1   Variability in species composition and distribution of forage fish in the Gulf of Alaska

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14 **ABSTRACT**

15 In the Gulf of Alaska (GOA), forage fish species, such as age-0 walleye pollock (*Gadus chalcogrammus*),

16 capelin (*Mallotus villosus*), Pacific herring (*Clupea pallasii*), and mesopelagic fishes (e.g. *Myctophidae*),

17 are ecologically important as both consumers of zooplankton, and as prey for fish, seabirds, and marine

18 mammals. As part of the Gulf of Alaska Integrated Ecosystem Research Program, an acoustic-trawl

19 survey was conducted in the summers and falls of 2011 and 2013 to quantify variability in species

20 composition, density, and distributions of forage fish over the continental shelf and slope in the central

21 and eastern regions of the GOA. The forage fish community in 2011 was characterized by the absence

22 of age-0 pollock and lower densities of capelin, herring, and mesopelagics compared to observations in

23 2013. Age-0 pollock were abundant across both regions in summer 2013, but were rarely observed in

24 fall. In contrast, summer observations of herring were rare, while aggregations of herring were

25 observed over the eastern GOA shelf in fall of both years. Seasonal changes in community composition

26 are attributed to the transport of age-0 pollock from offshore waters in summer to nearshore waters in

27 fall, and to immigration of herring to the eastern GOA shelf in fall. Forage fish spatial patterns varied

28 within and between regions due to intra- and interspecific differences in horizontal and vertical

29 distributions that were correlated with bottom depth. Observed spatial and temporal variability in

30 community composition and distributions of forage fish species may potentially impact predator

31 foraging in the GOA, as well as the effectiveness of monitoring to detect changes in forage fish biomass.

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33 Key Words: Capelin, distribution, forage fish, Gulf of Alaska, mesopelagic, Pacific herring, walleye

34 pollock, wavelets

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36 **1. INTRODUCTION**

37 In pelagic marine ecosystems, planktivorous fish occupy an intermediate trophic position where they

38 function as both predator and prey, facilitating the transfer of energy from primary consumers to

39 piscivores. Collectively referred to as forage fish, these include small, schooling pelagic fish, early life

40 stages of piscivorous fish, and mesopelagic fish species (Springer and Speckman, 1997). Throughout the

41 Northeast Pacific, the forage fish community is comprised of small pelagic species such as capelin

42 (*Mallotus villosus*) and Pacific herring (*Clupea pallasii*, hereafter herring), juvenile groundfish such as

43 walleye pollock (*Gadus chalcogrammus*, hereafter pollock) and Pacific cod (*Gadus macrocephalus*),

44 juvenile salmonids, and mesopelagic fish (*e.g.* myctophids) species (Mecklenburg et al., 2002; Springer

45 and Speckman, 1997). Forage fish serve as key prey for many seabirds, marine mammals, and

46 commercially important fish species (Dragoo et al., 2012; Womble and Sigler, 2006; Yang et al., 2005).

47 As predators, forage fish can regulate the biomass (Freon et al., 2005; Gjøsæter et al., 2002; Micheli,

48 1999) and species composition (Cury et al., 2000; Frank et al., 2011) of their zooplankton prey, and may

49 potentially influence recruitment of their predators by consuming fish eggs and larvae (Fauchald, 2010;

50 Kornilovs et al., 2001).

51

52 Forage fish are temporally and spatially variable in their abundance and distribution, arising from

53 differences in life histories among species. Fluctuations in the abundance of small pelagic species

54 primarily result from high recruitment variability and relatively short life spans (Freon et al., 2005).

55 Spawning stocks comprised of only 1 or 2 age classes cannot withstand multiple years of poor

56 recruitment (Freon et al., 2005; Pikitch et al., 2012; Springer and Speckman, 1997), making populations

57 of short-lived species more susceptible to large variations in abundance compared to those of longer-

58 lived species. Reduced abundance may result in contracted distributions (Hay et al., 2001; Ingvaldsen

59 and Gjøsæter, 2013; MacCall, 1990); while strong recruitment can rapidly increase abundance and/or

60   expand distributions (*e.g.* Bertrand et al., 2004; Chavez et al., 2003; Schwartzlose et al., 1999). In high

61   latitude ecosystems, abrupt changes in abundance and/or distribution have been observed in

62   populations of small pelagic species including capelin (Anderson and Piatt, 1999; Carscadden et al.,

63   2013a, 2013b) and herring (*Clupea* spp.) (Hay et al., 2001). Abundance of juvenile stages of longer-lived,

64   demersal fish species are also variable (*e.g.* Duffy-Anderson et al., 2015); with juvenile abundances

65   influenced by environmental conditions, rather than age structures and biomass of spawning stocks

66   (Szuwalski et al., 2015).

67

68   Independent of abundance, distributions of forage fish may also be influenced by environmental

69   processes that operate across a range of spatial and temporal scales (Freon et al., 2005; Hunt et al.,

70   1999; Ingvaldsen and Gjøsæter, 2013).   The distribution, intensity, and duration of oceanographic

71   gradients varies over scales ranging from 100s of m to 100s of km and hours to months (*e.g.* Stabeno et

72   al., 2004; Cheng et al., 2012; Ladd and Cheng, 2015). This environmental variability changes the

73   availability of preferred habitat and/or prey, which can influence forage fish distributions (*e.g.* Arimitsu

74   et al., 2008; Obradovich et al., 2014; Speckman et al., 2005). Vertical structure in the water column can

75   also influence forage fish distributions by limiting habitat (Bertrand et al., 2010; Sogard and Olla, 1998),

76   concentrating prey (Hunt et al., 1999; Grados et al., 2012), or providing refuge from predators (Hrabik et

77   al., 2006). Predators can directly influence forage fish distributions (*e.g.* a "halo" of local prey depletion,

78   Ashmole, 1963; Lewis et al., 2001), or indirectly by causing anti-predator behavioral responses, such as

79   shifts in vertical position (*e.g.* Hrabik et al., 2006; Mowbray, 2002; Scheuerell and Schindler, 2003).

80

81   From a resource management perspective, spatial and temporal variability in the species composition,

82   abundance and distribution of forage fish is potentially relevant when assessing the availability of food

83   to managed piscivorous species and the design of monitoring efforts. Variability in the availability of

84   forage fish as prey may impact predator growth, fitness, and/or reproductive success (*e.g.* Cury et al.,

85   2011; Gjøsæter et al., 2009; Robinson et al., 2015).   The magnitude of any impact will depend on the

86   predator's foraging behavior (*e.g.* Benoit-Bird et al., 2013; Fauchald, 2009), spatial constraints (*e.g.*

87   mobile versus central place forager, Orians and Pearson, 1979), and energetic requirements (*e.g.*

88   breeding versus non-breeding life stage). Similarly, variability in the species composition and

89   distribution of forage fish may restrict their availability to population abundance estimate surveys. The

90   precision and accuracy of survey abundance estimates will depend on the survey's timing, sample

91   resolution and extent, and gear selection.

92

93   To support an ecosystem-based approach to fisheries management in the Gulf of Alaska (GOA),

94   characterization of spatial and temporal variability in forage fish distributions is needed to improve our

95   understanding of how changes in forage fish biomass and availability potentially impact predators

96   (Livingston et al., 2005). Despite their ecological importance, information on the distribution and

97   community structure of forage fish over the GOA continental shelf and slope is limited (Ormseth, 2014).

98   Resource assessment surveys conducted in U.S. Federal waters of the GOA are designed to estimate the

99   population abundance of commercially important demersal species. These surveys are not designed to

100   sample small pelagic (*e.g.* capelin, herring) and age-0 groundfish (*e.g.* pollock, Pacific cod) species

101   (Ormseth, 2014), yet are often the only data series available for the description of community

102   composition, distribution, and abundance of forage fish in the GOA.

103

104   As part of the Gulf of Alaska Integrated Ecosystem Research Program (GOAIERP -

105   http://www.nprb.org/gulf-of-alaska-project), this study conducted an acoustic-trawl survey in the

106   summers and falls of 2011 and 2013 to quantify horizontal and vertical distributions of forage fish over

107   the GOA shelf and slope. The GOAIERP was an inter-disciplinary effort to investigate how physical and

108   biological processes in the GOA marine ecosystem determine the survival of five commercially and

109   ecologically important demersal species during their first year of life. Our contribution was to

110   characterize spatial and temporal variability in species composition and distributions of forage fish, and

111   to infer potential effects on forage fish predators and distribution/abundance survey efforts.

112

113

114   **2. METHODS**

115   **2.1 Survey Design**

116   The GOAIERP was designed to compare patterns in the central and eastern regions of the GOA during

117   multiple seasons and years (Fig. 1). The central GOA (CGOA) region extended from the southeast side of

118   Kodiak Island to the mouth of Amatuli Trough. The eastern GOA (EGOA) region extended from Cross

119   Sound to Cape Ommaney (southern tip of Baranof Island). Acoustic-trawl surveys were conducted in

120   each region during the summers (July-August) and falls (September-October) of 2011 and 2013 (Table

121   1). Acoustic measurements and midwater trawls sampled along parallel transects orthogonal to the

122   coast that extended from coastal (< 50 m bottom depth) to basin waters beyond the 2000 m isobath

123   (Fig. 1). Each region's sampling grid included fixed stations spaced equidistant along transects. In the

124   CGOA, 53 stations spaced at 37.0 km (20 nmi) intervals were sampled along 10 transects (4 to 6 stations

125   per transect depending on width of the shelf). In the EGOA, the sampling grid in 2011 was composed of

126   52 stations spaced 18.5 km (10 nmi) apart along 13 transects (4 stations each). In 2013, the EGOA

127   sampling grid was increased to 72 stations along 8 transects (9 stations each), which expanded the

128   spatial extent to approximately 150 km offshore. All EGOA stations remained spaced at 18.5 km along

129   each transect, while spacing between the 5 southernmost transects (A to K) increased to 37.0 km.

130

131   **2.2 Data Collection**

132   Acoustic data were collected during seasonal surveys in 2011 and 2013 from the F/V *Northwest Explorer*

133   and the NOAA Ship *Oscar Dyson* (Table 1). Simrad ES60 echosounders (Kongsberg Maritime) with hull-

134   mounted, split-beam transducers (38 and 120 kHz, 7° beamwidths measured at half-power points) were

135   used on the *Northwest Explorer*. Acoustic data were collected on the *Oscar Dyson* using Simrad EK60

136   echosounders and centerboard-mounted, split-beam transducers (38 and 120 kHz, 7° beamwidths).

137   Data were continuously collected during daytime hours (sunrise to sunset) along each transect at a

138   speed of approximately 5 m/s (10 knots) on the *Northwest Explorer* and 6.2 m/s (12 knots) on the *Oscar*

139   *Dyson*. Prior to the start of summer surveys, all echosounders were calibrated using a 38.1 mm tungsten

140   carbide sphere following Foote et al. (1987).

141

142   Fish were sampled using a 198 m midwater rope trawl (Cantrawl model 400, Cantrawl Nets Ltd) with a

143   1.2 mm mesh codend liner. Trawls were towed at 1.6 ± 0.26 m/s (mean ± SE). Surface trawls (with

144   additional floats attached to the headrope) were conducted at each station (Fig. 1). Midwater trawls

145   were conducted opportunistically to identify acoustic targets at headrope depths ranging from 10 to 250

146   m. Gear and time limitations precluded the trawl from being fished at depths exceeding 250 m. To

147   monitor headrope depth and measure the net opening during trawling, a Simrad FS900 trawl sonar was

148   used on the *Northwest Explorer* and a Simrad FS70 trawl sonar was used on the *Oscar Dyson*. The net

149   opening vertical height averaged 34.7 ± 4.3 m during surface trawls and 16.9 ± 2.4 m during midwater

150   trawls. The horizontal spread of the net averaged 39.5 ± 2.8 m during surface trawls and 62.6 ± 8 m

151   during midwater trawls. Surface trawls were fished for 30 minutes once the trawl sonar confirmed the

152   net was fully opened. Midwater trawl fishing times averaged 20 minutes (range 4 to 35 minutes) based

153   on acoustic densities observed on the echosounder and trawl sonar displays. Trawl catches were sorted

154   by species. For each species or age-group (*i.e.* juvenile or adult), length and weight were individually

155   measured for up to 50 fish, and an additional subsample of up to 200 fish were counted and bulk

156 weighed to estimate the total number of fish in larger catches. Pollock less than 130 mm standard

157 length were classified as age-0 (Brodeur and Wilson, 1996a).

158

159 **2.3 Acoustic Data Processing and Classification**

160 The 38 kHz data were analyzed for the 2011 survey, and 38 and 120 kHz data were used for analysis of

161 the 2013 survey. ES60 data were corrected to remove the triangle-wave error following Keith et al.

162 (2005). All other acoustic data processing was completed using Echoview v5.4 (Echoview Software Pty

163 Ltd). A surface exclusion line was set at 10 m on the *Northwest Explorer* and 15 m on the *Oscar Dyson* to

164 account for transducer depth (4.9 and 9.1 m), and to exclude data within twice the near-field of the 38

165 kHz transducer (Simmonds and MacLennan, 2005). The seafloor was detected in the 38 kHz data,

166 followed by visual inspection and manual correction. A bottom exclusion line was set 1 m above the

167 corrected seafloor to exclude the acoustic deadzone (Ona and Mitson, 1996). Only data between the

168 surface and bottom exclusion lines were analyzed. 38 kHz data were analyzed to a maximum depth of

169 500 m, and the 120 kHz data to a maximum depth of 250 m. All acoustic data were visually inspected to

170 exclude electrical noise spikes or ping dropouts (*i.e.* transmissions in which a bottom echo was not

171 received at the transducer). Excluded data were removed/not included in estimates of integrated

172 backscatter. Ambient and vessel-generated noise were removed based on methods described by De

173 Robertis and Higginbottom (2007). For each frequency, linear measurements of volume backscatter (s_v,

174 m^{-1}) (MacLennan et al., 2002) were averaged in 20 pings (horizontal) by 10 m (vertical) cells and

175 converted to logarithmic units (i.e. mean volume backscattering strength (MVBS) dB re 1 m^{-1}, hereafter

176 dB). A -110 dB maximum noise threshold and a minimum signal-to-noise ratio filter of 10 dB were

177 applied to each analytic cell.

178

179   Acoustic backscatter data were classified using ten single or mixed species categories (Table 2) to a

180   maximum depth of 250 m with the exception of the mesopelagic layer and unknown categories, which

181   were classified to 500 m. Data classification followed a multistep procedure (Fig. 2) that discriminated

182   macrozooplankton from fish, identified surface and mesopelagic layers, and then created analysis

183   regions for single or multispecies fish aggregations by matching observed backscatter patterns to

184   species compositions sampled from trawl catches (details for each category follow).

185

186   *Discriminating macrozooplankton from fish*

187   Classification of acoustic data was consistent between the 2011 and 2013 surveys, with the exception of

188   macrozooplankton. Addition of the 120 kHz frequency to the 2013 survey facilitated discrimination of

189   macrozooplankton from fish using differences in MVBS (Kang et al., 2002) between 120 and 38 kHz data

190   (ΔMVBS $_{(120\text{-}38)}$, measured in the logarithmic domain). Backscatter measurements within the upper 250

191   m of the water column were averaged into 20 ping horizontal by 3 m vertical cells for each frequency.

192   Cells with ΔMVBS $_{(120\text{-}38)}$ values greater than 8.6 dB were classified as macrozooplankton, and all

193   remaining cells were classified as "fish" (Fig. 2). The ΔMVBS $_{(120\text{-}38)}$ 8.6 dB value is 1 standard deviation

194   greater than the ΔMVBS $_{(120\text{-}38)}$ for eulachon (*Thaleichthys pacificus*, 5.8 ± 2.8 dB), the highest difference

195   value among common North Pacific fish species observed by De Robertis et al. (2010). Among

196   macrozooplankton, the ΔMVBS $_{(120\text{-}38)}$ 8.6 dB value is less than that observed for copepods (*Neocalanus*

197   spp., Murase et al., 2009) and euphausiids (*Euphausia pacifica*, Kang et al., 2002; McKelvey and Wilson,

198   2006; Murase et al., 2009; and *Thysanoessa* spp., De Robertis et al., 2010) in the North Pacific, which

199   have ΔMVBS $_{(120\text{-}38)}$ values greater than 10 dB. The 120 kHz data were used to assign backscatter values

200   to macrozooplankton cells, while "fish" cells were assigned a -999 dB value which is equivalent to 0 in

201   the linear domain. A -80 dB data threshold was applied to the 120 kHz data prior to export of the

202   macrozooplankton category (cf. Ressler et al., 2012).

203

204 *Layer detection*

205 The 38 kHz data were used to classify the 20 ping x 3 m "fish" cells to all other backscatter categories

206 (Fig. 2). To classify "fish" cells, 20 ping x 3 m cells were re-assigned 38 kHz backscatter values at the

207 original measurement resolution of 1 ping (horizontal) by 0.187 m (vertical). Macrozooplankton cells

208 were assigned a -999 dB value (*i.e.* 0 in the linear domain). Acoustic backscatter associated with surface

209 and mesopelagic layers within the water column were identified using the "schools detection" SHAPES

210 algorithm in Echoview (Barange, 1994; Coetzee, 2000). Detection parameter values included: 300 m

211 minimum total length and maximum horizontal linking distance; 10 m minimum candidate length; and 5

212 m minimum total school height, minimum candidate height, and maximum vertical linking distance. To

213 detect schools as continuous layers, a -90 dB data threshold was applied to backscatter within the upper

214 50 m (classified as surface layer) and a -80 dB threshold was applied to backscatter between a depth

215 range of 150 to 500 m (mesopelagic layer). When a continuous layer extended beyond these depth

216 boundaries, the school detection depth range was extended to include the layer. Backscatter located

217 between 250 to 500 m and not associated with a layer (*e.g.* dense aggregations at shelf breaks) were

218 classified as unknown due to a lack of midwater trawl samples below 250 m. A -75 dB threshold was

219 applied to the surface and mesopelagic categories prior to export to include weak scatterers associated

220 with each group, such as jellyfish in the surface layer (De Robertis and Taylor, 2014) and mesopelagic

221 fish lacking gas-filled swimbladders (Davison, 2011). Surface and mesopelagic layers were then removed

222 (*i.e.* masked) from 38 kHz data by reassigning backscatter in classified cells a -999 dB value (*i.e.* 0 in the

223 linear domain).

224

225 *Discriminating aggregations*

226   All remaining backscatter was classified using trawl samples associated with homogenous echogram

227   patterns (Fig. 2). Backscatter observed during trawls in which one classification category accounted for

228   at least 90% of the catch (by number; Table 3) was treated as a characteristic echogram pattern for

229   subsequent visual classification of that category. Distinguishing characteristics for echogram patterns

230   associated with a particular category included, but were not limited to: aggregation shape, acoustic

231   density, vertical position, bottom depth, and proximity to other characteristic patterns. A -67 dB data

232   threshold was applied to exclude weak scatterers (*e.g.* jellyfish and macrozooplankton) from fish

233   backscatter (De Robertis and Taylor, 2014; Parker-Stetter et al., 2013). Analysis regions were created

234   and classified to single species categories (capelin and herring) when similar echogram patterns were

235   observed in the acoustic data. Echogram patterns associated with trawl samples comprised of multiple

236   forage fish species or overlapping patterns of two or more categories were classified as mixed categories

237   (*e.g.* forage fish mix, forage fish/piscivore mix). Other backscatter patterns that were not sampled by

238   trawls were classified as unknown. Analysis regions for capelin, herring, forage fish mix, forage fish /

239   piscivores mix, and unknown backscatter were then masked and backscatter in these cells were

240   assigned a -999 dB value prior to proceeding to the final classification step.

241

242   *Depth stratification*

243   Analysis regions for age-0 pollock and piscivores were stratified by depth (Fig. 2). Trawl data for age-0

244   pollock and piscivores during the summer 2013 survey indicated that the two categories were vertically

245   separated above/below 100 m across most of the CGOA and EGOA. An editable line was initially set at

246   100 m depth, and then adjusted in areas where trawl samples indicated a change in vertical distribution

247   (*e.g.* shallow waters inside the 100 m isobath) of age-0 pollock or piscivores. All remaining backscatter

248   between 10 m and the edited 100 m line was classified as age-0 pollock. Backscatter between the

249   edited 100 m line and either a depth of 250 m or the bottom exclusion line, whichever was shallower,

11

250   was classified as piscivores. Although age-0 pollock were infrequently observed in all 2011 and fall 2013

251   surveys, the edited 100 m line was used as the upper boundary for piscivore analysis regions in all

252   surveys. When age-0 pollock were absent, backscatter above the edited 100 m line that was not

253   assigned to other categories was classified as unknown.

254

255   Along-transect estimates of acoustic density (nautical area scattering coefficient, s_A, m^2 nmi^{-2},

256   MacLennan et al., 2002) for each fish classification category (Table 2, Fig. 2) were calculated by

257   integrating backscatter through the water column from the surface exclusion line (*i.e. Northwest*

258   *Explorer* = 10 m; *Oscar Dyson* = 15 m) to 250 m in 200 m horizontal bins. Mesopelagic and unknown

259   backscatter were integrated to a maximum depth of 500 m. At the 200 m horizontal resolution, each

260   bin contained a minimum of 5 pings when the echosounder was operated at the slowest pulse rate of 1

261   ping per 7 seconds.

262

263   **2.4 Identifying Scales of Variability**

264   The choice of horizontal resolution to characterize distributions of age-0 pollock, capelin, herring, and

265   mesopelagic backscatter categories (collectively referred to as forage fish categories) was determined by

266   identifying scales that maximize variability in distributions of acoustic density, s_A. A wavelet analysis was

267   conducted to quantify significant scales of variability along individual transects for each forage fish

268   backscatter category by survey (*e.g.* Grados et al., 2012). Background information describing how

269   wavelet analysis was used is provided as supplementary material (S.1). The frequency of occurrence of

270   significant scales was summed across transects for each forage fish category during all surveys to

271   determine the smallest scale that was most prevalent among all forage fish categories. Acoustic density

272   estimates, s_A, for each forage fish category were then horizontally binned at this resolution and

273   exported using the same data thresholds as the original data exports (section 2.3).

12

274

275   Computation of wavelet functions and significance testing was completed in Matlab v8.1.0.604 (The

276   MathWorks Inc) using an adapted Matlab package provided by C. Torrence and G. Compo

277   (http://paos.colorado.edu/research/wavelets/). Wavelet plots and summary of wavelet outputs were

278   completed in R v3.1.2 (The R Foundation) using the "biwavelet" package (version 0.17.5) provided by T.

279   Gouhier and A. Grinsted (http://github.com/tgouhier/biwavelet).

280

281   **2.5 Forage Fish Distributions**

282   For each forage fish category, changes in acoustic density, s_A, were quantified by region (CGOA/EGOA),

283   season (summer/fall), and year (2011/2013). Acoustic density estimates were binned at the spatial

284   resolution identified by the wavelet analysis (section 2.4, referred to as analysis resolution). A

285   preliminary analysis examined differences in mean density relative to distance from shore and by

286   bottom depth (Supplementary material, S.2), to account for differences in survey design between the

287   GOAIERP stations (systematic, fixed distance from shore) and acoustic measurements (continuous

288   sampling across bathymetric gradients). This analysis indicated that densities for all forage fish

289   categories were strongly correlated with bottom depth, and that comparisons between regions and

290   years that were based on distance from shore were confounded by regional differences in shelf width

291   and the extension of the EGOA grid further offshore in 2013 (Fig. 1).

292

293   Based on the preliminary analysis results (S.2), spatial and temporal changes in forage fish density and

294   vertical distribution were examined relative to bottom depth only where fish were present (*i.e.* $s_A > 0$,

295   referred to as nonzero density) (Bez and Rivoirard, 2001; Woillez et al., 2007). This approach accounts

296   for limitations in survey design, where the frequency of zero density values in a sample is sensitive to

297   changes in the extent of the survey domain (Table 1 and Fig. 1), and acoustic classification (*i.e.*

298   backscatter assigned to the forage fish mix, forage fish/piscivore mix, or unknown categories). To

299   summarize differences in horizontal distribution by bottom depth, nonzero densities of forage fish were

300   averaged between isobaths (bottom depth ranges for isobath groups: < 100 m, 100-199 m, 200-499 m,

301   500-999 m, 1,000-1,999 m, and > 2,000 m). Vertical distributions for each forage fish category were

302   similarly summarized between isobaths. Estimates of s_A for each forage fish category were exported in 1

303   m vertical depth layers. The mean vertical location, or center of mass (CM) in the water column within

304   each acoustic bin, was derived following Urmy et al. (2012) , in which a weighted mean of volumetric

305   density (s_v, m^{-1}) was calculated from all depth layers using Python v2.7 (Python Software Foundation).

306   CM values for each forage fish category were averaged by isobath group to quantify changes in vertical

307   distribution relative to bottom depth.

308

309   Notched boxplots and pairwise comparisons were used to quantify differences in forage fish density and

310   vertical distributions between isobath groups and surveys (Chambers et al., 1983; McGill et al., 1978).

311   Notches that do not overlap are considered significantly different at the 95% confidence level. Multiple

312   two-sample comparisons were conducted within each classification category using the Wilcoxon rank-

313   sum test (Zar, 2010) to measure differences in median nonzero density and CM between isobath groups

314   and surveys. A two-tailed null hypothesis, that each set of medians were equal, was tested at $\alpha = 0.05$

315   significance level. Samples with less than 30 observations were not tested.

316

317

318   **3. RESULTS**

319   **3.1 Sampling**

320   A total of 83 midwater trawls were conducted, with 41 in 2011 and 42 in 2013 (Table 3). Among these

321   samples, 47 trawls (19 in 2011 and 28 in 2013) contained one backscatter category that accounted for at

322   least 90% of the catch (by number) (Table 3). These samples were used as representative echogram

323   patterns for classification of backscatter categories (Table 2). Of the 382 surface trawl samples

324   collected, 16 trawls (4 in 2011 and 12 in 2013) were also used to classify acoustic data (Table 3).

325

326   *Acoustic classification*

327   Total backscatter was 4 to 12 times higher in 2013 than in 2011 in both seasons and regions (Fig. 3A).

328   Classification of acoustic backscatter is summarized for each survey by the proportion of total

329   backscatter assigned to each category from all samples ($s_{A,T}$) and in waters less than 500 m bottom

330   depth ($s_{A,T<500}$) in (Fig. 3B). The surface layer accounted for less than 12 % of total backscatter in all

331   surveys. The mesopelagic layer accounted for the largest proportion of total backscatter in 3 of 4 EGOA

332   surveys (> 66 % $s_{A,T}$, not including fall 2011), and a relatively large fraction of backscatter in the CGOA

333   (range 22 to 34 % $s_{A,T}$, not including fall 2013). Changes in mesopelagic density should be interpreted

334   with caution as observed changes may be biased by species-specific and ontogenetic differences in

335   scattering properties among mesopelagic fish and invertebrates (Davison, 2011; Davison et al., 2015).

336   The piscivores category accounted for a high proportion of total backscatter during all surveys in the

337   CGOA (29 to 40 % $s_{A,T}$) and over the shelf in the EGOA (18 to 56 % $s_{A,T<500}$). Backscatter was only

338   assigned to the age-0 pollock category in summer 2013, accounting for less than 6 % $s_{A,T}$. Backscatter

339   was only assigned to the herring category in both EGOA fall surveys, with discrete aggregations observed

340   in less than 5 % of total samples (*i.e.* 200 m acoustic bins) in 2011 (*n* = 109) and less than 1 % of samples

341   in 2013 (*n* =20). Backscatter was only assigned to the capelin category in the CGOA, accounting for 14 to

342   37 % $s_{A,T<500}$ over the shelf. Backscatter was assigned to the forage fish mix category in the fall 2013

343   EGOA (12 % $s_{A,T<500}$) and both CGOA fall surveys (<1 % and 10 % $s_{A,T<500}$, in 2011 and 2013). The forage

344   fish/piscivores mix category accounted for a small fraction of total backscatter over the shelf among all

345   surveys (< 6 % $s_{A,T<500}$). Backscatter that was classified as unknown varied widely among surveys (1.4 to

346   51% $s_{A,T}$). Distribution maps of acoustic density, s_A, for each backscatter category in 200 m horizontal

347   bins are available in the GOAIERP Middle Trophic Level final report (Ormseth et al. 2016).

348

349   **3.2 Scales of Variability**

350   Significant periods were detected in all forage fish distributions (*i.e.* age-0 pollock, capelin, herring, and

351   mesopelagic backscatter categories), indicating spatial structure across a range of scales (Fig. 4). The

352   occurrence of significant periods at scales less than 4 km (*i.e.* fine) was more frequent among transects

353   and surveys for each species group than the occurrence of significant periods at scales greater than 8 km

354   (*i.e.* coarse). Herring had the fewest (n=5) and narrowest range of significant periods (0.41 to 0.55 km),

355   likely reflecting the limited number of discrete, monospecific schools observed during all surveys.

356   Distributions of age-0 pollock and capelin had similar distinct modes of fine- (pollock = 0.41 to 1.34 km,

357   capelin = 0.41 to 3.54 km) and coarse-scale structure (pollock = 14.17 to 60.76 km, capelin = 8.14 to

358   60.76 km). The bimodal peaks in distribution scales likely corresponded to aggregations of fish schools

359   (fine-scales), and the width of submarine banks in the CGOA and the EGOA shelf (coarse-scales).

360   Significant periods of mesopelagic distribution scales occurred between 0.41 to 11.51 km, which are

361   consistent with observed chord distances of high density shoals within the mesopelagic layer. There

362   was higher spatial and temporal variability in significant periods in mesopelagic distributions, resulting in

363   a broader range of significant periods compared to age-0 pollock and capelin distributions (Fig. 4).

364

365   The significant period most prevalent across transects and surveys for all forage fish categories ranged

366   from 0.44 to 0.55 km (38% of transects with herring were significant at 0.44km; 83% with age-0 pollock

367   and 85% with capelin at 0.51 km; 52% with mesopelagics at 0.55 km). Therefore, a resolution of 0.5 km

368   was selected for analysis of all forage fish distributions.

369

370 **3.3 Forage Fish Distributions**

371 Changes in species composition and distribution of forage fish communities were observed between

372 years, seasons, and regions. In the CGOA (Fig. 5), the forage fish community was primarily comprised of

373 capelin over the shelf and mesopelagics beyond the shelf break in both years. Age-0 pollock were

374 abundant across the shelf in summer 2013, but rarely observed during other CGOA surveys. A low

375 density, mixed aggregation of age-0 pollock and capelin at the northwest end of the 201 and 205

376 transects (Fig. 1) in fall 2011 was the only observed concentration of age-0 pollock verified by trawl

377 samples in 2011. Herring aggregations were not observed in midwater trawl catches in the CGOA.

378 Infrequent, surface trawl catches of small numbers of herring (< 10 fish per trawl) were the only

379 indication of their presence (Moss et al., 2016).

380

381 In the EGOA (Fig. 6), mesopelagics were the only forage fish group consistently present in summer and

382 fall of both years. Age-0 pollock were distributed over shelf, slope, and basin waters in summer 2013,

383 but were rare in the fall and throughout 2011. A small number of age-0 pollock were caught in

384 midwater trawls off nearshore stations on the M transect (Fig. 1), mixed with other forage fish species in

385 fall 2013. Herring aggregations were observed during fall surveys, both in dense monospecific or mixed

386 aggregations with other forage and/or piscivorous fish (*e.g.* adult pollock, rockfish). Herring were

387 primarily distributed over the shelf or within the Yakobi Sea Valley off Cross Sound (Fig. 1). A herring

388 aggregation was also observed over slope waters within the mesopelagic layer. Summer observations of

389 herring were rare in both years, limited to a small number of fish caught in surface trawls over the shelf.

390 Capelin observations were not frequently observed in the EGOA. In summer 2011, capelin occurred in a

391 mixed aggregation along with longfin smelt (*Spirinchus thaleichthys*) and pollock (≥ 305 mm in length)

392 within the Yakobi Sea Valley on the L transect (Fig. 1). In fall 2013, high density aggregations of capelin

393 co-occurred with herring over the shelf northwest of the Yakobi Sea Valley on the M transect. Even

394   though capelin did not occur in midwater or surface trawl catches in summer 2013, capelin were

395   observed in the stomachs of Chinook (*Oncorhynchus tshawytscha*) and coho (*Oncorhynchus kisutch*)

396   salmon collected from the surface trawl at the nearshore station on the M transect (E. Fergusson

397   unpublished data).

398

399   *Horizontal distributions of nonzero fish density relative to bathymetry*

400   In 5 of the 7 surveys, nonzero densities of mesopelagics were positively correlated with bottom depth

401   (Fig.7). With the exception of the EGOA fall 2011 and summer 2013 distributions, mesopelagic nonzero

402   densities were lowest between the 200 and 500 m isobaths, and then increased over deeper water

403   before stabilizing (Wilcoxon rank-sum, α = 0.05 two-tailed, Table S.1). Median nonzero densities of

404   mesopelagics were significantly higher during 2013 within each isobath group (Wilcoxon rank-sum, α =

405   0.05 two-tailed, Table S.2), with peak mesopelagic density observed in fall 2013 over bottom depths

406   greater than 1000 m (median $s_A \geq 1522$ m^2 nmi^{-2}) in the EGOA.

407

408   Nonzero densities of capelin, age-0 pollock, and herring were typically higher over shallow, shelf waters,

409   declining over deeper water beyond the shelf break outside the 500 m isobath (Fig. 7). Over the shelf,

410   median nonzero densities of capelin were significantly higher inside the 100 m isobath in summer of

411   both years (Table S.1), with the peak capelin density (median $s_A = 411$ m^2 nmi^{-2}) occurring in summer

412   2013 (Table S.2). In fall, capelin nonzero density inside the 100 m isobath significantly declined from

413   summer maxima to similar levels in fall of both years. Density increased from summer to fall in 2011

414   within the 100 to 200 m isobaths (W = 2025, $n_{2GOA11, 100-200m}$ = 71, $n_{4GOA11, 100-200m}$ = 89, P < 0.05), to levels

415   higher than those observed in shallower waters (W = 9748, $n_{4GOA11, <100m}$ = 271, $n_{4GOA11, 100-200m}$ = 89, P <

416   0.05). Median nonzero density of age-0 pollock inside the 100 m isobath (median $s_A = 22$ m^2 nmi^{-2}) was

417   also significantly higher compared to all other isobath groups in the CGOA (median $s_A \leq 5.2$ m^2 nmi^{-2},

418   Table S.1). In the EGOA, peak age-0 pollock nonzero densities (median $s_A \geq 33$ m^2 nmi^{-2}) occurred over a

419   broader range of bottom depths inside 500 m (Table S.1). Outside the 100 m isobath, median nonzero

420   densities of age-0 pollock in the EGOA were significantly higher than in the CGOA within each isobath

421   group (Table S.2). No statistical comparisons of median nonzero density of herring across depths or

422   between years were attempted due to small sample sizes ($n < 30$) in 4 of 5 isobath groups (Table S.1).

423

424   *Vertical distributions of fish relative to bathymetry*

425   Significant differences in the center of mass (CM) of capelin and age-0 pollock (Fig. 7) were observed

426   within and between species (Wilcoxon rank-sum, $\alpha = 0.05$ two-tailed, Table S.3 and Table S.4). The

427   median CM of capelin inside the 100 m isobath (median CM = 55 m) was significantly shallower than

428   outside 100 m (median CM ≥ 110 m) in summer 2013, and in both seasons in 2011 (Table S.3). There

429   were no significant differences in capelin CM within isobath groups between years and seasons, with the

430   exception of summer 2013 and fall 2011 within 100 to 200 m ($W = 5979$, $n_{2GOA13} = 173$, $n_{4GOA11} = 89$, $P <$

431   0.05) and inside 100 m in fall 2013 with the other CGOA surveys (Table S.4). Compared to capelin, age-0

432   pollock in the CGOA were consistently located shallower in the water column within all isobath groups

433   (Fig. 7). The median CM of age-0 pollock between the 100 and 200 m isobaths (median CM = 44 m) was

434   significantly deeper compared to both inside the 100 m isobath (median CM = 31 m) ($W = 210,693$,

435    $n_{2GOA13,<100m} = 860$, $n_{2GOA13, 100-200m} = 1016$, $P < 0.05$) and between the 200 and 500 m isobaths (median CM

436   = 33 m) ($W = 251,169$, $n_{2GOA13,100-200m} = 1016$, $n_{2GOA13, 200-500m} = 365$, $P < 0.05$). Outside the 500 m isobath,

437   age-0 pollock CM was more variable compared to observations over the shelf, with a 1st and 3rd quartile

438   depth range of 13 to 93 m (Fig. 7).

439

440   Vertical distributions of age-0 pollock also differed between regions. In the EGOA, the median CM of

441   age-0 pollock was significantly deeper within each isobath group than in the CGOA between the 100 to

442   2000 m isobaths (Table S.4). The vertical position of age-0 pollock in the EGOA was deepest between

443   the 200 to 1000 m isobaths at median CM depths of 73 and 82 m (W = 5700, $n_{1GOA13, 200-500m}$ = 153,

444    $n_{1GOA13,500-1,000m}$ = 82, P = 0.25), and significantly shallower both over the shelf between the 100 and 200

445   m isobaths (median CM = 59 m) (W = 15,267, $n_{1GOA13,100-200m}$ = 332, $n_{1GOA13, 200-500m}$ = 153, $P < 0.05$) and

446   beyond the 1000 and 2000 m isobaths (median CM depth $\leq$ 65 m) (W = 10,571, $n_{1GOA13,500-1,000m}$ = 82,

447    $n_{1GOA13, 1,000-2,000m}$ = 218, $P < 0.05$).

448

449   Vertical distributions of mesopelagics varied seasonally and regionally between a CM interquartile range

450   of 241 to 336 m depth in the CGOA, and 214 to 405 m in the EGOA (Fig. 7). Mesopelagics within the

451   Yakobi Sea Valley were as shallow as 125 m.

452

453   Vertical distributions of herring within the 100 to 200 m isobaths were similar between years (median

454   CM = 111 and 112 m). Although sample sizes were too small for statistical comparison, the median CM

455   decreased from 158 to 172 m between the 200 to 1000 m isobaths in fall 2011. Between the 1000 and

456   2000 m isobaths, discrete herring schools were located at a median CM of 165 m within the mesopelagic

457   layer. The midwater trawl that collected these samples was paired with a surface trawl in which no

458   herring were caught, making it unlikely that herring in the midwater sample were caught near the

459   surface as the net was deployed or recovered.

460

461

462   **4. DISCUSSION**

463   Recognizing that changes in the availability of forage fish as prey may impact predators of commercial

464   and/or ecological importance (Livingston et al., 2005), an ecosystem-based approach in fisheries

465   management requires an understanding of how distributions of forage fish biomass vary in time and

466   space. In this study, we observed variability in species composition and distributions of forage fish in

467   the GOA between years, seasons, and regions. The forage fish community in 2011 was characterized by

468   the absence of age-0 pollock and lower densities of capelin, herring, and mesopelagics, compared to

469   observations in 2013. Age-0 pollock were abundant across both regions in summer 2013, but were

470   rarely observed in fall. In contrast, summer observations of herring were rare, while aggregations of

471   herring were observed over the EGOA shelf in fall of both years. Observed seasonal changes in

472   community composition are attributed to the transport of age-0 pollock from offshore waters in

473   summer to nearshore waters in fall, and to immigration of herring to the EGOA shelf in fall. Forage fish

474   distribution patterns varied within and between regions due to intra- and interspecific differences in

475   horizontal and vertical distributions that were correlated with bottom depth. Observed spatial and

476   temporal variability in the species composition and distributions of forage fish likely resulted in reduced

477   foraging opportunities for predators in 2011 compared to 2013. Differences in forage fish distribution

478   patterns between species may also impact surveys attempting to monitor changes in forage fish

479   abundance and distribution.

480

481   **4.1 Characterization of Forage Fish Community Composition and Distribution Patterns**

482   4.1.1 *Variability between years*

483   Observed differences in forage fish density between 2011 and 2013, including higher densities of capelin

484   in 2013 and the lack of age-0 pollock in 2011, were also detected by other GOA resource assessment

485   surveys. The National Marine Fisheries Service (NMFS) Alaska Fisheries Science Center's (AFSC) GOA

486   bottom trawl survey estimated higher capelin abundance in 2013 compared to 2011, which was the

487   second highest recorded in the survey since 1984 (Ormseth, 2014). Ichthyoplankton surveys conducted

488   in spring of both years as part of the GOAIERP also measured significantly lower abundances of pollock

489   eggs and larvae in 2011 (Siddon et al., 2016). In the AFSC's late summer midwater trawl survey, age-0

490   pollock catch-per-unit-effort (CPUE) in 2013 was the highest observed since 2005, while CPUE in 2011

491   was among the lowest (NPFMC, 2013). A small-mesh demersal survey, conducted by NMFS and the

492   Alaska Department of Fish and Game (ADFG) in nearshore bays around Kodiak and along the Alaska

493   Peninsula coastline in the western GOA, also recorded the highest CPUEs for juvenile pollock (< 20 cm)

494   in 2013 since 1979 (NPFMC, 2014), while CPUE in 2011 was below average (NPFMC, 2012).

495

496   Recent annual stock assessments have shown that the pronounced difference in age-0 pollock

497   abundance in 2011 and 2013 was reduced in subsequent measurements of year class strength. Each

498   cohort was initially sampled as age-1's in winter by the AFSC's Shelikof Strait acoustic-trawl survey, with

499   much fewer age-1 pollock observed from the 2011 cohort in 2012 (95 million fish) compared to age-1's

500   from the 2013 cohort in the 2014 survey (576 million fish) (Dorn et al., 2014). Updates to the

501   assessment model continue to estimate the 2011 cohort as among the smallest year classes observed

502   since the early 1970s (Dorn et al., 2015). In contrast, abundance estimates for the 2013 cohort have

503   been lowered each year and the relative year class strength is average to below average (Dorn et al.,

504   2015). These observations indicate that high age-0 pollock abundance in summer does not necessarily

505   persist to subsequent life stages, as has been previously documented in the eastern Bering Sea (EBS)

506   (Hunt et al., 2011).

507

508   The lack of age-0 pollock in 2011 has been attributed to high mortality experienced between the larval

509   and age-0 stages, likely due to insufficient zooplankton prey (Moss et al., 2016). The spring bloom in

510   2011 was relatively weak, with anomalously low chlorophyll levels (Stabeno et al., 2015). Phytoplankton

511   biomass was much lower in 2011 and was dominated by small-cell picophytoplankton that are less

512   efficient at transferring energy to zooplankton compared to larger-cell diatoms that were more

513   abundant in 2013 (Strom et al., 2015). The weak bloom and low phytoplankton biomass in 2011,

514   combined with a high abundance of salps in spring and summer (Li et al., 2016), are believed to have

515   resulted in lower abundances of small copepods in spring and large copepods in summer 2011 relative

516   to 2013 (Hopcroft et al., 2016). It is unknown what factors led to lower densities of other forage fish

517   species in 2011.

518

519   4.1.2 *Variability between seasons*

520   In 2013, change in age-0 pollock abundance shifted the seasonal composition of the GOA forage fish

521   community. Pollock were distributed across both regions in summer, but were rare in fall and only

522   observed near coastal areas off Cross Sound in the EGOA. The shift in age-0 pollock abundance is

523   consistent with transport from offshore to nearshore waters (Brodeur and Wilson, 1996a; Hinckley et

524   al., 1991; Moss et al., 2016; Parada et al., 2015) in late-summer/early-fall. Presence within coastal

525   embayments could not be verified during fall 2013 (Ormseth et al., 2016). Alternative explanations for

526   the lack of age-0 pollock in fall 2013 include: settlement within the study area (Moss et al., 2016);

527   transport outside the study area (Parada et al., 2015); or high mortality.

528

529   In contrast to the seasonal inshore movement of age-0 pollock, the occurrence of herring over the EGOA

530   shelf in fall of both years suggests herring migrate from inshore waters and embayments in summer

531   (Ormseth et al., 2016) to offshore overwintering grounds. Herring have been extensively monitored

532   within Alaska state waters (< 3 nmi from shore) by ADFG (*e.g.* Hebert, 2014; Hollowell et al., 2015), yet

533   Information on herring distributions over the EGOA shelf is lacking. Previous studies have reported that

534   herring descend to deeper waters in fall once the water column destratifies (Carlson, 1980; Csepp et al.,

535   2011; Sigler and Csepp, 2007). Similarly, herring in the EBS feed over the shelf in summer and

536   overwinter offshore over deeper waters near the Pribilof Islands (Funk, 1990). Some populations of

537   Atlantic herring (*Clupea harengus*) in the western Atlantic, Iceland, and North Sea also migrate to deeper

538   coastal waters or over the shelf to overwinter (Hay et al., 2001). Observations of herring within the

539   mesopelagic layer in fall 2011 trawl samples suggests that they are not limited to the shelf, and opens

540   the possibility that a portion of the population may overwinter over the EGOA slope.

541

542   The presence of dense aggregations of capelin in summer and fall over the CGOA shelf in both years

543   suggests a non-migratory distribution. Since the 1980s, AFSC bottom trawl catches of capelin over the

544   Kodiak shelf have higher CPUEs than other areas of the GOA (Ormseth, 2014), suggesting that capelin

545   may consistently aggregate over the CGOA shelf in summer and fall. The AFSC's GOA pollock acoustic-

546   trawl stock assessment survey (hereafter pollock AT survey) has also estimated capelin abundance in

547   summer 2003, 2005, 2011, and 2013; each year capelin aggregations were similarly concentrated east of

548   Kodiak Island (Guttormsen and Yasenak, 2007; Jones et al., 2015, 2014). The length frequency

549   distribution of capelin caught in this study and the GOA pollock AT survey (Guttormsen and Yasenak,

550   2007; Jones et al., 2015, 2014) indicates that these fish were primarily immature age-1 and age-2 fish

551   (cf. Brown, 2002). If capelin in the Northeast Pacific behave consistently with capelin in the Northwest

552   Atlantic, Iceland, and Barents Sea (Carscadden et al., 2013b), then we hypothesize that the CGOA shelf

553   east of Kodiak island serves as a summer feeding area for immature age-1 and -2 fish. Capelin are

554   predicted to remain offshore over the GOA shelf until they mature at age-2 or -3, and then migrate to

555   coastal waters to spawn near beaches in late spring and early summer (Brown, 2002; Pahlke, 1985).

556

557   4.1.3 *Spatial variability*

558   Forage fish distribution patterns reflect intra- and interspecific differences in spatial distributions within

559   and between regions. In the CGOA, the highest capelin and age-0 pollock densities occurred inside the

560   100 m isobath over Albatross and Portlock Banks. Spatial separation between these species was

561   apparent over each bank; capelin concentrated along bank/trough edges while age-0 pollock were more

562   widely distributed from the edges to the shallower tops of both banks. Aggregations of capelin located

563   along edges of Albatross and Portlock Banks were also observed during the pollock AT survey in summer

564   2003 and 2013 (Guttormsen and Yasenak, 2007; Jones et al., 2014). Vertical separation between capelin

565   and age-0 pollock was common over both banks and troughs, with capelin consistently deeper.

566   Variability in the distribution of capelin and age-0 pollock in this and other studies suggests that both

567   species are sensitive to changes in the environment. Spatial separation between these species may be

568   indicative of interspecific differences in habitat preferences, prey resource utilization, and/or predator

569   avoidance (e.g. Logerwell et al., 2010; Wilson et al., 2006). Changes in distributions of capelin and age-0

570   pollock over the Kodiak shelf and in the western GOA have been attributed to oceanographic conditions

571   and the location of water masses (Hollowed et al., 2007; Logerwell et al., 2007), areas of relatively weak

572   currents (Wilson, 2009), and the composition and distribution of zooplankton prey (Logerwell et al.,

573   2010; Wilson et al., 2006). Although capelin and age-0 pollock have been hypothesized to potentially

574   compete for shared prey resources (Logerwell et al., 2010; Wilson et al., 2006), vertical distributions of

575   capelin in summer were not different in 2011 when pollock were absent, compared to 2013 when

576   pollock were abundant.

577

578   Even though capelin were the dominant forage fish species over the CGOA shelf in summer and fall of

579   both years, observations of capelin in the EGOA were rare and only occurred in summer 2011 and fall

580   2013. The limited observations of capelin in the EGOA are potentially due to bathymetric and

581   oceanographic differences between the two regions. The narrow EGOA shelf is much deeper than the

582   shallow banks and troughs that penetrate the broad CGOA shelf where capelin densities were highest.

583   Aggregations of capelin were observed within the Yakobi Sea Valley in summer 2011 and over the

584   relatively shallow shelf, northwest of Cross Sound in fall 2013. This area receives mixed, nutrient-rich

585   waters from Cross Sound (Stabeno et al., 2015). North of Cross Sound, capelin distributions within

586   Glacier Bay have been associated with areas near tidewater glaciers that are relatively cooler, more

587   turbid, have higher dissolved oxygen, and lower chlorophyll concentrations (Arimitsu et al., 2008). The

588   frequent occurrence of capelin in diets of rhinoceros auklets (*Cerorhinca monocerata*) sampled at St.

589   Lazaria Island in 2011 and 2013 (Slater and Fety, 2015) suggests that capelin were present in the region,

590   but likely distributed inshore or to the north of the study area.

591

592   Compared to distribution patterns in the CGOA, age-0 pollock in the EGOA were concentrated in higher

593   densities closer to shore near the shelf break or within the Yakobi Sea Valley. The vertical distribution of

594   age-0 pollock in the EGOA was significantly deeper than in the CGOA out to the 1000 m isobath,

595   occupying maximum depths of 125 m. This maximum depth falls within the depth range reported for

596   age-0 pollock in summer and fall in the Northeast Pacific (Bailey, 1989; Brodeur and Wilson, 1996b;

597   Parker-Stetter et al., 2015). Variability in vertical distributions of age-0 pollock were associated with

598   bottom depth in this study, often occurring over relatively short horizontal distances due to strong

599   bathymetric gradients in both regions. Variability in vertical position may serve an important role in

600   transport of age-0 pollock over 100s of km to nearshore nursery areas (Smart et al., 2013). The

601   horizontal movement of fish located above the pycnocline would be more susceptible to wind-forced

602   circulation, while subsurface currents would have a greater impact on the trajectory of fish occupying

603   deeper waters (Duffy-Anderson et al., 2015).

604

605   Mesopelagics in the EGOA were also distributed relatively close to shore compared to distributions in

606   the CGOA, and occasionally at relatively shallow depths of 125 m within the Yakobi Sea Valley. Catches

607   of myctophids in the AFSC bottom trawl survey have also typically occurred off the Yakobi Sea Valley,

608   near the southern tip of Baranof Island, and near the shelf break off Kayak Island and Yakutat (Ormseth,

609   2014). The relatively close proximity (< 20 km) of mesopelagics to the EGOA coast and shallow vertical

610 distribution within the Yakobi Sea Valley may provide an important energy source to coastal piscivores

611 (*e.g.* Robards et al., 2003; Slater and Fety, 2015) given the high energy density and lipid content of

612 mesopelagic species (Van Pelt et al., 1997; Vollenweider et al., 2011).

613

614 **4.2 Potential Impact of Forage Fish Variability on Predators**

615 The absence of age-0 pollock and lower acoustic densities of all other forage fish species in 2011

616 suggests that foraging opportunities for piscivorous predators in the GOA were less favorable compared

617 to 2013. The anomalously weak spring bloom, observed differences in phytoplankton community

618 composition (Stabeno et al., 2015; Strom et al., 2015), and lower mesozooplankton biomass (Hopcroft et

619 al., 2016) suggest that poor foraging conditions persisted from spring through fall in 2011. Prey

620 compositions estimated from tufted puffin (*Fratercula cirrhata*) and common murre (*Uria aalge*) bill-

621 loads at East Amatuli Island during summer breeding season surveys in 2011 differed from those in 1995

622 to 2014 (Kettle et al., 2015). Capelin were present as prey items in all years, while gadids were absent

623 from seabird diets in 3 (puffin) and 5 (murre) of the years, including 2011 for both species (Kettle et al.,

624 2015). Seabird recruitment failures were observed across the GOA in 2011 (NPFMC, 2012). In contrast

625 to 2011, higher forage fish densities, and high summer abundance of age-0 pollock observed in this and

626 other surveys, likely increased predator foraging opportunities in 2013. At East Amatuli Island, age-0

627 pollock were the dominant prey item in puffin chick diets in 2013, accounting for 72% of the total

628 number of sampled prey items (Kettle et al., 2015). The diet shift coincided with higher mean growth in

629 puffin chicks, with daily mass gain increasing from 4.7 g d^{-1} in 2011 to 9.6 g d^{-1} in 2013 (Kettle et al.,

630 2015). Across the western GOA, seabird production was categorized as good or above average for most

631 monitored species in 2013 (NPFMC, 2014).

632

633 In 2011, foraging predators may have required greater energy expenditures to locate and capture prey

634 compared to 2013. Densities of capelin, herring, and mesopelagics were all significantly lower in 2011

635 compared to 2013, potentially affecting the foraging success of predators that are sensitive to local prey

636 density (*e.g.* Benoit-Bird et al., 2013). Piatt et al. (2007) demonstrated that the allocation of time spent

637 foraging and incubating chicks by common murres, and the breeding success of black-legged kittiwakes

638 (*Rissa tridactyla*) exhibited strong non-linear relationships with prey density. In addition, age-0 pollock

639 were observed at shallower depths than most other forage fish species in summer 2013, with juvenile

640 salmon in the surface layer being the one notable exception. When age-0 pollock were absent, diving

641 and epipelagic predators would have to dive deeper to forage during daytime. Vertical shifts of prey to

642 greater depths reduces potential encounter rates with prey as reaction distances of visual foragers

643 decreases under low light (Vogel and Beauchamp, 1999). Diving and epipelagic predators are further

644 constrained by the vertical distribution of prey due to the physiological costs of diving and the limited

645 time available to search for prey per dive when swimming to greater depths (Acevedo-Gutiérrez et al.,

646 2002; Wilson et al., 1992). Higher energy density and lipid content among capelin, herring, and

647 myctophids compared to age-0 pollock (Vollenweider et al., 2011) would potentially offset some of

648 these increased foraging costs. Yet, widespread recruitment failures among seabirds across the GOA in

649 2011 indicate that the prey supply was likely insufficient (NPFMC, 2012).

650

651 **4.3 Study Limitations**

652 This study's characterization of forage fish distributions in the two regions is potentially limited by the

653 absence of other known forage fish species in the GOA, classification of acoustic data to species, and the

654 loss of data due to logistic constraints. Juvenile salmon were not included in the analysis of GOA forage

655 fish. Juvenile salmon are primarily distributed in the upper 50 m of the water column (Orsi and

656 Wertheimer, 1995), often concentrating within 15 m of the surface (Beamish et al., 2000; Emmett et al.,

657   2004; Farley et al., 2005). The shallow vertical distribution of juvenile salmon, and co-occurrence with

658   adult salmon and other epipelagic fish and invertebrate species, prevented acoustic estimates of salmon

659   to species and/or length classes in this study. This group of species was assigned to the surface

660   category. Juvenile salmon distribution patterns based on GOAIERP surface trawl data are described by

661   Moss et al. (2016).

662

663   This study's description of GOA forage fish is also potentially limited by infrequent observations of

664   eulachon and the absence of Pacific sand lance (*Ammodytes hexapterus*) in trawl samples. But the lack

665   of observations for either species in this study is not attributed to selectivity of the Cantrawl net. In fall

666   2013, small numbers of eulachon (8 to 24 fish per trawl) were caught in 3 midwater samples. Sand lance

667   has also comprised 2% of non-salmonid catches (approximately 11,400 sand lance) during a fall 2002

668   survey (Farley et al., 2005) that sampled the EBS using the same Cantrawl net. Although known to

669   burrow in the bottom (Meyer et al., 1979), sand lance are primarily distributed in the water column

670   during daytime (Hobson, 1986), making them accessible to both the Cantrawl net and acoustic sampling

671   (*e.g.* Ostrand et al., 2005).

672

673   The lack of eulachon and sand lance observations in this study is attributed to the extent of the survey

674   domain. From 2007 to 2013, AFSC bottom trawl survey catches of eulachon were concentrated to the

675   west of the CGOA study area within the Shelikof Sea Valley, within Amatuli Trough (partially covered by

676   the CGOA grid), and inside Sitka Sound (Ormseth, 2014). Sand lance typically occur in shallow, coastal

677   and intertidal waters (Blackburn and Anderson, 1997; Haynes et al., 2008; Johnson et al., 2008). In

678   Prince William Sound, sand lance were caught close to shore in less than 40 m bottom depth, and were

679   not observed over depths greater than 60 m (Ostrand et al., 2005). Shallow waters (< 50 m) were rarely

680   sampled in this study, suggesting that sand lance likely occurred inshore of the survey domain.

681   Offshore, AFSC bottom trawl survey catches of sand lance have historically occurred over Albatross

682   Bank, but sand lance were mostly absent from bottom trawl catches in 2007 to 2013 (Ormseth, 2014).

683

684   Analysis of the acoustic data was further constrained by the ability to classify observed backscatter to

685   species. The proportion of acoustic backscatter categorized as mixed species and/or unclassified varied

686   between surveys due to uncertainty in net selectivity and the lack of trawl samples. Mixed species

687   catches were not used to apportion backscatter by percent composition due to an inability to correct for

688   net selectivity (*e.g.* Williams et al., 2011). Logistic constraints associated with equipment failures, poor

689   weather, and decreased sampling time on shorter days in fall also reduced the number of trawl samples

690   used to verify observed echogram patterns. As a result, a higher proportion of backscatter in some

691   surveys was classified as unknown, limiting interpretation of observed changes in forage fish

692   distributions.

693

694   The U.S. government shutdown in 2013 resulted in the loss of 10 survey days in the fall CGOA survey,

695   limiting sampling effort to only the southern portion of the survey grid over the shelf. Only two

696   midwater and 10 surface trawls were conducted and 248 km of transect sampled, compared to at least

697   10 midwater and 37 surface trawls and 933 km sampled in the other CGOA surveys. Reduced survey

698   effort increased the proportion of backscatter assigned to the forage fish mix, forage fish/piscivores mix,

699   and unknown backscatter (10, 6, and 29 % $s_{A,T}$) categories compared to other surveys. No samples were

700   collected over waters deeper than 500 m, preventing any meaningful coverage of mesopelagics. Limited

701   coverage and relatively poor resolution of the acoustic data prevented most spatial or temporal

702   comparisons with other GOAIERP surveys for all forage fish species.

703

704   **4.4 Implications for Survey Design for Forage Fish**

705   Observed variability in forage fish distributions highlight timing, sample resolution and extent, and gear

706   selection factors that should be considered in future monitoring of the GOA forage fish community.

707   Design choices will differ if surveys target individual species, and compromises are required if the goal is

708   to survey all forage fish species in the GOA.

709

710   The optimal time to monitor interannual differences in the distribution and abundance of forage fish is

711   July and August. Age-0 pollock are widely distributed across the shelf and slope in summer where they

712   overlap with capelin and mesopelagics. A summer survey would also coincide with groundfish

713   assessment surveys (*i.e.* pollock AT survey, bottom trawl survey, and AFSC bottom-longline survey) and

714   breeding season surveys of seabirds (Dragoo et al., 2015) and pinnipeds (Womble et al., 2009; Womble

715   and Sigler, 2006). Stomach and bill-load samples are typically collected during these surveys, which are

716   used to characterize foraging habits and energy intake of predators (*e.g.* Kettle et al., 2015; Yang et al.,

717   2005). Temporal overlap of a dedicated forage fish survey with these long-running surveys would

718   quantify changes in the forage base with predator abundances, distributions, growth, prey selection,

719   and reproductive success. A summer survey would also be consistent with international efforts to

720   survey capelin populations off Iceland and in the Barents Sea when immature age-1 and -2 fish are

721   distributed offshore (Carscadden et al., 2013a).

722

723   Spatial distributions observed in this study can be used to delineate the spatial extent of a forage fish

724   survey. The relative stability of mesopelagic density within each isobath suggests that it would be

725   inefficient to delineate a survey grid by a fixed distance offshore; a depth-stratified survey design would

726   provide an estimate of relative abundance between major isobaths (*e.g.* 100, 200, 500, 1000 m).

727   Similarly, even though age-0 pollock were observed in low densities over the EGOA basin, all

728   aggregations were located within the 200 m isobath in the CGOA and most were within the 1000 m

729   isobath in the EGOA. Extending a forage fish survey beyond the 2000 m isobath would not be an

730   efficient allocation of resources if the objective of the survey was to produce an index of forage fish

731   abundance over shelf and slope habitats. There were also specific bathymetric locations, such as CGOA

732   banks and the Yakobi Sea Valley, where consistent, high concentrations of forage fish highlighted the

733   importance of identifying specific locations or habitats where fish aggregate to increase accuracy of

734   biomass estimates through increased sampling effort.

735

736   Choice of survey gear and sampling resolution should ensure that forage fish are sampled through their

737   full vertical range at horizontal scales that maximize variability in their distributions. In this study, high

738   variability in the vertical distribution of age-0 pollock and capelin between isobath groups and regions

739   highlights the necessity of sampling the whole water column. Variance in vertically integrated,

740   horizontal distributions was decomposed using wavelets, which identified two modes of significant

741   spatial scales that were attributed to bathymetric features associated with high fish density (coarse-

742   scale) and aggregations of fish schools (fine-scale). To ensure that distribution patterns are detected in

743   discrete grid (*e.g.* GOAIERP stations) or a systematic transect (*e.g.* acoustic survey), samples should be

744   spaced by half the distance of the peak coarse-scale mode (*i.e.* the Nyquist frequency; Spellerberg,

745   1991). For example, the peak coarse-scale for age-0 pollock was approximately 30 km, therefore

746   stations and/or transects would be spaced at a resolution of 15 km or less. In contrast, capelin (peak

747   mode = 46 km) would be sampled by stations/transects no more than 23 km apart. Continuous

748   horizontal sampling (*e.g.* acoustics) would be necessary to sample patchy forage fish distributions that

749   are structured at fine-scales (<1 km). It is acknowledged that acoustic samples are constrained by

750   surface and bottom exclusions, discrimination of species, and determining length composition within

751   mixed aggregations (Simmonds and MacLennan, 2005), but acoustic surveys typically include direct

752   samples such as midwater trawls. Integration of surface and midwater trawls with multifrequency

753   acoustic sampling would ensure that important forage species located near the surface, such as juvenile

754   salmonids and herring, are also sampled.

755

756   A complete forage fish survey should also include species that were not well sampled in this study. The

757   lack of summer observations of herring suggests that herring are unlikely to be well sampled in an

758   offshore summer survey unless the survey area was extended into coastal embayments (Ormseth et al.,

759   2016). To include eulachon, sand lance, and age-0 Pacific cod, the survey domain would need to be

760   expanded or additional sampling methodologies would need to be incorporated to increase the

761   likelihood that these species would be captured. For sand lance, this includes identifying when they

762   occupy pelagic waters and are available to both acoustic and trawl sampling (Freeman et al., 2004;

763   Greenstreet et al., 2006).

764

765   **4.5 Conclusion**

766   An ecosystem approach to fisheries management in the GOA requires accurate estimates of forage fish

767   abundance and distribution to track the forage base utilized by piscivorous fish, seabirds, and marine

768   mammals. Results from this study indicate that spatial and temporal variability observed in the species

769   composition and distribution of forage fish alters their availability to apex predators and monitoring

770   survey sampling gears. We highlight considerations for improving monitoring efforts of biomass in the

771   GOA, recognizing that additional efforts are needed to evaluate how the GOA forage fish community will

772   respond to changing climate conditions. Additional effort is needed to quantify the relative importance

773   of physical and biological factors that influence changes in densities and distributions of forage fish

774   observed in GOAIERP surveys.

775

776

794 **5. REFERENCES**

795 Acevedo-Gutiérrez, A., Croll, D.A., Tershy, B.R., 2002. High feeding costs limit dive time in the largest

796   whales. J. Exp. Biol. 205, 1747–1753.

797 Anderson, P.J., Piatt, J.F., 1999. Community reorganization in the Gulf of Alaska following ocean climate

798   regime shift. Mar. Ecol. Prog. Ser. 189, 117–123.

799 Arimitsu, M.L., Piatt, J.F., Litzow, M.A., Abookire, A.A., Romano, M.D., Robards, M.D., 2008. Distribution

800   and spawning dynamics of capelin (*Mallotus villosus*) in Glacier Bay, Alaska: A cold water

801   refugium. Fish. Oceanogr. 17, 137–146. doi:10.1111/j.1365-2419.2008.00470.x

802 Ashmole, N.P., 1963. The regulation of numbers of tropical oceanic birds. Ibis 103b, 458–473.

803   doi:10.1111/j.1474-919X.1963.tb06766.x

804 Bailey, K.M., 1989. Interaction between the vertical distribution of juvenile walleye pollock *Theragra*

805   *chalcogramma* in the eastern Bering Sea, and cannibalism. Mar. Ecol. Prog. Ser. 53, 205–213.

806 Barange, M., 1994. Acoustic identification, classification and structure of biological patchiness on the

807   edge of the Agulhas Bank and its relation to frontal features. S. Afr. J. Mar. Sci. 14, 333–347.

808   doi:10.2989/025776194784286969

809 Beamish, R.J., McCaughran, D., King, J.R., Sweeting, R.M., McFarlane, G.A., 2000. Estimating the

810   abundance of juvenile coho salmon in the Strait of Georgia by means of surface trawls. N. Am. J.

811   Fish Manage. 20, 369–375. doi:10.1577/1548-8675(2000)020<0369:ETAOJC>2.3.CO;2

812 Benoit-Bird, K.J., Battaile, B.C., Heppell, S.A., Hoover, B., Irons, D., Jones, N., Kuletz, K.J., Nordstrom, C.A.,

813   Paredes, R., Suryan, R.M., Waluk, C.M., Trites, A.W., 2013. Prey patch patterns predict habitat

814   use by top marine predators with diverse foraging strategies. PLoS ONE 8, e53348.

815   doi:10.1371/journal.pone.0053348

816 Bertrand, A., Ballón, M., Chaigneau, A., 2010. Acoustic observation of living organisms reveals the upper

817   limit of the oxygen minimum zone. PLoS ONE 5, e10330. doi:10.1371/journal.pone.0010330

818   Bertrand, A., Segura, M., Gutierrez, M., Vasquez, L., 2004. From small-scale habitat loopholes to decadal

819   cycles: A habitat-based hypothesis explaining fluctuation in pelagic fish populations off Peru.

820   Fish Fish. 5, 296–316. doi:10.1111/j.1467-2679.2004.00165.x

821   Blackburn, J.E., Anderson, P.J., 1997. Pacific sand lance growth, seasonal availability, movements, catch

822   variability, and food in the Kodiak-Cook Inlet area of Alaska (No. AK-SG-97-01), Forage Fishes in

823   Marine Ecosystems. Alaska Sea Grant College Program, Fairbanks, Alaska, USA.

824   Bradshaw, G.A., Spies, T.A., 1992. Characterizing canopy gap structure in forests using wavelet analysis.

825   J. Ecol. 80, 205–215. doi:10.2307/2261007

826   Brodeur, R.D., Wilson, M.T., 1996a. A review of the distribution, ecology and population dynamics of

827   age-0 walleye pollock in the Gulf of Alaska. Fish. Oceanogr. 5, 148–166. doi:10.1111/j.1365-

828   2419.1996.tb00089.x

829   Brodeur, R.D., Wilson, M.T., 1996b. Mesoscale acoustic patterns of juvenile walleye pollock (*Theragra*

830   *chalcogramma*) in the western Gulf of Alaska. Can. J. Fish. Aquat. Sci. 53, 1951–1963.

831   doi:10.1139/cjfas-53-9-1951

832   Brown, E.D., 2002. Life history, distribution, and size structure of Pacific capelin in Prince William Sound

833   and the northern Gulf of Alaska. ICES J. Mar. Sci. 59, 983–996. doi:10.1006/jmsc.2002.1281

834   Carlson, H.R., 1980. Seasonal distribution and environment of Pacific herring near Auke Bay, Lynn Canal,

835   Southeastern Alaska. Trans. Am. Fish. Soc. 109, 71–78. doi:10.1577/1548-

836   8659(1980)109<71:SDAEOP>2.0.CO;2

837   Carscadden, J.E., Gjøsæter, H., Vilhjálmsson, H., 2013a. Recruitment in the Barents Sea, Icelandic, and

838   eastern Newfoundland/Labrador capelin (*Mallotus villosus*) stocks. Prog. Oceanogr., Norway-

839   Canada Comparison of Marine Ecosystems (NORCAN) 114, 84–96.

840   doi:10.1016/j.pocean.2013.05.006

841   Carscadden, J.E., Gjøsæter, H., Vilhjálmsson, H., 2013b. A comparison of recent changes in distribution

842   of capelin (*Mallotus villosus*) in the Barents Sea, around Iceland and in the Northwest Atlantic.

843   Prog. Oceanogr., Norway-Canada Comparison of Marine Ecosystems (NORCAN) 114, 64–83.

844   doi:10.1016/j.pocean.2013.05.005

845   Chambers, J.M., Cleveland, W.S., Kleiner, B., Tukey, P.A., 1983. Graphical Methods for Data Analysis, The

846   Wadsworth Statistics/Probability Series. Wadsworth International Group, Belmont, California.

847   Chavez, F.P., Ryan, J., Lluch-Cota, S.E., Ñiquen C., M., 2003. From anchovies to sardines and back:

848   Multidecadal change in the Pacific Ocean. Science 299, 217–221. doi:10.1126/science.1075880

849   Cheng, W., Hermann, A.J., Coyle, K.O., Dobbins, E.L., Kachel, N.B., Stabeno, P.J., 2012. Macro- and micro-

850   nutrient flux to a highly productive submarine bank in the Gulf of Alaska: A model-based analysis

851   of daily and interannual variability. Prog. Oceanogr. 101, 63–77.

852   doi:10.1016/j.pocean.2012.01.001

853   Coetzee, J., 2000. Use of a shoal analysis and patch estimation system (SHAPES) to characterise sardine

854   schools. Aquat. Living Resour. 13, 1–10. doi:10.1016/S0990-7440(00)00139-X

855   Csepp, D.J., Vollenweider, J.J., Sigler, M.F., 2011. Seasonal abundance and distribution of pelagic and

856   demersal fishes in southeastern Alaska. Fish. Res. 108, 307–320.

857   doi:10.1016/j.fishres.2011.01.003

858   Cury, P.M., Bakun, A., Crawford, R.J.M., Jarre, A., Quinones, R.A., Shannon, L.J., Verheye, H.M., 2000.

859   Small pelagics in upwelling systems: patterns of interaction and structural changes in "wasp-

860   waist" ecosystems. ICES J. Mar. Sci. 57, 603–618. doi:10.1006/jmsc.2000.0712

861   Cury, P.M., Boyd, I.L., Bonhommeau, S., Anker-Nilssen, T., Crawford, R.J.M., Furness, R.W., Mills, J.A.,

862   Murphy, E.J., Österblom, H., Paleczny, M., Piatt, J.F., Roux, J.-P., Shannon, L., Sydeman, W.J.,

863   2011. Global seabird response to forage fish depletion: One-third for the birds. Science 334,

864   1703–1706. doi:10.1126/science.1212928

865 Davison, P., 2011. The specific gravity of mesopelagic fish from the northeastern Pacific Ocean and its

866   implications for acoustic backscatter. ICES J. Mar. Sci. 68, 2064–2074.

867   doi:10.1093/icesjms/fsr140

868 Davison, P., Lara-Lopez, A., Anthony Koslow, J., 2015. Mesopelagic fish biomass in the southern

869   California current ecosystem. Deep-Sea Res. Part II 112, 129–142.

870   doi:10.1016/j.dsr2.2014.10.007

871 De Robertis, A., Higginbottom, I., 2007. A post-processing technique to estimate the signal-to-noise ratio

872   and remove echosounder background noise. ICES J. Mar. Sci. 64, 1282–1291.

873 De Robertis, A., McKelvey, D.R., Ressler, P.H., 2010. Development and application of an empirical

874   multifrequency method for backscatter classification. Can. J. Fish. Aquat. Sci. 67, 1459–1474.

875   doi:10.1139/F10-075

876 De Robertis, A., Taylor, K., 2014. In situ target strength measurements of the scyphomedusa *Chrysaora*

877   *melanaster*. Fish. Res. 153, 18–23. doi:10.1016/j.fishres.2014.01.002

878 Dorn, M., Aydin, K., Jones, D., McCarthy, A., Palsson, W., Spalinger, K., 2015. Assessment of walleye

879   pollock stock in the Gulf of Alaska, Stock Assessment and Fishery Evaluation Report for the

880   Groundfish Resources of the Gulf of Alaska. North Pacific Fishery Management Council, 605 W

881   4th Avenue, Suite 306 Anchorage, AK 99501.

882 Dorn, M., Aydin, K., Jones, S., Palsson, W., Spalinger, K., 2014. Assessment of walleye pollock stock in the

883   Gulf of Alaska, Stock Assessment and Fishery Evaluation Report for the Groundfish Resources of

884   the Gulf of Alaska. North Pacific Fishery Management Council, 605 W 4th Avenue, Suite 306

885   Anchorage, AK 99501.

886 Dragoo, D.E., Renner, H.M., Irons, D.B., 2015. Breeding status and population trends of seabirds in

887   Alaska, 2014 (Report No. AMNWR 2015/03). U.S. Fish and Wildlife Service, Alaska Maritime

888   National Wildlife Refuge, 95 Sterling Highway, Suite 1 Homer, AK 99603.

889   Dragoo, D.E., Renner, H.M., Irons, D.B., 2012. Breeding status, population trends and diets of seabirds in

890   Alaska, 2009 (Report No. AMNWR 2012/01). U.S. Fish and Wildlife Service, Alaska Maritime

891   National Wildlife Refuge, 95 Sterling Highway, Suite 1 Homer, AK 99603.

892   Duffy-Anderson, J.T., Barbeaux, S.J., Farley, E., Heintz, R., Horne, J.K., Parker-Stetter, S.L., Petrik, C.,

893   Siddon, E.C., Smart, T.I., 2015. The critical first year of life of walleye pollock (*Gadus*

894   *chalcogrammus*) in the eastern Bering Sea: Implications for recruitment and future research.

895   Deep-Sea Res. Part II. doi:10.1016/j.dsr2.2015.02.001

896   Emmett, R.L., Brodeur, R.D., Orton, P.M., 2004. The vertical distribution of juvenile salmon

897   (*Oncorhynchus* spp.) and associated fishes in the Columbia River plume. Fish. Oceanogr. 13,

898   392–402. doi:10.1111/j.1365-2419.2004.00294.x

899   Farley, E.V., Murphy, J.M., Wing, B.W., Moss, J.H., Middleton, A., 2005. Distribution, migration

900   pathways, and size of western Alaska juvenile salmon along the eastern Bering Sea shelf. Alsk.

901   Fish. Res. Bull. 11, 15–26.

902   Fauchald, P., 2010. Predator–prey reversal: a possible mechanism for ecosystem hysteresis in the North

903   Sea? Ecology 91, 2191–2197. doi:10.1890/09-1500.1

904   Fauchald, P., 2009. Spatial interaction between seabirds and prey: review and synthesis. Mar. Ecol. Prog.

905   Ser. 391, 139–151. doi:10.3354/meps07818

906   Foote, K.G., Knudsen, H.P., Vestnes, G., MacLennan, D.N., Simmonds, E.J., 1987. Calibration of acoustic

907   instruments for fish density estimation: a practical guide (Cooperative Research Report No. 144).

908   International Council for the Exploration of the Sea.

909   Frank, K.T., Petrie, B., Fisher, J., Leggett, W.C., 2011. Transient dynamics of an altered large marine

910   ecosystem. Nature 477, 86–98. doi:10.1038/nature10285

911   Freeman, S., Mackinson, S., Flatt, R., 2004. Diel patterns in the habitat utilisation of sandeels revealed

912   using integrated acoustic surveys. J. Exp. Mar. Biol. Ecol. 305, 141–154.

913   doi:10.1016/j.jembe.2003.12.016

914   Freon, P., Cury, P., Shannon, L., Roy, C., 2005. Sustainable exploitation of small pelagic fish stocks

915   challenged by environmental and ecosystem changes: a review. Bull. Mar. Sci. 76, 385–462.

916   Funk, F., 1990. Migration of Pacific herring in the eastern Bering Sea as inferred from 1983-88 joint

917   venture and foreign observer information (Regional Information Report No. 5J90-04). Alaska

918   Department of Fish and Game, Juneau, Alaska.

919   Gjøsæter, H., Bogstad, B., Tjelmeland, S., 2009. Ecosystem effects of the three capelin stock collapses in

920   the Barents Sea. Mar. Biol. Res. 5, 40–53. doi:10.1080/17451000802454866

921   Gjøsæter, H., Dalpadado, P., Hassel, A., 2002. Growth of Barents Sea capelin (*Mallotus villosus*) in

922   relation to zooplankton abundance. ICES J. Mar. Sci. 59, 959–967. doi:10.1006/jmsc.2002.1240

923   Grados, D., Fablet, R., Ballon, M., Bez, N., Castillo, R., Lezama-Ochoa, A., Bertrand, A., 2012. Multiscale

924   characterization of spatial relationships among oxycline depth, macrozooplankton, and forage

925   fish off Peru using geostatistics, principal coordinates of neighbor matrices (PCNMs), and

926   wavelets. Can. J. Fish. Aquat. Sci. 69, 740–754. doi:10.1139/F2012-017

927   Greenstreet, S.P.R., Armstrong, E., Mosegaard, H., Jensen, H., Gibb, I.M., Fraser, H.M., Scott, B.E.,

928   Holland, G.J., Sharples, J., 2006. Variation in the abundance of sandeels *Ammodytes marinus* off

929   southeast Scotland: an evaluation of area-closure fisheries management and stock abundance

930   assessment methods. ICES J. Mar. Sci. 63, 1530–1550. doi:10.1016/j.icesjms.2006.05.009

931   Guttormsen, M.A., Yasenak, P.T., 2007. Results of the 2003 and 2005 echo integration-trawl surveys in

932   the Gulf of Alaska during summer, Cruises MF2003-09 and OD2005-01 (No. AFSC Processed Rep.

933   2007-04). Alaska Fisheries Science Center, NOAA, National Marine Fisheries Service, 7600 Sand

934   Point Way NE, Seattle WA 98115.

935   Hay, D.E., Toresen, R., Stephenson, R., Thompson, M., Claytor, R., Funk, F., Ivshina, E., Jakobsson, J.,

936   Kobayashi, T., McQuinn, I., Melvin, G., Molloy, J., Naumenko, N., Oda, K.T., Parmanne, R., Power,

937   M., Radchenko, V., Schweigert, J., Simmonds, J., Sjöstrand, B., Stevenson, D.K., Tanasichuk, R.,

938   Tang, Q., Watters, D.L., Wheeler, J., 2001. Taking stock: an inventory and review of world herring

939   stocks in 2000, in: Herring: Expectations for a New Millennium. Alaska Sea Grant College

940   Program, Fairbanks, Alaska, USA, pp. 381–454.

941   Haynes, T.B., Robinson, C.K.L., Dearden, P., 2008. Modelling nearshore intertidal habitat use of young-

942   of-the-year Pacific sand lance (*Ammodytes hexapterus*) in Barkley Sound, British Columbia,

943   Canada. Environ. Biol. Fish. 83, 473–484. doi:10.1007/s10641-008-9374-2

944   Hebert, K.P., 2014. Operational plan: Southeast Alaska herring stock assessment surveys and sampling,

945   2014 (Regional Operational Plan No. CF.1J.14-01). Alaska Department of Fish and Game, Division

946   of Commercial Fisheries, Juneau, Alaska.

947   Hinckley, S., Bailey, K., Picquelle, S., Schumacher, J., Stabeno, P., 1991. Transport, distribution, and

948   abundance of larval and juvenile walleye pollock (*Theragra chalcogramma*) in the Western Gulf

949   of Alaska. Can. J. Fish. Aquat. Sci. 48, 91–98. doi:10.1139/f91-013

950   Hobson, E.S., 1986. Predation on the Pacific sand lance, *Ammodytes hexapterus* (Pisces: Ammodytidae),

951   during the transition between day and night in southeastern Alaska. Copeia 1986, 223–226.

952   doi:10.2307/1444914

953   Hollowed, A.B., Wilson, C.D., Stabeno, P.J., Salo, S.A., 2007. Effect of ocean conditions on the cross-shelf

954   distribution of walleye pollock (*Theragra chalcogramma*) and capelin (*Mallotus villosus*). Fish.

955   Oceanogr. 16, 142–154. doi:10.1111/j.1365-2419.2006.00418.x

956   Hollowell, G., Otis, E.O., Ford, E., 2015. 2014 Lower Cook Inlet area finfish management report (Fishery

957   Management Report No. No 15-32). Alaska Department of Fish and Game, Anchorage, Alaska.

958   Hopcroft, R.R., Aguilar-Islas, A.M., Ladd, C., Matarese, A.C., Mordy, C.W., Rember, R., Stabeno, P.J.,

959   Strom, S.L., 2016. The role of cross-shelf and along-shelf transports as controlling mechanisms

960   for nutrients, plankton and larval fish in the coastal Gulf of Alaska (No. NPRB GOA Project G83 &

961   G85 Lower Trophic Level Final Report), Gulf of Alaska Integrated Ecosystem Research Program.

962   North Pacific Research Board.

963   Hrabik, T.R., Jensen, O.P., Martell, S.J.D., Walters, C.J., Kitchell, J.F., 2006. Diel vertical migration in the

964   Lake Superior pelagic community. I. Changes in vertical migration of coregonids in response to

965   varying predation risk. Can. J. Fish. Aquat. Sci. 63, 2286–2295. doi:10.1139/f06-124

966   Hunt, G.L., Coyle, K.O., Eisner, L.B., Farley, E.V., Heintz, R.A., Mueter, F., Napp, J.M., Overland, J.E.,

967   Ressler, P.H., Salo, S., Stabeno, P.J., 2011. Climate impacts on eastern Bering Sea foodwebs: a

968   synthesis of new data and an assessment of the Oscillating Control Hypothesis. ICES Journal of

969   Marine Science 68, 1230–1243. doi:10.1093/icesjms/fsr036

970   Hunt, G.L., Mehlum, F., Russell, R.W., Irons, D., Decker, M.B., Becker, P.H., 1999. Physical processes, prey

971   abundance, and the foraging ecology of seabirds, in: Proceedings of the International

972   Ornithological Congress. pp. 2040–2056.

973   Ingvaldsen, R.B., Gjøsæter, H., 2013. Responses in spatial distribution of Barents Sea capelin to changes

974   in stock size, ocean temperature and ice cover. Mar. Biol. Res. 9, 867–877.

975   doi:10.1080/17451000.2013.775450

976   Johnson, S.W., Thedinga, J.F., Munk, K.M., 2008. Distribution and use of shallow-water habitats by

977   Pacific sand lances in southeastern Alaska. Trans. Am. Fish. Soc. 137, 1455–1463.

978   doi:10.1577/T07-194.1

979   Jones, D.T., Ressler, P.H., Stienessen, S.C., McCarthy, A.L., Simonsen, K.A., 2014. Results of the acoustic-

980   trawl survey of walleye pollock (*Gadus chalcogrammus*) in the Gulf of Alaska, June-August 2013

981   (DY2013-07) (AFSC Processed Rep. No. 2014–6). Alaska Fish. Sci. Cent., NOAA, Natl. Mar. Fish.

982   Serv., 7600 Sand Point Way NE, Seattle WA 98115.

983   Jones, D.T., Stienessen, S.C., Simonsen, K.A., Guttormsen, M.A., 2015. Results of the acoustic-trawl

984   survey of walleye pollock (*Gadus chalcogrammus*) in the Gulf of Alaska, June-August 2011

985   (DY2013-07) (AFSC Processed Rep. No. 2015–4). Alaska Fish. Sci. Cent., NOAA, Natl. Mar. Fish.

986   Serv., 7600 Sand Point Way NE, Seattle WA 98115.

987   Kang, M., Furusawa, M., Miyashita, K., 2002. Effective and accurate use of difference in mean volume

988   backscattering strength to identify fish and plankton. ICES J. Mar. Sci. 59, 794–804.

989   doi:10.1006/jmsc.2002.1229

990   Keith, G.J., Ryan, T.E., Kloser, R.J., 2005. ES60adjust. jar. Java software utility to remove a systematic

991   error in Simrad ES60 data.

992   Kettle, A.B., Bargmann, N., Winnard, S., 2015. Biological monitoring at East Amatuli Island, Alaska in

993   2014 (Report No. AMNWR 2015/06). U.S. Fish and Wildlife Service, Alaska Maritime National

994   Wildlife Refuge, 95 Sterling Highway, Suite 1 Homer, AK 99603.

995   Kornilovs, G., Sidrevics, L., Dippner, J.W., 2001. Fish and zooplankton interaction in the Central Baltic

996   Sea. ICES J. Mar. Sci. 58, 579–588. doi:10.1006/jmsc.2001.1062

997   Ladd, C., Cheng, W., 2015. Gap winds and their effects on regional oceanography Part I: Cross Sound,

998   Alaska. Deep-Sea Res. Part II. doi:10.1016/j.dsr2.2015.08.006

999   Lewis, S., Sherratt, T.N., Hamer, K.C., Wanless, S., 2001. Evidence of intra-specific competition for food in

1000   a pelagic seabird. Nature 412, 816–819. doi:10.1038/35090566

1001 Li, K., Doubleday, A.J., Galbraith, M.D., Hopcroft, R.R., 2016. High abundance of salps in the coastal Gulf

1002   of Alaska during 2011: A first record of bloom occurrence for the northern Gulf. Deep Sea

1003   Research Part II: Topical Studies in Oceanography. doi:10.1016/j.dsr2.2016.04.009

1004 Livingston, P.A., Aydin, K., Boldt, J., Ianelli, J., Jurado-Molina, J., 2005. A framework for ecosystem

1005   impacts assessment using an indicator approach. ICES J. Mar. Sci. 62, 592–597.

1006   doi:10.1016/j.icesjms.2004.12.016

1007 Logerwell, E.A., Duffy-Anderson, J., Wilson, M., McKelvey, D., 2010. The influence of pelagic habitat

1008   selection and interspecific competition on productivity of juvenile walleye pollock (*Theragra*

1009   *chalcogramma*) and capelin (*Mallotus villosus*) in the Gulf of Alaska. Fish. Oceanogr. 19, 262–

1010   278. doi:10.1111/j.1365-2419.2010.00542.x

1011 Logerwell, E.A., Stabeno, P.J., Wilson, C.D., Hollowed, A.B., 2007. The effect of oceanographic variability

1012   and interspecific competition on juvenile pollock (*Theragra chalcogramma*) and capelin

1013   (*Mallotus villosus*) distributions on the Gulf of Alaska shelf. Deep-Sea Res. Part II 54, 2849–2868.

1014   doi:10.1016/j.dsr2.2007.08.008

1015 MacCall, A.D., 1990. Dynamic geography of marine fish populations. Washington Sea Grant Program

1016   Seattle, Washington.

1017 MacLennan, D.N., Fernandes, P.G., Dalen, J., 2002. A consistent approach to definitions and symbols in

1018   fisheries acoustics. ICES J. Mar. Sci. 59, 365–369. doi:10.1006/jmsc.2001.1158

1019 McGill, R., Tukey, J.W., Larsen, W.A., 1978. Variations of box plots. Am. Stat. 32, 12–16.

1020   doi:10.2307/2683468

1021 McKelvey, D.R., Wilson, C.D., 2006. Discriminant classification of fish and zooplankton backscattering at

1022   38 and 120 kHz. Trans. Am. Fish. Soc. 135, 488–499. doi:10.1577/T04-140.1

1023 Mecklenburg, C.W., Mecklenburg, T.A., Thorsteinson, L.K., 2002. Fishes of Alaska. American Fisheries

1024   Society, Bethesda, Md.

1025 Meyer, T.L., Cooper, R.A., Langton, R.W., 1979. Relative abundance, behavior, and food habits of the

1026   American sand lance, *Ammodytes americanus*, from the Gulf of Maine. Fish. Bull 77, 243–253.

1027 Mi, X.C., Ren, H.B., Ouyang, Z.S., Wei, W., Ma, K.P., 2005. The use of the Mexican Hat and the Morlet

1028   wavelets for detection of ecological patterns. Plant Ecol. 179, 1–19. doi:10.1007/s11258-004-

1029   5089-4

1030 Micheli, F., 1999. Eutrophication, fisheries, and consumer-resource dynamics in marine pelagic

1031   ecosystems. Science 285, 1396–1398. doi:10.1126/science.285.5432.1396

1032 Moss, J.H., Shotwell, S.K., Heintz, R.A., Atkinson, S., Debenham, C., Fournier, W., Golden, N., Heifetz, J.,

1033   Mueter, F.J., Pirtle, J.L., Reid, J.A., Slater, L., Sreenivasan, A., Will, A., Zaleski, M., Zimmermann,

1034   M., 2016. Surviving the Gauntlet: A comparative study of the pelagic, demersal, and spatial

1035   linkages that determine groundfish recruitment and diversity in the Gulf of Alaska ecosystem

1036   (No. NPRB GOA Project G84 Upper Trophic Level Final Report), Gulf of Alaska Integrated

1037   Ecosystem Research Program. North Pacific Research Board.

1038 Mowbray, F., 2002. Changes in the vertical distribution of capelin (*Mallotus villosus*) off Newfoundland.

1039   ICES J. Mar. Sci. 59, 942–949. doi:10.1006/jmsc.2002.1259

1040 Murase, H., Ichihara, M., Yasuma, H., Watanabe, H., Yonezaki, S., Nagashima, H., Kawahara, S.,

1041   Miyashita, K., 2009. Acoustic characterization of biological backscatterings in the Kuroshio-

1042   Oyashio inter-frontal zone and subarctic waters of the western North Pacific in spring. Fish.

1043   Oceanogr. 18, 386–401. doi:10.1111/j.1365-2419.2009.00519.x

1044 National Atlas of the United States, 2014. 1:1,000,000-Scale Coastline of the United States.

1045 NPFMC, 2014. Ecosystem Considerations 2014. North Pacific Fishery Management Council, 605 W. 4th

1046   Avenue, Suite 306, Anchorage, AK 99301.

1047 NPFMC, 2013. Ecosystem Considerations 2013. North Pacific Fishery Management Council, 605 W. 4th

1048   Avenue, Suite 306, Anchorage, AK 99301.

1049 NPFMC, 2012. Ecosystem Considerations 2012. North Pacific Fishery Management Council, 605 W. 4th

1050   Avenue, Suite 306, Anchorage, AK 99301.

1051 Obradovich, S.G., Carruthers, E.H., Rose, G.A., 2014. Bottom-up limits to Newfoundland capelin

1052   (*Mallotus villosus*) rebuilding: the euphausiid hypothesis. ICES J. Mar. Sci. 71, 775–783.

1053   doi:10.1093/icesjms/fst184

1054 Ona, E., Mitson, R.B., 1996. Acoustic sampling and signal processing near the seabed: the deadzone

1055   revisited. ICES J. Mar. Sci. 53, 677–690. doi:10.1006/jmsc.1996.0087

1056 Orians, G.H., Pearson, N.E., 1979. On the theory of central place foraging, in: Horn, D.J., Stairs, G.R.,

1057   Mitchell, R.D. (Eds.), Analysis of Ecological Systems. Ohio State University Press, Columbus, OH,

1058   pp. 155–177.

1059 Ormseth, O., 2014. Appendix 2. Forage species report for the Gulf of Alaska (Stock Assessment and

1060   Fishery Evaluation Report for the Groundfish Resources of the Gulf of Alaska). North Pacific

1061   Fishery Management Council, 605 W. 4th Avenue, Suite 306, Anchorage, AK 99301.

1062 Ormseth, O.A., Budge, S., De Robertis, A., Horne, J., McGowan, D., Rand, K., Wang, S., 2016. Temporal

1063   and spatial axes of variability in the structure of Gulf of Alaska forage fish communities (No.

1064   NPRB GOA Project G82 Middle Trophic Level Final Report), Gulf of Alaska Integrated Ecosystem

1065   Research Program. North Pacific Research Board.

1066 Orsi, J., Wertheimer, A., 1995. Marine vertical distribution of juvenile chinook and coho salmon in

1067   southeastern Alaska. Trans. Am. Fish. Soc. 124, 159–169. doi:10.1577/1548-

1068   8659(1995)124<0159:MVDOJC>2.3.CO;2

1069 Ostrand, W.D., Gotthardt, T.A., Howlin, S., Robards, M.D., Orr, J.W., 2005. Habitat selection models for

1070   Pacific sand lance (*Ammodytes hexapterus*) in Prince William Sound, Alaska. Northwest. Nat. 86,

1071   131–143. doi:10.1898/1051-1733(2005)086[0131:SMFPSL]2.0.CO;2

1072 Pahlke, K.A., 1985. Preliminary studies of capelin (*Mallotus villosus*) in Alaskan waters. Alaska

1073   Department of Fish and Game.

1074   Parada, C., Hinckley, S., Horne, J., Mazur, M., Hermann, A., Curchister, E., 2015. Modeling connectivity of

1075   *walleye pollock* in the Gulf of Alaska: Are there any linkages to the Bering Sea and Aleutian

1076   Islands? Deep Sea Research Part II: Topical Studies in Oceanography.

1077   doi:10.1016/j.dsr2.2015.12.010

1078   Parker-Stetter, S.L., Horne, J.K., Farley, E.V., Barbee, D.H., Andrews III, A.G., Eisner, L.B., Nomura, J.M.,

1079   2013. Summer distributions of forage fish in the eastern Bering Sea. Deep-Sea Res. Part II 94,

1080   211–230. doi:10.1016/j.dsr2.2013.04.022

1081   Parker-Stetter, S.L., Horne, J.K., Urmy, S.S., Heintz, R.A., Eisner, L.B., Farley, E.V., 2015. Vertical

1082   distribution of age-0 pollock during late-summer: Biophysical coupling or ontogeny? Mar. Coast.

1083   Fish. 7, 349–369. doi:10.1080/19425120.2015.1057307

1084   Piatt, J.F., Harding, A.M.A., Shultz, M., Speckman, S.G., Pelt, T.I. van, Drew, G.S., Kettle, A.B., 2007.

1085   Seabirds as indicators of marine food supplies: Cairns revisited. Mar. Ecol. Prog. Ser. 352, 221–

1086   234. doi:10.3354/meps07078

1087   Pikitch, E.K., Boersma, P.D., Boyd, I.L., Conover, D.O., Cury, P., Essington, T., Heppell, S.S., Houde, E.D.,

1088   Mangel, M., Pauly, D., Plaganyi, E., Sainsbury, K., Steneck, R.S., 2012. Little fish, big impact:

1089   managing a crucial link in ocean food webs. Lenfest Ocean Program, Washington, DC.

1090   Ressler, P.H., De Robertis, A., Warren, J.D., Smith, J.N., Kotwicki, S., 2012. Developing an acoustic survey

1091   of euphausiids to understand trophic interactions in the Bering Sea ecosystem. Deep-Sea Res.

1092   Part II 65–70, 184–195. doi:10.1016/j.dsr2.2012.02.015

1093   Robards, M.D., Abookire, A., Anson, J.M., Bodkin, J.L., Drew, G., Hooge, P., Piatt, J.F., Speckman, S.G.,

1094   2003. Ecology of selected marine communities in Glacier Bay: zooplankton, forage fish, seabirds

1095   and marine mammals. United States Geological Survey, Alaska Science Center, Biological Science

1096   Office, Anchorage, AK.

1097   Robinson, W.M.L., Butterworth, D.S., Plagányi, É.E., 2015. Quantifying the projected impact of the South

1098   African sardine fishery on the Robben Island penguin colony. ICES J. Mar. Sci. fsv035.

1099   doi:10.1093/icesjms/fsv035

1100   Saunders, S.C., Chen, J.Q., Drummer, T.D., Gustafson, E.J., Brosofske, K.D., 2005. Identifying scales of

1101   pattern in ecological data: a comparison of lacunarity, spectral and wavelet analyses. Ecol.

1102   Complex. 2, 87–105. doi:10.1016/j.ecocom.2004.11.002

1103   Scheuerell, M.D., Schindler, D.E., 2003. Diel vertical migration by juvenile sockeye salmon: empirical

1104   evidence for the antipredation window. Ecology 84, 1713–1720. doi:10.1890/0012-

1105   9658(2003)084[1713:DVMBJS]2.0.CO;2

1106   Schwartzlose, R.A., Alheit, J., Bakun, A., Baumgartner, T.R., Cloete, R., Crawford, R.J.M., Fletcher, W.J.,

1107   Green-Ruiz, Y., Hagen, E., Kawasaki, T., Lluch-Belda, D., Lluch-Cota, S.E., MacCall, A.D., Matsuura,

1108   Y., Nevarez-Martinez, M.O., Parrish, R.H., Roy, C., Serra, R., Shust, K.V., Ward, M.N., Zuzunaga,

1109   J.Z., 1999. Worldwide large-scale fluctuations of sardine and anchovy populations. S. Afr. J. Mar.

1110   Sci. 21, 289–347.

1111   Siddon, E.C., De Forest, L.G., Blood, D.M., Doyle, M.J., Matarese, A.C., 2016. Early life history ecology for

1112   five commercially and ecologically important fish species in the eastern and western Gulf of

1113   Alaska. Deep Sea Research Part II: Topical Studies in Oceanography.

1114   doi:10.1016/j.dsr2.2016.06.022

1115   Sigler, M.F., Csepp, D.J., 2007. Seasonal abundance of two important forage species in the North Pacific

1116   Ocean, Pacific herring and walleye pollock. Fish. Res. 83, 319–331.

1117   doi:10.1016/j.fishres.2006.10.007

1118   Simmonds, E.J., MacLennan, D.N., 2005. Fisheries Acoustics: Theory And Practice, 2nd ed. Blackwell

1119   Science, Oxford, UK.

1120   Slater, L., Fety, S., 2015. Biological monitoring at St. Lazaria Island, Alaska, in 2014 (Report No. AMNWR

1121   2015/09). U.S. Fish and Wildlife Service, Alaska Maritime National Wildlife Refuge, 95 Sterling

1122   Highway, Suite 1 Homer, AK 99603.

1123   Smart, T.I., Siddon, E.C., Duffy-Anderson, J.T., 2013. Vertical distributions of the early life stages of

1124   walleye pollock (*Theragra chalcogramma*) in the Southeastern Bering Sea. Deep-Sea Res. Part II

1125   94, 201–210. doi:10.1016/j.dsr2.2013.03.030

1126   Sogard, S.M., Olla, B.L., 1998. Behavior of juvenile sablefish, *Anoplopoma fimbria* (Pallas), in a thermal

1127   gradient: Balancing food and temperature requirements. J. Exp. Mar. Biol. Ecol. 222, 43–58.

1128   doi:10.1016/S0022-0981(97)00137-8

1129   Speckman, S.G., Piatt, J.F., Minte-Vera, C.V., Parrish, J.K., 2005. Parallel structure among environmental

1130   gradients and three trophic levels in a subarctic estuary. Prog. Oceanogr. 66, 25–65.

1131   doi:10.1016/j.pocean.2005.04.001

1132   Spellerberg, I.F., 1991. Monitoring Ecological Change, 1st ed. Cambridge University Press, Cambridge,

1133   U.K.

1134   Springer, A.M., Speckman, S.G., 1997. A forage fish is what? Summary of the symposium (No. AK-SG-97-

1135   01), Forage Fishes in Marine Ecosystems. Alaska Sea Grant College Program, Fairbanks, Alaska,

1136   USA.

1137   Stabeno, P., Bond, N., Hermann, A., Kachel, N., Mordy, C., Overland, J., 2004. Meteorology and

1138   oceanography of the Northern Gulf of Alaska. Cont. Shelf Res. 24, 859–897.

1139   Stabeno, P.J., Bond, N.A., Kachel, N.B., Ladd, C., Mordy, C.W., Strom, S.L., 2015. Southeast Alaskan shelf

1140   from southern tip of Baranof Island to Kayak Island: Currents, mixing and chlorophyll-*a*. Deep-

1141   Sea Res. Part II. doi:10.1016/j.dsr2.2015.06.018

1142 Strom, S.L., Fredrickson, K.A., Bright, K.J., 2015. Spring phytoplankton in the eastern coastal Gulf of

1143   Alaska: Photosynthesis and production during high and low bloom years. Deep-Sea Res. Part II.

1144   doi:10.1016/j.dsr2.2015.05.003

1145 Szuwalski, C.S., Vert-Pre, K.A., Punt, A.E., Branch, T.A., Hilborn, R., 2015. Examining common

1146   assumptions about recruitment: a meta-analysis of recruitment dynamics for worldwide marine

1147   fisheries. Fish Fish. 16, 633–648. doi:10.1111/faf.12083

1148 Torrence, C., Compo, G.P., 1998. A practical guide to wavelet analysis. Bull. Amer. Meteorol. Soc. 79, 61–

1149   78. doi:10.1175/1520-0477(1998)079<0061:APGTWA>2.0.CO;2

1150 Urmy, S.S., Horne, J.K., Barbee, D.H., 2012. Measuring the vertical distributional variability of pelagic

1151   fauna in Monterey Bay. ICES J. Mar. Sci. 69, 184–196. doi:10.1093/icesjms/fsr205

1152 Vollenweider, J.J., Heintz, R.A., Schaufler, L., Bradshaw, R., 2011. Seasonal cycles in whole-body

1153   proximate composition and energy content of forage fish vary with water depth. Mar. Biol. 158,

1154   413–427. doi:10.1007/s00227-010-1569-3

1155 Williams, K., Punt, A.E., Wilson, C.D., Horne, J.K., 2011. Length-selective retention of walleye pollock,

1156   *Theragra chalcogramma*, by midwater trawls. ICES J. Mar. Sci. 68, 119–129.

1157   doi:10.1093/icesjms/fsq155

1158 Wilson, M.T., 2009. Ecology of small neritic fishes in the western Gulf of Alaska. I. Geographic

1159   distribution in relation to prey density and the physical environment. Mar. Ecol. Prog. Ser. 392,

1160   223–237. doi:10.3354/meps08160

1161 Wilson, M.T., Jump, C.M., Duffy-Anderson, J.T., 2006. Comparative analysis of the feeding ecology of two

1162   pelagic forage fishes: capelin *Mallotus villosus* and walleye pollock *Theragra chalcogramma*.

1163   Mar. Ecol. Prog. Ser. 317, 245–258. doi:10.3354/meps317245

1164 Wilson, R.P., Hustler, K., Ryan, P.G., Burger, A.E., Noldeke, E.C., 1992. Diving birds in cold water: do

1165   Archimedes and Boyle determine energetic costs? Amer. Nat. 140, 179–200.

1166   Womble, J.N., Sigler, M.F., 2006. Seasonal availability of abundant, energy-rich prey influences the

1167   abundance and diet of a marine predator, the Steller sea lion *Eumetopias juhatus*. Mar. Ecol.

1168   Prog. Ser. 325, 281–293. doi:10.3354/meps325281

1169   Womble, J.N., Sigler, M.F., Willson, M.F., 2009. Linking seasonal distribution patterns with prey

1170   availability in a central-place forager, the Steller sea lion. J. Biogeogr. 36, 439–451.

1171   doi:10.1111/j.1365-2699.2007.01873.x

1172   Yang, M.S., Aydin, K., Greig, A., Lang, G., Livingston, P., 2005. Historical Review of Capelin (*Mallotus*

1173   *villosus*) Consumption in the Gulf of Alaska and Eastern Bering Sea (No. NMFS-AFSC-155).

1174   National Marine Fisheries Service, Alaska Fisheries Science Center.

1175   Zar, J.H., 2010. Biostatistical analysis, 5th ed. Prentice-Hall/Pearson, Upper Saddle River, N.J.

1176

1177 **FIGURE CAPTIONS**

1178 **Figure 1 –** Survey domain and stations sampled in 2011 and 2013. Individual transects are labeled in

1179 CGOA (181 to 217) and EGOA (A to M). Key geographic features are labeled in black, bathymetric

1180 features labeled in blue.

1181

1182 **Figure 2 –** Classification procedure for acoustic backscatter data. Key steps (in boxes) correspond to

1183 subheadings in section 2.3. Backscatter categories are bold. Note 10 m depth range minimum refers to

1184 the *Northwest Explorer*. A minimum depth range of 15 m was used for the *Oscar Dyson*.

1185

1186 **Figure 3 –** Summary of acoustic backscatter measurements by survey. Mean density (**A**) for "fish" backscatter

1187 from 38 kHz data and macrozooplankton from 120 kHz is shown for each survey, with *n* indicating the number of

1188 200 m samples. The proportion of "fish" backscatter assigned to each classification category (**B**) is shown by

1189 survey for all samples (left) and only samples located inside 500 m bottom depth (right). Backscatter categories

1190 include: "PO" = age-0 pollock; "CA" = capelin; "HE" = herring; "FF" = forage fish mix; "FP" = forage fish/piscivores

1191 mix; "MP" = mesopelagic, "SU" = surface; "PI" = piscivores; "UN" = unknown backscatter.

1192

1193 **Figure 4 –** Summary of significant periods for each forage fish category by transect identified by wavelet

1194 analysis. Y-axis is an octave scale. For each transect, significant periods are indicated by year (gray circles

1195 = 2011, black circles = 2013) and season (closed circles = summer, open circles = fall). Frequency

1196 distributions (right panel) indicate peak period (dashed line) that was most prevalent across all surveys

1197 for each category (herring values are gray).

1198

1199 **Figure 5 –** Forage fish distributions in CGOA by year and season. Acoustic densities, s_A (m^2 nmi^{-2}), are in

1200 500 m horizontal bins. "FF present" = forage fish mix and forage fish / piscivores mix categories.

1201

1202   **Figure 6 –** Forage fish distributions in EGOA by year and season. Acoustic densities, s_A (m^2 nmi^{-2}), are in

1203   500 m horizontal bins. "FF present" = forage fish mix and forage fish / piscivores mix categories.

1204

1205   **Figure 7 –** Distributions for each forage fish category between isobaths by year, season, and region. Box

1206   plots on left show horizontal distributions of nonzero acoustic density ($s_A > 0$ m^2 nmi^{-2}) between

1207   isobaths. Box plots on right show vertical distributions (*i.e.* center of mass, m) between isobaths. Box

1208   plot notches that do not overlap indicate strong evidence of differences between medians at the 95%

1209   confidence level. Box plots are not notched if *n* < 30 or during the CGOA fall 2013 survey due to limited

1210   survey coverage of the study area.

TABLES

Table 1 – Temporal coverage for each region ("EGOA" = eastern Gulf of Alaska; "CGOA" = central GOA) by survey.

Season (Seas): "S"=summer; "F"=fall. Survey vessel ("NWE" = F/V *Northwest Explorer*; "DY" = NOAA Ship *Oscar Dyson*), echosounders and operating frequencies, transducer input power by frequency, pulse duration (PD), transmit rate (TR, number of seconds between pulses), and amount of acoustic transect data (Dist, km). Transmit rate was determined by recording depth on the NWE (1 s per 600 m).

Survey	Year	Seas	Dates	Region	Vessel	Echosounders (kHz)	Power (W)	PD (ms)	TR (s)	Dist (km)
1GOA11	2011	S	3-17 Jul	EGOA	NWE	ES60 (38)	2000	1.024	1-7	602
2GOA11	2011	S	5-21 Aug	CGOA	NWE	ES60 (38)	2000	1.024	1-7	1,301
3GOA11	2011	F	8-19 Sep	EGOA	NWE	ES60 (38)	2000	1.024	1-7	435
4GOA11	2011	F	25 Sep-8 Oct	CGOA	NWE	ES60 (38)	2000	1.024	1-7	933
1GOA13	2013	S	3-21 Jul	EGOA	NWE	ES60 (38, 120)	2000, 200	1.024	1-7	1,005
2GOA13	2013	S	6-21 Aug	CGOA	NWE	ES60 (38, 120)	2000, 200	1.024	1-7	1,288
3GOA13	2013	F	10-24 Sep	EGOA	NWE	ES60 (38)*	2000	1.024	1-7	683
4GOA13	2013	F	24-28 Sep	CGOA	DY	EK60 (38, 120)**	2000, 500	0.512	1.4	248

* 120 kHz were recorded at an uncalibrated power setting and these data were not used in this study.

** EK60 data were also collected at 18, 70, and 200 kHz, but were not used in this study.

Table 2 – Backscatter category definitions for acoustic data. Survey(s) in which backscatter was assigned to each classification category are listed, along with the category water column depth range. Reported lengths are derived from trawl samples, while corresponding ages are inferred from literature-based, length-age relationships.

Classification Category	Survey				Depth Range * (m)	Acoustic Threshold (dB)	Definition
	1GOA11 / 1GOA13	2GOA11 / 2GOA13	3GOA11 / 3GOA13	4GOA11 / 4GOA13			
Surface	x / x	x / x	x / x	x / x	10 - 50	-75	May include but not limited to adult and juvenile salmon, epipelagic fish, squid, jellyfish
Mesopelagic	x / x	x / x	x / x	x / x	125 – 500	-75	Comprised of myctophids (*e.g.* northern lanternfish, *Stenobrachius leucopsarus*) and other mesopelagics
Piscivores	x / x	x / x	x / x	x / x	10 – 250	-67	Includes all groundfish (*e.g.* pollock, rockfish) greater than 158 mm in length
Age-0 Pollock	/ x	/ x	/	/	10 – 125	-67	Pollock 26 to 88 mm in length; may also include age-0 Pacific cod (45 to 77 mm in length) in 2GOA13
Capelin	/	x / x	/	x / x	10 – 250	-67	Capelin 54 to 204 mm in length
Herring	/	/	x / x	/	10 – 250	-67	Pacific herring 72 to 289 mm in length
Forage Fish Mix	/	/ x	/	x / x	10 -250	-67	Includes two or more of the following species: capelin, herring, age-0 pollock, age-0 Pacific cod **
Forage Fish/ Piscivores Mix	x /	x / x	x / x	/ x	10 – 250	-67	Includes at least 1 forage fish and 1 piscivore species
Unknown	x / x	x / x	x / x	x / x	10 - 500	-67	All backscatter that cannot be assigned to a category
Macrozooplankton	/ x	/ x	/	/ x	10 – 250	-80	Primarily euphausiids, copepods, and/or amphipods – 2013 only

* Minimum depth for all categories during the 4GOA13 survey is 15 m.

** Forage fish mix category may also include limited observations of other forage species such as eulachon, longfin smelt (*Spirinchus thaleichthys*), surf smelt (*Hypomesus pretiosus*), and Pacific sandfish (*Trichodon trichodon*).

Table 3 – Number of trawl samples by survey and the number

of trawl samples used for acoustic backscatter classification.

"ST" = surface trawl; "MWT" = midwater trawl; "FF" = forage

fish.

Survey	ST	MWT
1GOA11	52	11
2GOA11	54	10
3GOA11	40	10
4GOA11	37	10
1GOA13	71	11
2GOA13	55	19
3GOA13	63	10
4GOA13	10	2

Classification Category	2011		2013	
	ST	*MWT*	*ST*	*MWT*
Age-0 Pollock	0	0	6	8
Capelin	3	6	2	4
Herring	1	1	1	1
FF Mix	0	3	3	2
FF/Piscivores Mix	0	6	0	6
Piscivores	0	10	0	6
Mesopelagic	0	3	0	1