1 The influence of age and cohort on the distribution of walleye pollock

2 (*Gadus chalcogrammus*) in the eastern Bering Sea

3

4 Duane E. Stevenson[1], Stan Kotwicki[1], James T. Thorson[1], Giancarlo M. Correa[2], and Troy

5 Buckley[1]

6

7 [1]National Marine Fisheries Service, Alaska Fisheries Science Center, 7600 Sand Point Way NE,

8 Seattle, Washington 98115; E-mail: duane.stevenson@noaa.gov.

9 [2]Oregon State University, College of Earth, Ocean, and Atmospheric Sciences, Corvallis, Oregon

10 97330.

11 Corresponding author: Duane Stevenson (duane.stevenson@noaa.gov)

12

Abstract:

The spatial distributions of marine fish populations are influenced by environmental conditions, intrinsic properties of the populations, and prior distribution. The influence of these factors may not be consistent across age classes. For this study, age composition estimates for walleye pollock collected on bottom-trawl surveys in the Bering Sea were used to estimate range correlation indices, population centers of gravity, and effective area occupied. Age-specific density maps suggest a circular ontogenic migration during the summer feeding season, with the youngest and oldest groups most broadly distributed. Range correlation analysis among age groups and year classes provide clear evidence of a population cohort effect in the spatial distribution of the population. Variance decomposition analysis indicates that the in the spatial distribution of age groups during summer is influenced by the initial distribution of that cohort as recruits. Model-based analyses show that extrinsic temperature variables affect the youngest and oldest age classes the most, but provide no indication of age-related effects for intrinsic population factors. This study shows that both cohort and age-specific factors are important drivers of spatial distribution.

Keywords: demographics, age composition, distribution, walleye pollock, modeling, VAST

Introduction

The spatial distributions of fish populations are influenced by many factors. Environmental variables that define habitat suitability are clearly important. For example, physiological tolerances and resource availability directly affect the ability of a species to survive in a particular habitat. These factors have historically been used to define the fundamental and realized niche of a species, in the sense originally defined by Hutchinson (1957). However, other factors intrinsic to the population profoundly affect how a species occupies its realized niche. Recruitment dynamics, age structure, site fidelity, and behavioral preferences are some of the many intrinsic factors that may affect the spatial distribution of a population. Planque et al. (2011) list two categories of extrinsic drivers of spatial distribution (geographic attachment and environmental conditions), and four categories of intrinsic drivers (density-dependent habitat selection, spatial dependency, demographic structure, and species interactions). They also list a third type of driver (spatial memory), which is a product of the current and past distribution of the population and represents an extension of the entrainment hypothesis developed by Petitgas et al. (2006) and MacCall et al. (2019).

Because the distribution of a population can be influenced by both extrinsic environmental and intrinsic population factors, and is also dependent on past distribution, modeling efforts seeking to describe and predict the spatial distribution of a population may be improved by including both types of factors as well as a "memory" component. Models incorporating a combination of extrinsic and intrinsic factors can be used to assess the relative impacts of these factors using a variance decomposition process, in which variance in the spatial distribution of the population is decomposed into extrinsic and intrinsic effects to assess which effects are dominant. This "variance decomposition" approach avoids an artificial accept-reject

3

53   outcome that results from hypothesis testing (Thorson and Minto 2015) and is appropriate in a

54   world of multi-causality and tapering effects (Burnham and Anderson 2002). The relative effects

55   of spatial memory on the distribution of a population can also be assessed through spatial

56   comparisons of temporally distinct components of the population, such as recruitment classes

57   (cohorts).

58   In addition to assessing the relative importance of intrinsic and extrinsic factors on the

59   spatial distribution of a population, it may be desirable to know how these factors affect different

60   segments of that population. While the bulk of studies in spatial ecology have been focused on

61   population centroids (Pinsky et al. 2013) or range edges (Fredston-Hermann et al. 2020), there

62   has been comparatively little investigation of mechanisms defining shifts in the spatial

63   distribution in age-specific (or size-specific) segments of fish populations (but see Marquez et al.

64   2021). For species targeted by commercial fisheries, the distribution of desirable age (or size)

65   classes, and the factors that drive the spatial distributions of those population segments, are of

66   particular interest.

67   The walleye pollock (*Gadus chalcogrammus*) population of the eastern Bering Sea

68   supports one of the most valuable fisheries in the world, with approximately 1 million metric

69   tons harvested commercially each year for the past 50 years (Ianelli et al. 2019). Although

70   pollock biomass estimates have remained relatively stable in recent years, there is a growing

71   body of evidence that the Bering Sea ecosystem is changing. The formation of seasonal sea ice

72   that once acted as the prime driver of ecosystem functions in the Bering Sea has been declining

73   as the water temperatures in the region have warmed (Stabeno et al. 2017). As the water warms,

74   there is evidence that the pollock population of the eastern Bering Sea is moving north into the

4

75　Arctic (Stevenson and Lauth 2019) and west past the US-Russia convention line (O'Leary et al.

76　2021).

77　　　　The distribution and movements of pollock in the eastern Bering Sea have been studied in

78　a number of contexts. Spawning occurs in two major pulses, with the first in February-March

79　largely centering in the southeastern Bering Sea near Bogoslof and Unimak Islands, and the

80　second in April-May farther north, near the Pribilof Islands (Hinckley 1987; Kim et al. 1996;

81　Bacheler et al. 2010). The distribution of juvenile pollock has been studied in relation to many

82　factors, including the warm and cold stanzas that have dominated the eastern Bering Sea over the

83　past 20 years (Duffy-Anderson et al. 2017), resulting overlap between juvenile pollock and

84　predators/competitors (Thorson et al. 2021) and small-scale habitat heterogeneity (Benoit-Bird et

85　al. 2013). Kotwicki et al. (2005) described seasonal feeding migrations in pollock, noting that as

86　the water warms in the spring and summer, adult pollock migrate northwestward and onshore

87　from their spawning grounds in the eastern Bering Sea. Their results also suggested that juvenile

88　pollock complete similar annual migrations, but cover shorter distances. Ianelli (2005) briefly

89　described ontogenic migration, with younger fish more common on the northwestern part of the

90　EBS shelf and older fish moving progressively to the south and east of the EBS shelf.

91　　　　The walleye pollock is considered a semi-pelagic species, and the vertical distribution of

92　pollock in the water column is complex. Early life stages are generally found near the surface

93　(Smart et al. 2013, Parker-Stetter et al. 2015), but after the first year, they transition to midwater

94　and demersal habitats. Mid-water acoustic surveys and bottom-trawl surveys in Alaska suggest

95　that age-1 pollock tend to school close to the bottom, while age-2 and other juvenile pollock stay

96　higher in the water column, and adults are primarily demersal (Duffy-Anderson, 2003,

97　Honkalehto et al. 2010, Kotwicki et al. 2015, Lauth et al. 2019). The proportion of the population

98 available to the bottom trawl varies spatially, over time, and by age, although over 50% is

99 available to the bottom trawl in any year previously documented (Monnahan et al. 2021).

100   In this study, we seek to test three main questions about the distribution of walleye

101 pollock in the eastern Bering Sea:

102   1. Is there evidence of a memory/entrainment effect in the relative distributions of

103   cohorts (recruitment classes) in the population?

104   2. What are the relative influences of environmental conditions (year effects) and

105   memory/entrainment (cohort effects) on the population center of distribution?

106   3. Do intrinsic and extrinsic factors affecting the EAO by the population differ among

107   age classes?

108 We explore these questions using a combination of analyses that include model-based

109 predictions of density for age-specific segments of the walleye pollock population of the eastern

110 Bering Sea from 1982 through 2019. In addition, a variance decomposition procedure was used

111 to assess the relative importance of survey year and cohort to the variance in spatial distribution

112 among age-cohort combinations. The primary goal of these investigations was to evaluate the

113 relative contributions of survey year (year of collection) and cohort (year of birth) to the spatial

114 distributions of age-specific segments of the pollock population. The primary importance of this

115 study is that it assesses the relative magnitude of intrinsic, extrinsic, and cohort effects

116 influencing the spatial distribution of different age segments of a marine fish population.

117

118 **Materials and Methods**

119 **Data collection and age composition estimates**

120   Data used in this study were collected during bottom trawl surveys of the eastern Bering Sea

121   shelf, conducted annually by the Alaska Fisheries Science Center (AFSC) of the U.S. National

122   Marine Fisheries Service from 1982 through 2019 (e.g., Lauth et al. 2019). These fixed-station

123   surveys used an otter trawl with an effective fishing height of approximately 16 m for pollock

124   (Kotwicki et al. 2015). Thus, the spatial trends analyzed here apply only to the demersal portion

125   of the population available to the trawl. The survey grid consists of 376 stations, each of which is

126   sampled annually. At each station, random subsamples of length-frequency data were collected

127   (totaling roughly 20,000–50,000 lengths per year), as well as otoliths (totaling roughly 1000–

128   2000 otoliths per year) from either length-stratified (2006 and prior) or random (2007–2019)

129   subsamples of the total catch. Age data were then combined with length abundance information

130   to obtain age-specific abundances at each station using a model-based approach. This approach

131   consisted of using continuation ratio logits (CRL) to model the probability of being a specific

132   age at a given length, taking into account the spatial variability in size-at-age (Berg and

133   Kristensen 2012; Correa et al. 2020). Techniques used at the AFSC to age pollock have been

134   radiometrically validated up to age-8 (Kastelle and Kimura 2006), therefore all specimens with

135   estimated ages higher than 8 (approximately 25% of all aged specimens) were combined into the

136   "age-9+" class.

137   A data set including density-at-age estimates for each age class, for each survey station,

138   for each survey year was used to create a multispecies spatiotemporal model in VAST (Vector-

139   Autoregressive Spatio-temporal modeling package: Thorson and Barnett 2017), version 3.4.0, in

140   which age classes were treated as separate species in a multivariate model. VAST uses Template

141   Model Builder to identify maximum likelihood estimates (Kristensen et al. 2016), the stochastic

142   partial differential equation (SPDE) method to rapidly approximate spatial correlations (Lindgren

7

143 et al. 2011), and a generalization of the delta-method to calculate standard errors for parameters

144 and derived quantities (Tierney et al. 1989). We specify gamma-distributed positive catch rates

145 and the alternative "Poisson-linked" delta model using a log-link function for encounter

146 probabilities. The region specified was "eastern_bering_sea", corresponding to the spatial

147 footprint of the annual bottom trawl survey operated by AFSC in the eastern Bering Sea. The

148 spatial resolution was set at 500 knots, representing a relatively fine-scale mesh for density

149 predictions that is still computationally feasible, and corresponds roughly with the spatial

150 resolution of the samples (376 stations). We include both spatial and spatio-temporal

151 components as well as an annual intercept for each of two linear predictors, and do not estimate

152 any temporal autocorrelation in either intercepts or spatio-temporal components. By avoiding

153 any temporal autocorrelation, we ensure that resulting density predictions are "exchangeable" for

154 each of the ages and year-within-age. This, in turn, justifies our statistical analysis of density

155 patterns for each age and year, which we treat as independent for each age-year combination in

156 the analyses.

157   Outputs used from the VAST model included rasters (with the grid cell size of

158 approximately 100 km^2) of pollock density estimates by age (Supplementary File A), center of

159 gravity location, and estimates of EAO by age (Thorson et al. 2016). Cumulative density plots

160 for each age class were created by calculating the average estimated density across all years for

161 each of the 5000 grid cells from the VAST output raster, then sorting grid cells in order of

162 descending density and plotting the cells required to reach 75% of the cumulative average

163 density. The 75% threshold for cumulative density was chosen to visualize contrasts between

164 spatial distributions of age classes, and to align with the regional definition of "principal

165 Essential Fish Habitat area" (see Laman et al. 2018, Fig. 8). Centers of gravity were obtained for

166   each age class for each year using biomass-weighted eastings and northings in Universal

167   Transverse Mercator coordinates (see Thorson 2019: Table 2). Mean centers of gravity for each

168   age class were calculated as the simple average of the latitude and longitude of the centers of

169   gravity for each survey year. Longitude and latitude anomalies for each age-year combination

170   were obtained by subtracting the mean longitude/latitude (in UTM coordinates) from the mean of

171   the 38 longitude/latitude estimates for that age class. Temporal trends in COG (center of gravity)

172   were depicted by plotting these anomalies for all age classes over the study period (1982–2019).

173   VAST generates estimates of EAO for each age-year combination (see Thorson 2019: Table 2),

174   which are calculated as the area required to contain the population at its biomass-weighted

175   average density (Thorson et al. 2016).

176

177   **Question #1: Evidence of a cohort effect**

178   If the spatial distribution of pollock is being driven by contemporary factors, either intrinsic or

179   extrinsic, operating simultaneously on the entire population, then we expect correlations among

180   the distributions of all age classes within each year to be greater than correlations among

181   different survey years. However, if there is a memory effect operating on different cohorts to

182   influence the spatial distribution of pollock, then we expect correlations within cohorts (as they

183   are repeatedly sampled in successive survey years) to be greater than those among different

184   cohorts. We therefore used two metrics of range correlation, the global index of collocation

185   (GIC) and Schoener's D, to investigate spatial correlations among the distributions of pollock

186   age groups. GIC uses pairwise comparisons of population centers of gravity as an indicator of

187   large-scale similarity among distributions (Bez and Rivoirard 2000; Woillez et al. 2009;

188   Kotwicki and Lauth 2013), while Schoener's D (Schoener 1968) uses station-by-station pairwise

9

189 comparisons to assess fine-scale spatial similarity among distributions. We use both metrics,

190 given that fine-scale overlap (measured by Schoener's D) will capture high-resolution processes

191 while regional overlap (measured by GIC) will capture low-resolution processes.

192   Metrics of range correlation were calculated from the grid cell density predictions of the

193 VAST model (5,000 grid cells). GIC values were calculated in R using the method of Kotwicki

194 and Lauth (2013):

195 (1) $GIC_{1,2} = 1 - \frac{\Delta COG_{1,2}{}^2}{\Delta COG_{1,2}{}^2 + I_1 + I_2}$,

196 where ΔCOG is the distance between COGs for a given pair of age-year groups, I_1 is the

197 dispersion for group 1 and I_2 is the dispersion for group 2. The dispersion for each group is

198 calculated as:

199 (2) $I_1 = \frac{\sum_{i=1}^{n}(\Delta COG_{1,2})^2 z_{1i}}{\sum_{i=1}^{n} z_{1i}}$

200 Schoener's D values were calculated in R using the Species Association Analysis (spaa)

201 package, version 0.2.1 (Zhang 2016):

202 (3) $D = 1 - 0.5 * \sum_{i=1}^{n} |p_{x,i} - p_{y,i}|$

203 where $p_{x,i}$ and $p_{y,i}$ are the proportions of age-year x and y, respectively, at station i.

204   For each range correlation metric, GIC and Schoener's D, a matrix of pairwise

205 correlation statistics was generated for each age-year combination (9 ages * 38 data years = 342

206 x 342 matrix). A one-tailed t-test was then performed to determine whether the mean of within-

207 year correlations for each age pairing (e.g., age-1 vs. age-2 from 1982, $n = 38$) was significantly

208 higher than the mean of all possible age class correlations (e.g., age-1 from 1982 vs. age-2 from

209 1985, $n = 741$). Significant results for these t-tests were interpreted to indicate significant spatial

210 correlations between age classes within years. This same analysis was repeated for age-cohort

211 combinations (e.g., age-2 specimens collected in 1985 would represent the 1983 cohort, also a

212 342 X 342 matrix), and significant results were interpreted to indicate significant spatial

213 correlations between age classes within cohorts.

214

215 **Question #2: Relative importance of effects for center of gravity**

216 The relative importance of survey year and cohort to the variance explained in the linear model

217 predicting latitude/longitude of the COG estimates by age was assessed using a variance

218 decomposition procedure described in the R package *relaimpo*, which uses statistical metrics to

219 evaluate the relative importance of the regressors (Grömping 2006). Relative importance was

220 estimated using the following models:

221 lm1: lm(Ndev~factor(Year)+factor(Cohort))

222 lm2: lm(Edev~factor(Year)+factor(Cohort))

223 where Ndev and Edev are northing and easting deviations from the mean COG for a given age

224 class, and Year and Cohort are factors predicting distribution. The effect of Year is used to

225 capture all known and unknown year-specific effects that influence pollock distribution

226 including temperature (Kotwicki et al. 2005; Thorson et al. 2017; Eisner et al. 2020), light

227 conditions (Kotwicki et al. 2015), fish density, fishing pressure, ecological teleconnections

228 resulting from regional warm/cool conditions (Thorson et al. 2021), etc. The effect of Cohort is

229 used to capture all cohort-specific effects that influence pollock distribution including specifics

230 of cohort origination, cohort survival, multiyear effects on cohort distribution, differences in

231 ontogenetic migrations between cohorts, and other cohort related variables. Quantification of an

232 individual regressor's contribution to these regression models was estimated using three metric

233 outputs from the function *calc.relimp* in the R package *relaimpo* (Grömping 2006). The metric

234 "first" represents variance explained by each predictor alone; the metric "last" in this case

11

235   represents additional variance explained by each predictor when added to the model after the

236   variance explained by the first variable is accounted for; and the metric "lmg" is the average

237   contribution to variance explained for both orders of predictors (Christensen 1992; Grömping

238   2006).

239

240   **Question #3: Age-related factors influencing effective area occupied**

241   Finally, we seek to identify which intrinsic/extrinsic/memory effects are associated with larger or

242   smaller EAO for each combination of age and year. To do so, we used a generalized additive

243   modeling (GAM) procedure to assess the effects of some population parameters and

244   environmental variables, including age-1 abundance, spawning stock biomass, mean surface

245   temperature, cold pool area, and age class, on EAO. These models were constructed in R using

246   the "gam" function of the mgcv package, version 1.8-31 (Wood 2017). Age-1 abundance and

247   spawning stock biomass were obtained from the 2019 assessment of the walleye pollock stock in

248   the eastern Bering Sea (Ianelli et al. 2019: Table 32). Water temperatures were recorded by a

249   bathythermograph placed on the headrope of the net; surface temperature was recorded at -1 m

250   depth, and bottom temperature was recorded while the net was on bottom in fishing

251   configuration, ~3 m off bottom. Mean annual surface temperatures were calculated as the

252   average of water temperature samples from each survey station sampled by AFSC's eastern

253   Bering Sea bottom trawl survey, weighted by the proportion of their assigned stratum area. Four

254   different near-bottom temperature variables were tested in GAMs, including annual average

255   bottom temperature, calculated in the same way as surface temperature, and three different cold

256   pool area variables, calculated as in Kotwicki and Lauth (2013) for three different temperatures

257   (0, 1, and 2°C). EAO estimates were weighted by $1/SE^2$ in the model to correct for uncertainty,

258   where SE is the estimated standard error generated by VAST, and weighting by precision

259   accounts for heteroscedasticity when fitting the GAM model.

260   The initial model investigated was:

261   EAO ~ factor(age) + s(cpa, k=4) + s(temp, k=4) + s(ssb, k=4) + s(rec, k=4),

262   where EAO = effective area occupied (from VAST model, weighted by $1/SE^2$), age = age class,

263   cpa = cold pool area (the near-bottom temperature variable), stemp = mean annual surface

264   temperature, ssb = standing stock biomass, and rec = age-1 abundance. Smooth effects were

265   restricted to a maximum of 4 knots to minimize the possibility of overfitting. First, the best of the

266   four cold pool covariates (annual bottom temp, or cold pool area less than 0, 1, or 2°C) was

267   chosen by comparing four potential versions of the initial model above, using Akaike

268   Information Criterion (AIC). The model with the lowest AIC was used as the initial model for

269   testing for differences between the smooth effects by age, using "by" argument (e.g., s(cpa,

270   by=factor(age), k=4)). This age factor was added to initial model smooth covariates one by one

271   and tested for model improvements using AIC. The "by" parameter was retained in the covariate

272   for which the AIC was reduced the most. The process was repeated until no more reduction in

273   AIC could be achieved or until all variables included the "by" argument.

274

275   **Results**

276   **Describing age-specific densities**

277   The results of the VAST model show distinct differences in the spatial distribution of age classes

278   of pollock in the eastern Bering Sea. Predicted density plots for all survey years combined

279   (Fig.1) show that the youngest pollock (age-1) are on average broadly distributed across the shelf

280   to the north of the Pribilof Islands from the inner domain to the shelf edge. Age-1 and age-2

281   pollock are rarely encountered south of the Pribilof Islands. Progressing through the juvenile

282   stage (age-2 and 3), pollock are more concentrated near the shelf edge, becoming largely absent

283   from the inner shelf and remaining most densely distributed to the north of the Pribilof Islands.

284   Young adult pollock (age-4 through age-7) remain concentrated on the outer shelf, with their

285   distribution moving slightly to the south and west with each successive age class. For the oldest

286   age classes examined in this study (age-8 and age-9+), the distribution spreads back onto the

287   middle shelf, and high densities of pollock are increasingly found in the southern Bering Sea

288   near the Alaska Peninsula.

289   Mean COG calculated for each age class over the survey period summarizes the

290   distribution trends indicated in the density plots. These age-specific centers of gravity describe a

291   u-shaped, or nearly circular trend in centers of distribution as pollock age (Fig. 2). The transition

292   from age-1 to age-2 is marked by a notable northwestward shift in distribution, reflecting the

293   increasing concentration of individuals near the shelf edge in the northern part of the survey area.

294   All subsequent age transitions generally reflect a southward and eastward movement of the older

295   segments of the population. Transitions from age-3 through age-8 indicate only minor shifts in

296   distribution, and although the movement is directionally consistent, it appears gradual. The

297   transition from age-8 to the oldest age class (age-9+) appears more significant. The COG for this

298   oldest age group is shifted notably to the east, reflecting the spread of this population segment

299   back onto the middle shelf as well as the increasing proportion of the population in the

300   southeastern portion of the Bering Sea.

301   In addition to differences in their population COG, pollock occupy varying amounts of

302   space as they age. Mean estimates of EAO over the survey period indicate that age-1 pollock are

303   highly dispersed, occupying much more EAO than subsequent year classes (Fig. 3). Older

14

304   juveniles (age-2 through age-4) are much more concentrated, occupying on average less than half

305   the area of age-1 fish. Adult pollock (age-5 through age-9+), are progressively more dispersed,

306   with the oldest age classes occupying the largest area. These trends are also visible in the density

307   plots (Fig. 1).

308   Our data also show evidence of some temporal trends in pollock distribution. For

309   example, over the 38-year study period the COG averaged over all age classes of pollock moved

310   significantly northward (Fig. 4), although longitude did not shift significantly. Furthermore, the

311   average EAO has increased substantially, particularly over the last decade.

312

313   **Question #1: Evidence of a cohort effect**

314   Measures of spatial correlation based on range overlap metrics indicate strong correlations

315   among age groups both within year and within cohort. Within year, GIC values were

316   significantly correlated (Table 1) for all adjacent age groups (e.g., age-2 vs. age-3, age-3 vs. age-

317   4) as well as a few age groups separated by two years (e.g., age-4 vs. age-6). None of the more

318   distant age groups (3 or more age classes apart) were significantly correlated. Schoener's D

319   values (Table 2) within year were significantly correlated for nearly all pairwise comparisons,

320   regardless of age class, although age-1 and age-9+ comparisons were less universally significant.

321   Many of the pairwise comparisons of spatial correlation within cohort were also significant. GIC

322   values (Table 1) were significantly correlated among the majority of adjacent age groups, as well

323   as several non-adjacent age groups (e.g., age-3 vs. age-6). Schoener's D values (Table 2)

324   demonstrated a similar pattern, with nearly all adjacent comparisons significant, as well as many

325   of the non-adjacent comparisons.

15

326   Thus, the spatial distributions of pollock age classes were generally highly correlated

327   within a survey year, particularly those of the adjacent age classes. This effect was more

328   pronounced when measured using the finer-scale Schoener's D statistic. Correlation patterns

329   within a cohort were generally similar, indicating that the spatial distributions of individual

330   cohorts are highly correlated as they progress through time, again particularly across a single age

331   step. Significant pairwise correlations within a year indicate that the spatial distribution of age

332   classes within the population is being driven by extrinsic or intrinsic factors operating

333   simultaneously on the whole population, while the significant pairwise correlations within a

334   cohort for the majority of cohorts indicate that the spatial distribution of those cohorts is, to some

335   extent, driven by spatial memory or entrainment. For example, the distribution of age-3 pollock

336   in 1990 was significantly influenced by the distribution of age-2 pollock in 1989.

337

338   **Question #2: Centers of gravity**

339   The linear models in which age-specific COG (decomposed into deviations from the mean

340   latitude and longitude) are related to the factor variables "Year" and "Cohort" extend and clarify

341   the results of the range correlation metrics. In both the latitude and longitude models, year and

342   cohort contribute significantly to the overall variance of the model (Table 3) and explain the

343   majority of variation in the data ($> 60\%$). Furthermore, the relative contributions of the two

344   factors are similar in both models, with year contributing approximately two-thirds of the

345   variance, and cohort contributing approximately one-third. These results indicate that both year

346   and cohort contribute significantly to variation in both the latitudinal and longitudinal axes of

347   spatial variation in the distribution of pollock, though the magnitude of the year effect is clearly

348   greater.

349

Question #3: Effective area occupied

The results of the GAM modeling of EAO are presented in Tables 4 and 5. Of the near-bottom

temperature variables tested (cold pool area $< 0°C$, $< 1°C$, $< 2°C$, or mean annual bottom temp),

the cold pool area $< 0°C$ resulted in the lowest AIC. Differences in the smooth effect by age were

detected only for the environmental variables 'cpa' and 'stemp' (Table 4). Thus, in the final

model:

  EAO ~ factor(age) + s(cpa, by=factor(age), k=4) + s(stemp, by=factor(age), k=4) +

      s(ssb, k=4) + s(rec, k=4).

The final model explained a large proportion of the observed variation in EAO (80.6%). The

relationship between age and EAO reflected the same trend as above (Fig. 3), with the youngest

and oldest age classes occupying the most space, and the older juveniles (age-2 through age-4)

being the most concentrated (Fig. 5A). The age factor alone explained 61.4% of the variation in

EAO. For the population variables biomass (ssb) and age-1 abundance (rec) we did not detect

differences between smooth terms by age, but the results indicated that lower values of these

variables result in lower EAO (Fig. 5B, 5C). For biomass, results suggest that the EAO is smaller

than average for ssb values lower than 2500 (= 2.5 million tons). For recruitment, results indicate

that EAO is more extensive than average only for the six largest cohorts (based on age-1

abundance).

     The effects of environmental factors on the EAO by pollock differed by age class. The

effect of cold pool area was significant for age classes 1, 2, 7, 8, and 9+ (Fig. 6). In general, it

appears that EAO declines with increasing cold pool area. The effect of the cold pool on EAO of

age classes 3-6 was not significant and the partial effect was nearly constant, indicating that the

17

372   cold pool likely does not affect EAO for these ages. For surface temperature (Fig. 7), the

373   nonlinear interaction between surface temperature and EAO was significant for most adult

374   pollock (age-5 through age-9+), and partial effect plots showed a similar pattern of increasing

375   EAO with increasing surface temperatures for all significant age classes. This result indicates

376   that pollock of these ages are more concentrated in smaller areas in cooler temperatures, and

377   more dispersed in warmer conditions. However, this effect appears to be most pronounced only

378   for surface temperatures larger than 7°C, which indicates that this dispersion occurs only during

379   warm summers.

380

381   **Discussion**

382   This analysis describes the spatial distribution of walleye pollock in their summer feeding

383   habitat as a function of ontogeny and size. We also provide the first evidence for a cohort effect

384   in the spatial distribution of the walleye pollock of the eastern Bering Sea, and show that

385   intrinsic and extrinsic factors affect the spatial distribution of the population in age-specific

386   ways.

387   The youngest and oldest classes of walleye pollock are broadly dispersed across the

388   continental shelf in the eastern Bering Sea, although they are rarely encountered in the southern

389   portion of the survey range. In contrast, intermediate age classes are more concentrated in

390   feeding areas near the shelf edge. Although ontogenetic migration has been widely demonstrated

391   in marine fish species and has been previously examined in pollock (Bailey et al. 1999; Ianelli

392   2005) in the Bering Sea, previous studies have not accounted for spatial variability in age

393   structure. In contrast, our study accounted for spatiotemporal variability in age-length

394   relationships by using model-based age composition estimation. Ignoring this variability can lead

395   to biased outcomes of assessment models (Correa et al. 2020) and in spatiotemporal analysis of

396   ontogenetic migrations.

397   Our results suggest that the youngest and oldest age classes of pollock undertake more

398   limited summer feeding migrations than intermediate age classes, as they appear to be less

399   concentrated in summer feeding areas as demonstrated by EAO by age. Due to their size and

400   limited swimming performance, age-1 pollock have limited ability to cover large distances, and

401   their wide dispersal across the EBS shelf, and their absence from the southeastern portion of the

402   Bering Sea survey area, is likely a reflection of the distribution of the larval and age-0 population

403   distribution, which is driven by ocean currents. This advective extrinsic factor varies among

404   years (Wespestad et al. 2000). Kotwicki et al. (2005) also found that smaller pollock (< 29 cm,

405   roughly corresponding to age-1 and age-2) do not aggregate along the shelf edge as much as

406   older pollock. Larger juvenile and adult pollock can migrate over larger distances and form

407   tighter, more pelagic aggregations. These aggregations form predominantly on the shelf edge,

408   which is a primary pollock feeding ground (Kotwicki et al. 2005). As pollock mature, their

409   summer distribution moves progressively to the south along the shelf edge. Eventually, older

410   pollock disperse again over the shallow parts of the shelf. This dispersal coincides with the

411   transition of pollock from predominantly pelagic prey to more diverse prey that consists of both

412   pelagic and benthic animals (Buckley et al. 2016), limiting the requirement for an extensive

413   feeding migration. Previous studies have also suggested that juvenile pollock move offshore and

414   northward during the first few years of life, then generally move southward and back onto the

415   shelf after age-3 (Bailey et al. 1999; Ianelli 2005).

416   In addition to ontogenetic migration, our data show evidence of a recent northward shift

417   of the overall pollock COG in the Bering Sea, particularly during 2016-2019 for most age

19

418   classes. In recent years, this northward shift in distribution was accompanied by an increase in

419   EAO, which indicates that the recent expansion to the north does not coincide with

420   corresponding reductions of the area occupied in the south. If the warming trend continues in the

421   Bering Sea, we can expect further expansion of pollock distribution to the north (as demonstrated

422   in recent pollock studies in the NBS; Stevenson and Lauth 2019). This may hamper the ability of

423   the EBS bottom trawl survey to assess year-class strength and recruitment success, as was the

424   case for the 1992 year class, much of which was advected outside the survey area (Wespestad et

425   al. 2000; O'Leary et al. 2020). If further expansions to the north continue and the southern extent

426   of pollock distribution remains unchanged, we may see a further increase in the EAO of the

427   pollock population in the Bering Sea in the future. Such increases in summer EAO can

428   negatively affect the commercial fisheries because fish are more dispersed, and fishing quotas

429   require more time and effort to fill. This situation was observed in 2018–20 in the EBS pollock

430   summer fishing season, when it took longer than usual to catch the quota (Ianelli et al. 2021).

431   The effect of the expansion of the summer EAO on the population size and structure is unclear

432   and requires further investigation.

433   Our comparisons of spatial correlation among years and cohorts provide evidence of a

434   population-level "cohort effect". This effect is also clear from our decomposition of variance in

435   the center of gravity among years and cohorts. Marquez et al. (2021) showed a cohort effect in

436   the spatial autocorrelation in density for cod and haddock in the Barents Sea, and noted that this

437   effect was increasingly prevalent in older age classes in both species. Our results show an

438   analogous cohort effect in the temporal autocorrelation among age classes of pollock in the

439   Bering Sea, though we do not see clear evidence that this effect is more prevalent among older

440   age classes. The magnitude of the cohort effect demonstrated here is about half of the year effect,

441   so clearly it should not be omitted from studies of spatial dynamics in EBS pollock. Because our

442   variance decomposition analysis has compartmentalized spatial correlation into interannual

443   effects and cohort effects, and generalized across a large number of survey years, spatial variance

444   explained by the cohort effect should be due primarily to the initial distribution of the cohort.

445   This, in turn, should reflect the relative spawning success of the component spawning

446   aggregations that comprise the Bering Sea pollock population. The fact that we show here a clear

447   cohort effect implies that spawning success can differ among different spawning aggregations,

448   and that these differences in spawning success may lead to persistent differences in the spatial

449   distributions of cohorts as they recruit to the adult population.

450   The presence of a persistent cohort effect may indicate that there is some level of

451   metapopulation structure in the pollock of the Bering Sea. If this is the case, then mechanisms

452   must exist to maintain the structure in a region without clearly defined geographic boundaries.

453   These mechanisms could include physical oceanographic patterns, genetic predisposition and

454   environmental imprinting, or entrainment by learning adult migratory patterns. Spawning

455   aggregations of pollock in the EBS are broadly distributed in time and space (Hinckley 1987;

456   Stahl and Kruse 2008). Their eggs and larvae are subject to variable physical transport

457   (Wespestad et al. 2000) and mixing, resulting in multiple size-modes of larvae that overlap in

458   geographic distribution across the EBS (Nishimura et al. 1996; Traynor and Smith 1996). Thus,

459   larval retention in natal regions by physical oceanographic isolating mechanisms appears

460   unlikely. If a genetic and/or imprinted predisposition exists for spawning within a particular area

461   and time, then pollock would have a greater chance of spawning within aggregations of similarly

462   predisposed pollock than with others. Alternatively, juvenile pollock may learn migration

463   patterns by following adults to spawning locations, a process known as entrainment (Petitgas et

464 al. 2006), which could explain the increased area-occupied when spawning biomass is large

465 (MacCall et al. 2019). Our study cannot distinguish between these and other specific behavioral

466 mechanisms that may result in the spatio-temporal patterns identified here. However, the

467 presence of a persistent cohort effect in the spatial distribution of the population suggests that

468 this phenomenon requires more study, as the relative influences structuring mechanisms

469 (genetic/environmental imprinting vs. behavioral entrainment) may have important implications

470 for the ability of the species to colonize new habitat or recolonize historic spawning habitat.

471 Extrinsic environmental factors are clearly important in determining the spatial

472 distribution of walleye pollock. For example, our most effective measure of temperature

473 conditions near the sea floor, the cold pool area ($< 0°C$), has an inverse relationship with the

474 EAO by pollock on the Bering Sea shelf. In general, the more of the shelf is covered by the cold

475 pool, the less of the shelf pollock occupy. This effect is also evident in the relationship of EAO

476 to surface temperature, with pollock occupying more area on the shelf during years of warmer

477 overall surface temperatures. In general, this makes sense, as several previous studies have

478 concluded that adult pollock avoid low temperatures (Wyllie-Echeverria 1995; Wyllie-

479 Echeverria and Wooster 1998; Kotwicki 2005; Kotwicki and Lauth 2013), particularly $< 0°C$.

480 Some authors have suggested that juvenile pollock may use the cold pool as a refuge from

481 predatory pressures, including cannibalism by larger pollock (Hunsicker et al 2013, Uchiyama et

482 al 2020). However, whether this avoidance is the result of a direct physiological response or an

483 indirect response to ecological parameters such as prey populations or predator avoidance is still

484 unclear.

485 Our results also suggest that interannual temperature variations do not affect the spatial

486 distribution of all ages of pollock in the same way. The effect of bottom temperature was

487   significant for the youngest and oldest age classes of pollock, but not intermediate age classes. In

488   contrast, the effect of surface temperature was significant only for adults. These age-specific

489   differences in the response of pollock populations to temperature could be due to several factors.

490   Young pollock recruits are unable to escape colder temperatures (Buckley et al. 2016), but once

491   swimming speed allows active schooling and cross-shelf migration, behavioral adaptations to

492   maximize average feeding and survival success drive the distributions (Kotwicki et al. 2005). At

493   larger sizes, walleye pollock become less susceptible to predation, less dependent on small

494   pelagic prey (Buckley et al. 2016), more benthic in habit (Lynde 1984; Bakkala and Alton 1986;

495   Traynor et al. 1990), and disperse more widely over the EBS shelf during summer feeding

496   migrations (Kotwicki et al. 2005). Additionally, there is evidence that the influence of

497   temperature on bioenergetic parameters, such as respiration and digestion, declines with

498   increasing size in pollock (Buckley and Livingston 1994), so larger pollock may be less

499   metabolically dependent on optimum temperatures. Finally, the fact that bottom and surface

500   temperature have different relationships to pollock distribution may be due to the differing

501   seasonal dynamics of these environmental parameters. Surface temperature changes steadily over

502   the summer as the surface waters warm due to increased seasonal solar heating, while bottom

503   temperature, and particularly cold pool area, is driven more by the ice conditions of the previous

504   winter and often persists through much or all of the summer (Stabeno et al. 2007).

505   In addition to extrinsic factors, intrinsic population factors affect the spatial distribution

506   of walleye pollock, though not to the same extent. If density-dependent factors influence the

507   spatial distribution of pollock, then we would expect to see a strong relationship between

508   standing stock biomass (the overall size of the population) and the geographic area occupied by

509   the population. Our results do not show clear evidence of this effect at higher population levels,

510 but there is some indication that the area occupied by the population does contract when the

511 overall biomass is particularly low. Of course, pollock may expand their range into neighboring

512 regions at high abundance levels (e.g., Tsugi 1989; Stepanenko 1997), so at times the population

513 is likely expanding outside the survey area, into the northern Bering Sea, south into the Gulf of

514 Alaska, or west past the US-Russia convention line (O'Leary et al. 2021). If new recruits drive

515 the spatial distribution of the population, we would expect to see a strong relationship between

516 age-1 abundance and area occupied, assuming that the proportion of the population in the survey

517 area remains constant. Again, our results do not show clear evidence of this effect except for the

518 few largest cohorts in the time series, and adding an age interaction to the recruitment term in the

519 model degraded the fit. In fact, age-1 abundance was not significantly related to the area

520 occupied by the age-1 segment of the population. This suggests that either age-1 abundance is

521 not reaching sufficient levels for density to become limiting, or that more of the population

522 moves outside the survey area at higher abundance levels.

523   Although this study provides insight into the factors influencing the spatial distribution of

524 pollock in the Bering Sea, the analysis has some important limitations. First, the availability of

525 pollock to the survey trawl may be partially size-dependent. If age groups migrate differently

526 within the survey area, as this study and Kotwicki et al. (2005) suggest, then it is also possible

527 that the proportions of the population within the survey area, and therefore available to the trawl

528 survey, are not consistent among population segments and survey years. Additionally, the

529 vertical distribution of pollock in the water column largely influences their availability to the

530 bottom trawl gear. This vertical distribution may differ substantially among different age classes

531 of pollock, and the proportion of the population near the bottom varies both spatially and over

532 time (Monnahan et al. 2021). This study only examines the distribution of pollock available to

24

533 the bottom trawl survey, and subadult pollock in the 20-40cm size range are less commonly

534 encountered on AFSC bottom trawl surveys (Lauth et al. 2019). Therefore, estimates of the

535 spatial distribution for these age classes may be more uncertain than those of the other age

536 classes. We recommend additional research conducting similar analyses using a joint model of

537 bottom trawl and acoustic data to assess the pelagic portion of the population as well.

538 Secondly, our analyses do not address the possibility of time-lagged effects of intrinsic

539 and extrinsic factors. For example, the cold pool area in the survey year 2002 may have affected

540 the spatial distribution of the pollock population in 2003. Finally, the precision of density-at-age

541 estimation declines with species age class. Although our method of estimating age compositions

542 accounts for spatial differences in growth rates, the fact remains that the age-length-key assigns

543 larger pollock to an age class with less precision. This lack of precision may affect on the power

544 of our analyses to detect factors of influence for the older age classes.

545 Overall, the results of this study indicate that inter-annual variability in the spatial

546 distribution of the walleye pollock population in the eastern Bering Sea is strongly influenced by

547 extrinsic environmental factors, but that the population distribution also has a cohort component

548 that explains nearly one-third of the variance in center of gravity. Furthermore, this study shows

549 that intrinsic and extrinsic factors affect different age groups of the population in different ways.

550 Thus, when assessing the spatiotemporal distribution dynamics of marine fish populations, it is

551 essential not only to model intrinsic factors, extrinsic factors, and spatial cohort components, but

552 also to consider variability in how these factors influence the distribution of different age classes

553 in the population.

554

555 **Statement of Competing Interests**

556 The authors declare that they have no known competing financial interests or personal

557 relationships that could have appeared to influence the work reported in this paper.

558

559 **Data Availability**

560   Primary data used in this study can be located on the Alaska Fisheries Information

561 Network (https://akfin.psmfc.org/). Primary catch data for GAP bottom-trawl surveys can be

562 located at the NOAA Fisheries One Stop Shop (www.fisheries.noaa.gov/foss).

563

574

575 **References**

576 Bacheler N.M., Ciannelli L., Bailey K.M., and Duffy-Anderson J.T. 2010. Spatial and temporal

577   patterns of walleye pollock (*Theragra chalcogramma*) spawning in the eastern Bering

578   Sea inferred from egg and larval distributions. Fish. Oceanogr. 19:107–120.

579   Bailey K.M., Quinn T.J., Bentzen P., and Grant W.S. 1999. Population structure and dynamics of

580   walleye pollock *Theragra chalcogramma*. Adv. Mar. Biol. 37:179–255.

581   Bakkala R.G., and Alton M.S. 1986. Evaluation of demersal trawl survey data for assessing the

582   condition of eastern Bering Sea pollock. Int. N. Pac. Fish. Comm. Bull. 45:90–120.

583   Benoit-Bird K.J., McIntosh N.E., and Heppell S.A. 2013. Nested scales of spatial heterogeneity

584   in juvenile walleye pollock *Theragra chalcogramma* in the southeastern Bering Sea. Mar.

585   Ecol. Prog. Ser. 484:219–238.

586   Berg C.W., and Kristensen K. 2012. Spatial age-length key modelling using continuation ratio

587   logits. Fish. Res. 129–130:119–126.

588   Bez N., and Rivoirard J. 2000. Indices of collocation between populations. In: Checkley D.M.,

589   Hunter J.R., Motos L., and von der Lingen C.D.(eds). Workshop on the use of continuous

590   underway fish egg sampler (CUFES) for mapping spawning habitat of pelagic fish.

591   GLOBEC Report, pp. 48–52.

592   Buckley T.W., and Livingston P.A. 1994. A bioenergetics model of walleye pollock (*Theragra*

593   *chalcogramma*) in the eastern Bering Sea: structure and documentation. U.S. Dep.

594   Commer., NOAA Tech. Memo. NMFS-AFSC-37, 55 p.

595   Buckley T.W., Ortiz I., Kotwicki S., and Aydin K. 2016. Summer diet composition of walleye

596   pollock and predator-prey relationships with copepods and euphausiids in the eastern

597   Bering Sea, 1987–2011. Deep-Sea Res. II 134:302–311.

598   Burnham K.P., and Anderson D.R. 2002. Model selection and multimodel inference: a practical

599   information-theoretic approach. Springer-Verlag, New York, 488 pp.

600   Christensen R. 1992. Comment on Chevan and Sutherland. Am. Stat. 46:74.

601   Correa G.M., Ciannelli L., Barnett L.A.K., Kotwicki S., and Fuentes C. 2020. Improved

602   estimation of age composition by accounting for spatiotemporal variability in somatic

603   growth. Can. J. Fish. Aquat. Sci. 77:

604   Duffy-Anderson J.T., Ciannelli L., Honkalehto T., Bailey K.M., Sogard S.M., Springer A.M.,

605   and Buckley T. 2003. Distribution of age-1 and age-2 walleye pollock in the Gulf of

606   Alaska and eastern Bering Sea: sources of variation and implications for higher trophic

607   levels. In: Browman H.I., and Skiftesvik A.B. (eds). The Big Fish Bang. Proceedings of

608   the 26th Annual Larval Fish Conference. Institute of Marine Research, Bergen, Norway,

609   pp. 381–394.

610   Duffy-Anderson J.T., Stabeno P.J., Siddon E.C., Andrews A.G., Cooper D.W., Eisner L.B.,

611   Farley E.V., Harpold C.E., Heintz R.A., Kimmel D.G., Sewall F.F., Spear A.H., and

612   Yasumishii E.C. 2017. Return of warm conditions in the southeastern Bering Sea:

613   Phytoplankton – fish. PLoS ONE 12(6):e0178955.

614   Eisner L.S., Zuenko Y.I., Basyuk E.O., Britt L.L., Duffy-Anderson J.T., Kotwicki S., Ladd C.,

615   and Cheng W. 2021. Environmental impacts on walleye pollock (*Gadus chalcogrammus*)

616   distribution across the Bering Sea shelf. Deep Sea Res. II: Top. Stud. Oceanogr. 181–

617   182: https://doi.org/10.1016/j.dsr2.2020.104881.

618   Fredston-Hermann A., Selden R., Pinsky M., Gaines S.D., and Halpern B.S. 2020. Cold range

619   edges of marine fishes track climate change better than warm edges. Glob. Change Biol.

620   26:2908–2922.

621   Grömping U. 2006. Relative importance for linear regression in R: the package relaimpo. J. Stat.

622   Soft. 17:1–27.

623   Hinckley S. 1987. The reproductive biology of walleye pollock, *Theragra chalcogramma*, in the

624   Bering Sea, with reference to spawning stock structure. Fish. Bull. 85:481–498.

625   Hoff G.R. 2010. Identification of skate nursery habitat in the eastern Bering Sea. Mar. Ecol.

626   Prog. Ser. 403:243–254.

627   Honkalehto T., McCarthy A., Ressler P., Stienessen S., and Jones D. 2010. Results of the

628   acoustic-trawl survey of walleye pollock (*Theragra chalcogramma*) on the U.S. and

629   Russian Bering Sea shelf in June-August 2009 (DY0909). AFSC Processed Rep. 2010-

630   03, 57 p. Alaska Fish. Sci. Cent., NOAA, Natl. Mar. Fish. Serv., 7600 Sand Point Way

631   NE, Seattle WA 98115.

632   Hunsicker, M.E., Ciannelli, L., Bailey, K.M., Zador, S., and Stige, L.C. 2013. Climate and

633   demography dictate the strength of predator-prey overlap in a subarctic marine

634   ecosystem. PLoS ONE, 8, e66025.

635   Hutchinson G.E. 1957. Concluding remarks – Cold Spring Harbor Symposia on Quantitative

636   Biology 22:415–427.

637   Ianelli J. 2005. Assessment and fisheries management of eastern Bering Sea walleye pollock: is

638   sustainability luck? Bull. Mar. Sci. 76:321–335.

639   Ianelli J., Fissel B., Holsman K., Honkalehto T., Kotwicki S., Monnahan C., Siddon E.,

640   Stienessen S., and Thorson J. 2019. Chapter 1: Assessment of the walleye pollock stock

641   in the eastern Bering Sea, 169 p. In: Stock Assessment and Fishery Evaluation Report for

642   the Groundfish Resources of the Bering Sea/Aleutian Islands Regions; compiled by the

643   Plan Team for the Groundfish Fisheries of the Bering Sea and Aleutian Islands.

644 Kastelle C.R., and Kimura D.K. 2006. Age validation of walleye pollock (*Theragra*

645   *chalcogramma*) from the Gulf of Alaska using the disequilibrium of Pb-210 and Ra-226.

646   ICES J. Mar. Sci. 63:1520–1529.

647 Kim S., Kendall A.W. Jr, and Kang S. 1996. The abundance and distribution of pollock eggs and

648   some spawning characteristics in the southeastern Bering Sea in 1977. Ocean Res.

649   18(Special):59–67.

650 Kotwicki S., and Lauth R.R. 2013. Detecting temporal trends and environmentally-driven

651   changes in the spatial distribution of bottom fishes and crabs on the eastern Bering Sea

652   shelf. Deep-Sea Res. 94:231–243.

653 Kotwicki S., Buckley T.W., Honkalehto T., and Walters G. 2005. Variation in the distribution of

654   walleye pollock (*Theragra chalcogramma*) with temperature and implications for

655   seasonal migration. Fish. Bull. 103:574–587.

656 Kotwicki S., Horne J.K., Punt A.E., and Ianelli J.N. 2015. Factors affecting the availability of

657   walleye pollock to acoustic and bottom trawl survey gear. ICES J. Mar. Sci. 72:1425–

658   1439.

659 Kristensen K., Nielsen A., Berg C.W., Skaug H., and Bell B.M. 2016. TMB: automatic

660   differentiation and laplace approximation. J. Stat. Soft. 70:1–21.

661 Laman E.A., Rooper C.N., Turner K., Rooney S., Cooper D.W., and Zimmermann M. 2018.

662   Using species distribution models to describe essential fish habitat in Alaska. Can. J.

663   Fish. Aquat. Sci. 75:1230–1255.

664 Lauth R.R., Dawson E.J., and Conner J. 2019. Results of the 2017 eastern and northern Bering

665   Sea continental shelf bottom trawl survey of groundfish and invertebrate fauna. U.S. Dep.

666   Commer., NOAA Tech. Memo. NMFS-AFSC-396, 260 p.

667   Lindgren F., Rue H., and Lindström J. 2011. An explicit link between Gaussian fields and

668   Gaussian Markov random fields: the stochastic partial differential equation approach. J.

669   Roy. Stat. Soc. Ser. B Stat. Methodol. 73:423–498.

670   Lynde C.M. 1984. Juvenile and adult walleye pollock of the eastern Bering Sea: literature review

671   and results of ecosystem workshop. In: Ito D.H. (ed) Proceedings of the workshop on

672   walleye pollock and its ecosystem in the eastern Bering Sea. U.S. Dep. Commer., NOAA

673   Tech. Memo. NMFS-F/NWC-62, 292 p.

674   MacCall A.D., Francis T.B., Punt A.E., Siple M.C., Armitage D.R., Cleary J.S., Dressel S.C.,

675   Jones R.R., Kitka H., Lee L.C., Levin P.S., McIsaac J., Okamoto D.K., Poe M.,

676   Reifenstuhl S., Schmidt J.O., Shelton A.O., Silver J.J., Thornton T.F., Voss R., and

677   Woodruff J. 2019. A heuristic model of socially learned migration behavior exhibits

678   distinctive spatial and reproductive dynamics. ICES J. Mar. Sci. 76:598–608.

679   Marquez J.F., Saether B.-E., Aanes S., Engen S., Salthaug A., and Lee A.M. 2021. Age-

680   dependent patterns of spatial autocorrelation in fish populations. Ecology

681   00:e03523.10.1002/ecy.3523

682   Monnahan C.C., Thorson J.T., Kotwicki S., Lauffenberger N., Ianelli J.N., and Punt A.E. 2021.

683   Incorporating vertical distribution in index standardization accounts for spatiotemporal

684   availability to acoustic and bottom trawl gear for semi-pelagic species. ICES J. Mar. Sci.

685   fsab085, https://doi.org/10.1093/icesjms/fsab085

686   Nishimura A., Mito K., and Yanagimoto T. 1996. Hatch date and growth estimation of juvenile

687   walleye pollock, *Theragra chalcogramma*, collected in the Bering Sea in 1989 and 1990.

688   In: Brodeur R.D., Livingston P.A., Loughlin T.R., Hollowed A.B. (eds) Ecology of

689   juvenile walleye pollock, *Theragra chalcogramma*. NOAA Tech Rep NMFS 126, p 81-

690   87.

691 O'Leary C.A., Kotwicki S., Hoff G.R., Thorson J.T., Kulik V.V., Ianelli J.N., Lauth R.R., Nichol

692   D.G., Conner J., and Punt A.E. 2021. Estimating spatiotemporal availability of

693   transboundary fishes to fishery-independent surveys. J. App. Ecol. doi:10.1111/1365-

694   2664.13914.

695 Parker-Stetter S.L., Horne J.K., and Urmy S.S. 2015. Vertical distribution of age-0 walleye

696   pollock during late summer: environment or ontogeny? Mar. Coast. Fish. 7:349–369.

697 Petitgas P., Reid D., Planque B., Nogueira E., O'Hea B., and Cotano U. 2006. The entrainment

698   hypothesis: an explanation for the persistence and innovation in spawning migration and

699   life cycle patterns. ICES CM 2006/B:07

700 Pinsky M., Worm B., Fogarty M.J., Sarmiento J.L., and Levin S.A. 2013. Marine taxa track local

701   climate velocities. Science 341:1239–1242.

702 Planque B., Loots C., Petitgas P., Lindstrom U., and Vaz S. 2011. Understanding what controls

703   the spatial distribution of fish populations using a multi-model approach. Fish. Ocean.

704   20:1–17.

705 R Core Team. 2020. R: A language and environment for statistical computing. R Foundation for

706   Statistical Computing, Vienna, Austria. https://www.R-project.org/.

707 Schoener T.W. 1968. The *Anolis* lizards of Bimini: resource partitioning in a complex fauna.

708   Ecology 49:704–726.

709 Simpson S.C., Eagleton M.P., Olson J.V., Harrington G.A., and Kelly S.R. 2017. Final Essential

710   Fish Habitat (EFH) 5-year Review, Summary Report: 2010 through 2015. U.S. Dep.

711   Commer., NOAA Tech. Memo. NMFS-F/AKR-15, 115 p.

712   Stabeno P.J., Bond N.A., and Salo S.A. 2007. On the recent warming of the southeastern Bering

713   Sea shelf. Deep Sea Res. II: Top. Stud. Ocean. 54:2599–2618.

714   Stabeno P.J., Duffy-Anderson J.T., Eisner L., Farley E., Heintz R., and Mordy C.W. 2017.

715   Return of warm conditions in the southeastern Bering Sea: physics to fluorescence. PLoS

716   ONE 12:e0185464.

717   Stahl J.P., and Kruse G.H. 2008. Spatial and temporal variability in size of maturity of walleye

718   pollock in the eastern Bering Sea. Trans. Am. Fish. Soc. 137:1543–1557.

719   Stepanenko M.A. 1997. Variations from year to year in the spatial differentiation of the walleye

720   pollock, *Theragra chalcogramma*, and the cod, *Gadus macrocephalus*, in the Bering Sea.

721   J. Ichthyol. 37:14–20.

722   Stevenson D.E., and Lauth R.R. 2019. Bottom trawl surveys in the northern Bering Sea indicate

723   recent shifts in the distribution of marine species. Polar Biol. 42:407–421.

724   Thorson J.T. 2019. Guidance for decisions using the Vector Autoregressive Spatio-Temporal

725   (VAST) package in stock, ecosystem, habitat and climate assessments. Fish. Res.

726   210:143–161.

727   Thorson J.T., and Barnett L.A.K. 2017. Comparing estimates of abundance trends and

728   distribution shifts using single- and multispecies models of fishes and biogenic habitat.

729   ICES J. Mar. Sci. 74:1311–1321.

730   Thorson J.T., and Minto C. 2015. Mixed effects: A unifying framework for statistical modelling

731   in fisheries biology. ICES J. Mar. Sci. 72:1245–1256.

732   Thorson J.T., Ianelli J.N., and Kotwicki S. 2017. The relative influence of temperature and size-

733   structure on fish distribution shifts: a case-study on walleye pollock in the Bering Sea.

734   Fish Fish. 18:1073–1084.

735   Thorson J.T., Pinsky M.L., and Ward E.J. 2016. Model-based inference for estimating shifts in

736   species distribution, area occupied and centre of gravity. Methods Ecol. Evol. 7:990–

737   1002.

738   Thorson J.T., Arimitsu M.L., Barnett L.A.K., Cheng W., Eisner L.B., Haynie A.C., Hermann

739   A.J., Holsman K., Kimmel D.G., Lomas M.W., Richar J., and Siddon E.C. 2021.

740   Forecasting community reassembly using climate-linked spatio-temporal ecosystem

741   models. Ecography 44:1–14.

742   Tierney L., Kass R.E., and Kadane J.B. 1989. Fully exponential Laplace approximations to

743   expectations and variances of nonpositive functions. J. Amer. Stat. Assoc. 84:710–716.

744   Traynor J., and Smith D. 1996. Summer distribution and abundance of age-0 walleye pollock,

745   *Theragra chalcogramma*, in the Bering Sea. In: Brodeur R.D., Livingston P.A., Loughlin

746   T.R., Hollowed A.B. (eds) Ecology of juvenile walleye pollock, *Theragra*

747   *chalcogramma*. NOAA Tech Rep NMFS 126, p 57–59.

748   Traynor J.J., Karp W.A., Sample T.M., Furusawa M., Sasaki T., Teshima K., Williamson N.J.,

749   and Yoshimura T. 1990. Methodology and biological results from surveys of walleye

750   pollock (*Theragra chalcogramma*) in the eastern Bering Sea and Aleutian Basin in 1988.

751   Int. N. Pac. Fish Comm. Bull. 50:69–99.

752   Tsugi S. 1989. Alaska pollock population, *Theragra chalcogramma*, of Japan and its adjacent

753   waters, I: Japanese fisheries and population studies. Mar. Freshw. Behav. Physiol. 15:

754   147–205.

755   Uchiyama, T., Mueter, F.J., and Kruse, G.H. 2020. Multispecies biomass dynamics models

756   reveal effects of ocean temperature on predation of juvenile pollock in the eastern Bering

757   Sea. Fish. Ocean. 29:10–22.

758   Wespestad V.G., Fritz L.W., Ingraham W.J., and Megrey B.A. 2000. On relationships between

759   cannibalism, climate variability, physical transport and recruitment success of Bering Sea

760   walleye pollock, *Theragra chalcogramma*. ICES J. Mar. Sci. 57:272–278.

761   Woillez M., Rivoirard J., and Petitgas P. 2009. Notes on survey-based spatial indicators for

762   monitoring fish populations. Aquat. Living Resour. 22: 155–164.

763   Wood S. 2017. Generalized Additive Models: An Introduction with R, 2 edition. Chapman and

764   Hall/CRC.

765   Wylllie-Echeverria T. 1995. Sea-ice conditions and the distribution of walleye pollock (*Theragra*

766   *chalcogramma*) on the Bering and Chukchi shelf. In: Beamish R.J. (Ed.), Climate change

767   and northern fish populations. Canadian Special Publication in Fisheries and Aquatic

768   Science, National Research Council of Canada Ottawa 121:131–136.

769   Wyllie-Echeverria T., and Wooster W.S. 1998. Year-to-year variations in Bering Sea ice cover

770   and some consequences for fish distributions. Fish. Ocean. 7:159–170.

771   Zhang, J. 2016. R Package "spa". https://www.rdocumentation.org/packages/spaa/versions/0.2.2

772

FIGURE CAPTIONS

Figure 1. Plots of 75% cumulative estimated density (lat/long projected in NAD83), averaged over the survey period (1982-2019), for age classes of pollock. Plus signs (+) indicate the mean center of gravity for each age class, averaged over the survey period.

Figure 2. Estimated centers of gravity for each age class of pollock (lat/long projected in NAD83), averaged over the survey period (1982-2019).

Figure 3. Estimates of effective area occupied (+/- 2SE) for each age class of pollock, averaged over the survey period (1982-2019).

Figure 4. Temporal trends in centers of gravity by latitude (top) and longitude (center), as well as effective area occupied (bottom) for all age classes of pollock.

Figure 5. Partial effect plots from selected GAM model showing relationships between: A) age class and effective area occupied (EAO); B) standing stock biomass and EAO; and C) age 1 abundance and EAO for pollock in the eastern Bering Sea.

Figure 6. Partial effect plots from selected GAM model showing relationships between the estimated area of the cold pool (km^2 less than 0°C) and effective area occupied (EAO) for all ages of pollock in the eastern Bering Sea.

Figure 7. Partial effect plots from selected GAM model showing relationships between the mean annual surface temperature and effective area occupied (EAO) for all ages of pollock in the eastern Bering Sea.

Table 1. P values relating pairwise comparisons of global index of colocation (GIC) within year (above diagonal) or within cohort (below diagonal) to pairwise comparisons among age classes for all years/cohorts. Significant P values (<0.05, in bold) suggest greater correlation among age classes within year/cohort.

	age1	age2	age3	age4	age5	age6	age7	age8	age9
age1		**0.04**	0.47	0.75	0.67	0.72	0.38	0.18	0.34
age2	0.07		**0.02**	0.05	0.07	0.16	0.23	0.33	0.44
age3	0.52	0.07		**<0.01**	0.05	0.30	0.32	0.47	0.58
age4	0.45	0.19	**<0.01**		**<0.01**	**<0.01**	0.08	0.40	0.61
age5	0.43	0.08	**<0.01**	**<0.01**		**<0.01**	**<0.01**	0.07	0.40
age6	0.63	0.15	**<0.01**	**<0.01**	**<0.01**		**<0.01**	**<0.01**	0.29
age7	0.26	0.20	0.09	**0.04**	**<0.01**	**<0.01**		**<0.01**	**0.02**
age8	0.26	0.07	0.31	0.37	0.10	**<0.01**	**<0.01**		**<0.01**
age9	0.49	0.51	0.74	0.83	0.70	0.55	0.10	0.18	

Table 2. P values relating pairwise comparisons of Schoener's D within year (above diagonal) or within cohort (below diagonal) to pairwise comparisons among age classes for all years/cohorts. Significant P values (<0.05, in bold) suggest greater correlation among age classes within year/cohort.

	age1	age2	age3	age4	age5	age6	age7	age8	age9
age1		**<0.01**	**<0.01**	0.08	0.13	0.19	0.20	0.14	0.16
age2	0.13		**<0.01**	**<0.01**	**<0.01**	**<0.01**	**<0.01**	**<0.01**	0.07
age3	0.33	**<0.01**		**<0.01**	**<0.01**	**<0.01**	**<0.01**	**<0.01**	0.16
age4	0.28	0.05	**<0.01**		**<0.01**	**<0.01**	**<0.01**	**<0.01**	0.05
age5	0.15	0.10	**<0.01**	**<0.01**		**<0.01**	**<0.01**	**<0.01**	**<0.01**
age6	0.31	**0.01**	**0.02**	**<0.01**	**<0.01**		**<0.01**	**<0.01**	**<0.01**
age7	0.37	0.13	**<0.01**	**0.03**	**<0.01**	**<0.01**		**<0.01**	**<0.01**
age8	0.39	0.13	0.15	0.07	0.06	**<0.01**	**<0.01**		**<0.01**
age9	0.56	0.54	0.55	0.73	0.59	0.56	**0.01**	**<0.01**	

Table 3. Summary of variance decomposition, in which age-specific centers of gravity (decomposed into latitude and longitude) are related to the factor variables: year and cohort. First = variance explained by each predictor alone, last = variance explained when the predictor is added to the model as second.

	first	last	average
Latitude deviation ~ factor(Year) + factor(Cohort)			
Total variance explained: 0.633			
Factor(Year)	0.420	0.377	0.399
Factor(Cohort)	0.256	0.213	0.235
Longitude deviation ~ factor(Year) + factor(Cohort)			
Total variance explained: 0.610			
Factor(Year)	0.443	0.363	0.403
Factor(Cohort)	0.247	0.168	0.208

Table 4. Summary of variable selection process for the GAM modeling effective area occupied: "s" = variable modeled as a smooth term; "f" = variable modeled as a factor; "by=age" = variable modeled as a factor-smooth interaction with "age" as the factor. Asterisk indicates the final preferred model, using AIC as the optimality criterion (in which a lower value indicates a more optimized model).

| Model | btemp | cold pool area | | | stemp | ssb | rec | age | % var. explained | AIC |
		area <2°C	area <1°C	area <0°C						
Model_1	s				s	s	s	f	75.9	8115.1
Model_2		s			s	s	s	f	75.0	8125.3
Model_3			s		s	s	s	f	75.2	8122.2
Model_4				s	s	s	s	f	76.0	8110.5
Model_4.1				by=age	s	s	s	f	78.1	8102.7
Model_4.2				s	by=age	s	s	f	78.1	8101.7
Model_4.3				s	s	by=age	s	f	77.5	8108.3
Model_4.4				s	s	s	by=age	f	74.9	8140.2
Model_4.2.1*				by=age	by=age	s	s	f	80.6	8092.9
Model_4.2.2				s	by=age	by=age	s	f	79.2	8104.5
Model_4.2.3				s	by=age	s	by=age	f	77.2	8136.3
Model_4.2.1.1				by=age	by=age	by=age	s	f	80.9	8104.2
Model_4.2.1.2				by=age	by=age	s	by=age	f	79.6	8125.2