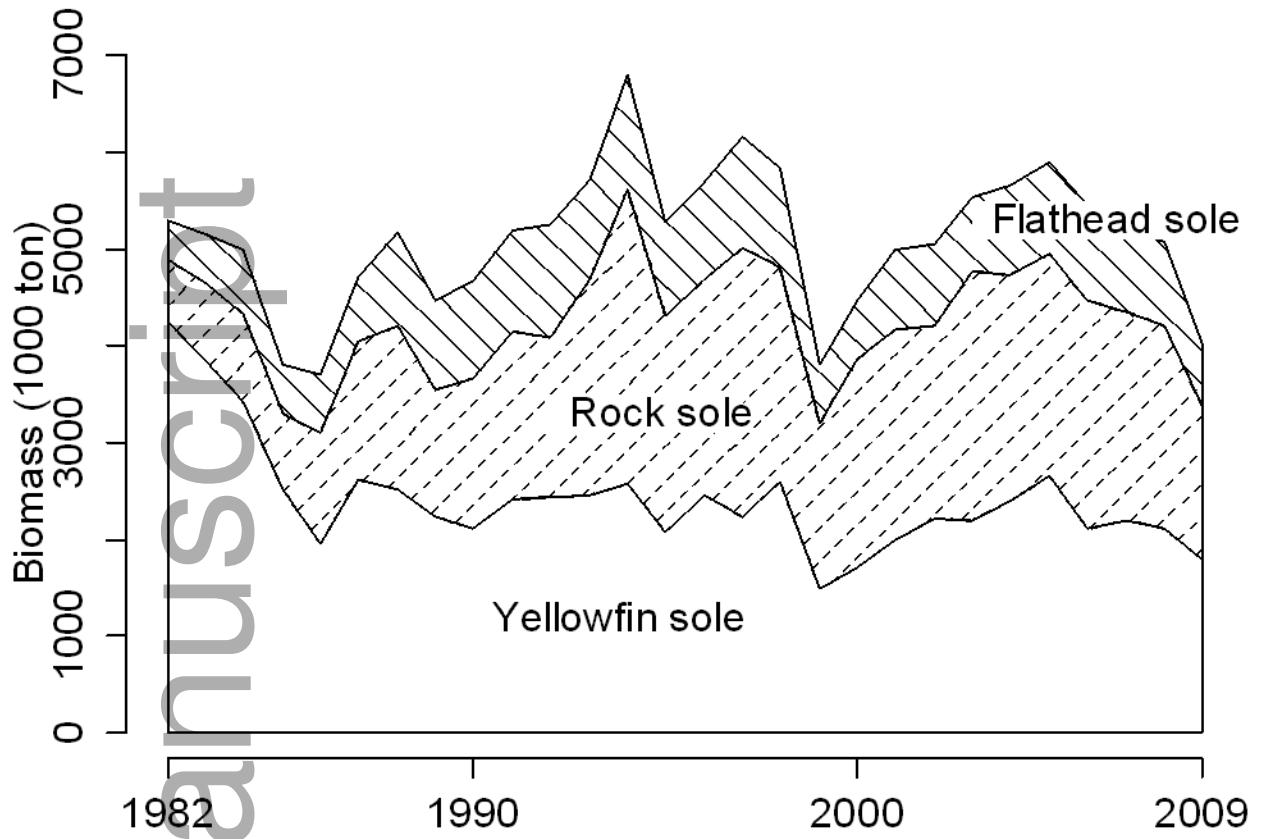
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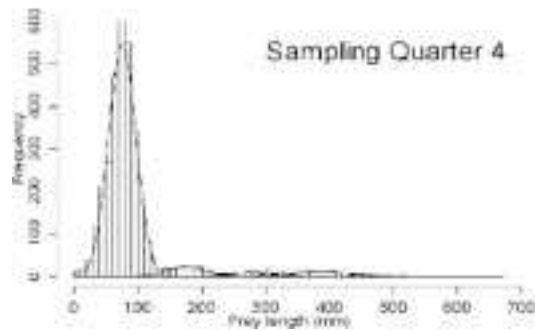
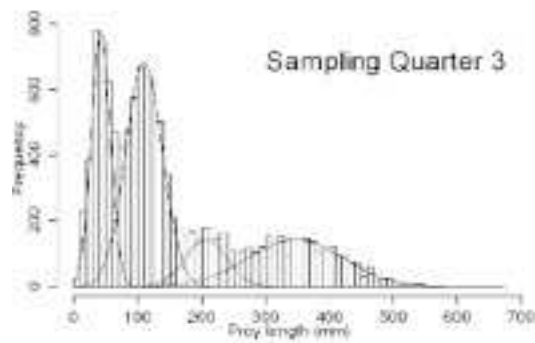
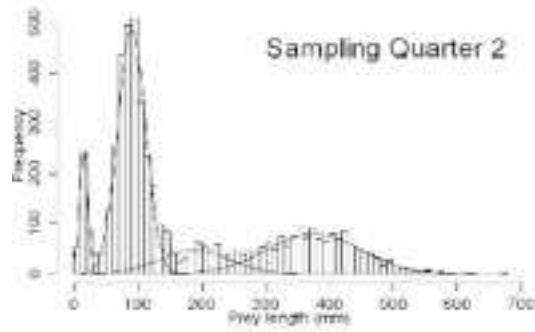
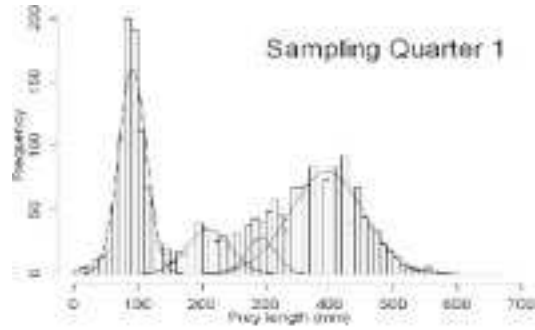


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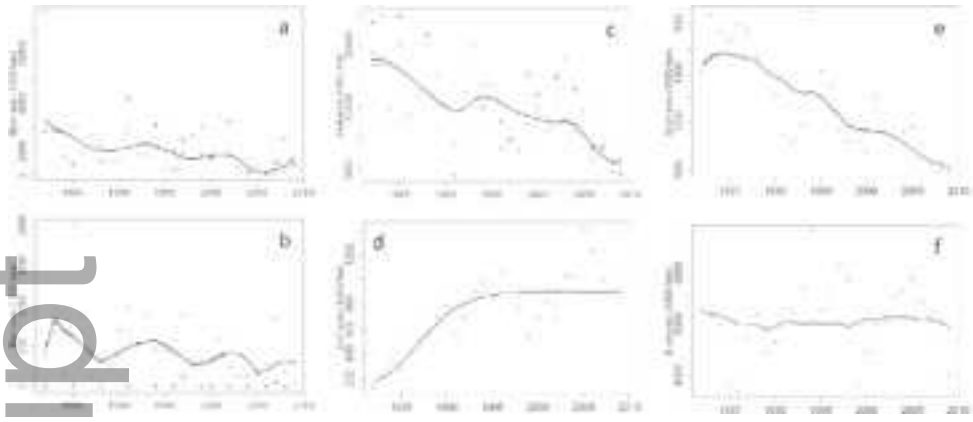
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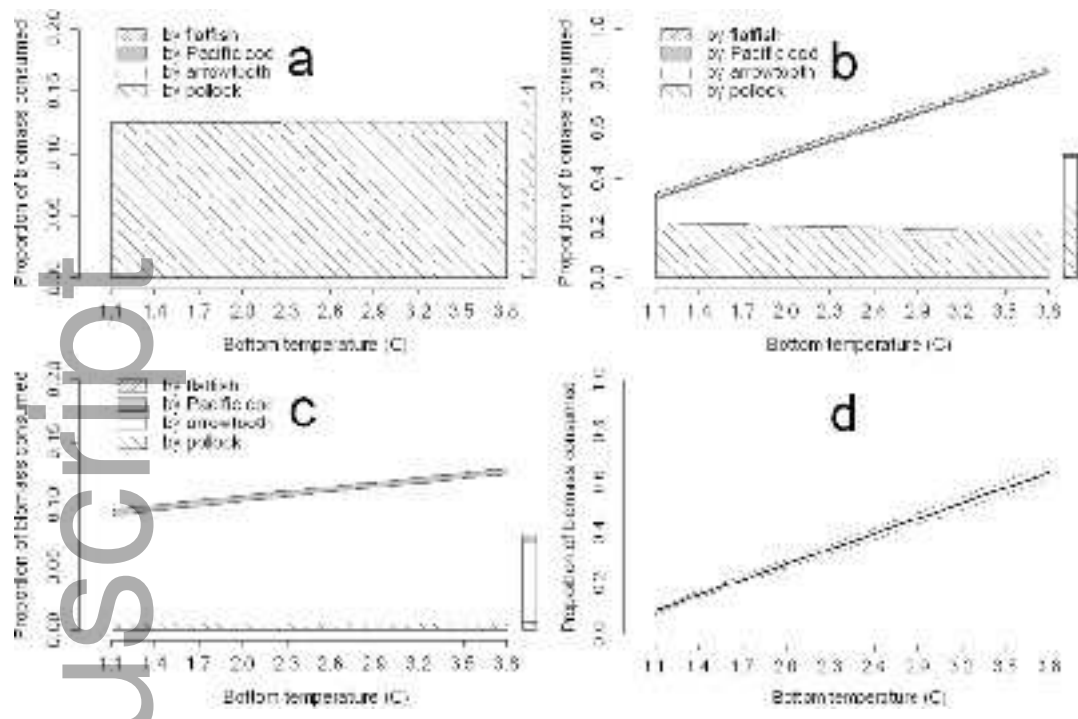
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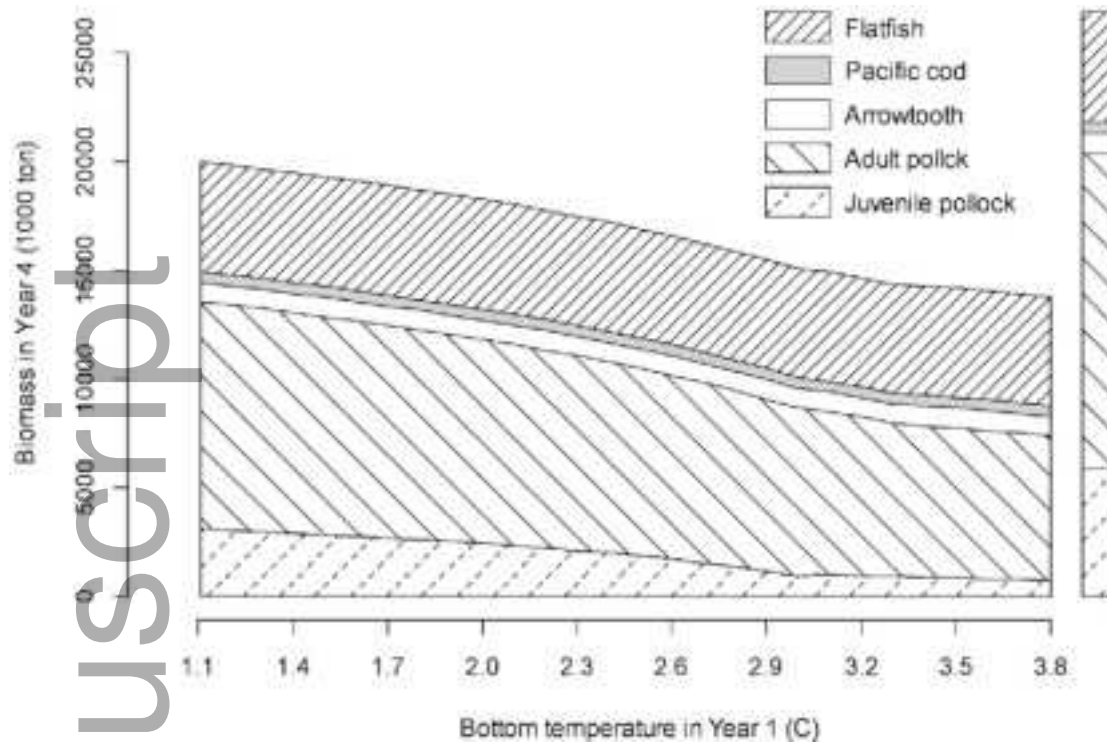
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