1   Detecting temporal trends and environmentally driven changes in the spatial

2   distribution of groundfishes and crabs in the eastern Bering Sea shelf

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19   ABSTRACT

20   This study uses a 30-year time series of standardized bottom trawl survey data (1982-

21   2011) from the eastern Bering Sea shelf to model between-year responses of global and local

22   spatial distribution indices for various bottom fishes and crabs against between-year differences

23   in the areal extent of the cold pool, fluctuations in population abundance, and the time lag

24   between surveys. The two density-independent factors, the areal extent of cold pool and the

25   survey time lag, together had a greater effect on the distributions for both spatial scales than did

26   the density-dependent factor population abundance. Spatial distributions were affected by

27   fluctuations in the extent and structure of the cold pool, generally showing a decreasing

28   similarity in spatial patterns with an increasing difference in the size of the cold pool. The model

29   iteratively selected among temperature levels within the cold pool at 0°, 1°, and 2°C for the

30   temperature with the best fit. The area of the cold pool contained within the 1° isotherm most

31   frequently affected spatial patterns of distribution on local and global scales. Temporal shifts in

32   populations varied considerably among species and directional vectors for some species were

33   greater in magnitude to the east or west than to the north. Results clearly show that the size of

34   the cold pool partly drives the short-term interannual variability in patterns of spatial distribution

35   on the eastern Bering Sea shelf, and that despite inclusion of data from the extended cold period

36   lasting from 2006-2010, there is a continuing broad scale community-wide temporal northward

37   shift. Based on our results, density-dependent or density-independent factors, other than a long

38   term warming trend, in the eastern Bering Sea are causing the observed northward temporal

39   shifts in distribution.

40

41   **Keywords**: spatial, distribution, scale, local, global, cold pool, fish, crab, temperature, Bering

42   Sea

1.   Introduction

The distributions of bottom fishes and crabs on the eastern Bering Sea continental shelf are affected by a host of biotic and abiotic factors. A subsurface layer of cold water ($<2°C$) known as the "cold pool" (Stabeno et al., 2010) is a major abiotic factor affecting the distribution of fish populations on the eastern Bering Sea shelf (Wyllie-Echeverria and Wooster, 1998; Sigler et al., 2011; Stabeno et al., *in press*), and retreating seasonal ice and the diminishing areal extent of the summer cold pool during a warm period lasting through 2005 was related to a community-wide northward shift in bottom fishes and invertebrates (Meuter and Litzow, 2008; Spencer, 2008). Studies have focused primarily on climate change and a general warming trend as the mechanism for basin-wide temporal shifts in the eastern Bering Sea. From 2006 to 2010, the eastern Bering Sea shelf environment entered into to relatively cold period when the spatial extent of winter sea ice and the summer cold pool both increased (Sigler et al., 2011). This is the first investigation to include an analysis of data for the 2006-2010 cold period to determine if increases in the size of the summer cold pool reversed the northward temporal shift in populations in the eastern Bering Sea and to investigate how distributions may be affected on a more local spatial scale.

A fundamental problem to studying ecological processes is that they are variable over a range of different spatial, temporal, and organizational scales (Levin, 1992). Spatial analyses of bottom fishes and crabs on the eastern Bering Sea shelf are complex because the physical and biological processes are dynamic, and the animals, as well as the cold pool, are not homogeneously distributed in space and time along latitudinal or longitudinal axes or gradients, which makes direct comparisons between years or over a broad scale difficult. Moreover, studies focusing on population shifts have lacked spatially explicit information about how a species is likely to respond to different temperature levels within the cold pool. From one year to

67   the next, the cold pool exhibits remarkable spatial heterogeneity during the late spring and

68   summer period. During warm years, the spatial extent of the cold pool is restricted to the

69   northern shelf, which contrasts sharply to the cold years when the spatial extent of the cold pool

70   extends down the middle shelf as far as the Alaska Peninsula and eastward into Bristol Bay (Fig.

71   1). There is obvious spatial heterogeneity in bottom temperatures between warm and cold

72   periods as well as spatial heterogeneity in the size and shape of the various isothermic

73   boundaries within the cold pool during any given year. Given the variability in the structure of

74   the cold pool, one might expect corresponding distributional changes in animal populations over

75   various spatial scales, especially for migratory temperate species having a lower tolerance for

76   water temperatures typically observed within the cold pool that can range between -2° to +2°C.

77   This study uses a 30-year time series of standardized bottom trawl survey data (1982-

78   2011) from the eastern Bering Sea shelf to model between-year responses of spatial distribution

79   indices of various bottom fishes and crabs against between-year differences in the areal extent of

80   the cold pool at three different bottom temperature levels. There are other factors besides

81   changes in bottom temperature that can affect distribution, including natural fluctuations in

82   population abundance (Spencer, 2008) and the temporal autocorrelation of spatial patterns (Pyper

83   and Peterman, 1998) also known as the time lag effect, i.e., snapshots of a spatial distribution for

84   a particular species that are closer in time may be more similar than those separated by longer

85   periods of time. Hence, in addition to temperature, we investigate variability in spatial

86   distribution patterns due to between year changes in population abundance as well as the time lag

87   between survey years.

88   The temporal scale we used was limited to the available survey data, but to determine

89   how distribution patterns varied over different spatial scales, we chose two indices for the model:

90   1) a global index comparing between-year responses of population centers across the eastern

91   Bering Sea shelf, and 2) a spatially explicit local index comparing between-year responses of

92   abundance location-by-location. A GAM (generalized additive model) framework is used to

93   model responses using the two spatial indices for all possible survey year combinations. The

94   basic thesis is that these models will explain the observed variability in spatial distribution of

95   populations and make it possible to determine the relative contribution of a changing cold pool,

96   fluctuating population abundance, and time lag between surveys to the distributional changes

97   observed in various bottom fishes and crabs on the eastern Bering Sea shelf.

98

99   **2.   Methods**

100   *2.1   Spatial indices*

101   Two spatial indices were used for analyzing pairwise comparisons among all bottom

102   trawl survey years: the global index of collocation (*GIC*) and the local index of collocation (*LIC*;

103   Bez, 2007).   The *GIC* and *LIC* provide different ways of quantifying the degree of similarity in a

104   population's spatial distribution between years. The *GIC* indicates whether a population center of

105   abundance has shifted between years using a pairwise comparison of center of gravity (*CG*)

106   within a defined geographical space taking into account the respective dispersion of that

107   population in each of those years. In contrast, the *LIC* indicates whether the local spatial

108   distribution changes between years using a location-by-location pairwise comparison of

109   standardized catch.

110   Figure 1 is a hypothetical grid for illustrating the difference between the *LIC* and the *GIC*

111   as well as showing the importance of spatial scale when choosing a metric for investigating

112   distributional change. Suppose each grid cell represents animal abundance or perhaps

113   temperature sampled annually during the same season in four consecutive years. Grid cells that

114   are $\leq 2.0°C$ are white to illustrate an environmental feature such as temperature. Regardless of

115   the obvious heterogeneity within the grid cells, all four years have an identical *CG* whether it is

116   for the animal population or temperature. A spatial analysis of either catch or temperature using

117   the *GIC* would not reveal a change in distribution since all six pairwise year comparisons would

118   have a *GIC* = 1.0. In contrast, a spatial analysis using the *LIC* captures the heterogeneity in

119   spatial distribution because the pairwise comparisons are spatially explicit. Moreover, using the

120   number of grid cells with temperature ≤ 2.0°C as a threshold, there is clearly a spatial difference

121   in temperature: *Year 1* = 0, *Year 2* = 6, *Year 3* = 4, and *Year 4* = 2.

122   The *GIC* (1) and the *LIC* (2) were calculated using data from the 30-year National Marine

123   Fisheries Service (NMFS) eastern Bering Sea shelf standardized bottom trawl survey, which

124   resulted in up to 435 pairwise comparisons of all the different year x year combinations for each

125   taxon. The possible values for both indices ranged from 0 to 1, where 1 indicated perfect

126   similarity between years and 0 indicated completely non-overlapping distributions between

127   years. The *GIC* compares the similarity in the *CG* for each pairwise year combination while

128   taking into account the change in dispersion (*I*) around the *CG*. The *GIC*'s were calculated using

129   the fixed set of stations common to all survey years (*n*=356).

130

131   1) $GIC = 1 - \dfrac{\Delta CG^2}{\Delta CG^2 + I_1 + I_2}$,

132
133

134   where ΔCG is the distance in kilometers (km) between the *CG*'s for a given pair of years (see

135   details below) and I_1 and I_2 are the dispersions for those years.

136
137   The *LIC* does a pairwise comparison at each survey station location between years,

138

139   2) $LIC = \dfrac{\sum z_{i1} z_{i2}}{\sqrt{\sum z_{i1}} \sqrt{\sum z_{i2}}}$,

140

141   where z_{i1} and z_{i2} are the fish densities at station i for the two years being compared (1 and 2). All

142   survey catch data were included for the *LIC* including the data from the additional stations

143   sampled in the northwest shelf since1987. This was acceptable because the *LIC* only used data

144   from stations when it was present for both years being compared. The ranges, means, and

145   standard deviations of *GIC* and *LIC* were combined for all years by species.

146   Both the latitude and longitude components of the $CG_{lat,long}$ were calculated by weighting

147   the station latitude (lat_i) or longitude ($long_i$) by z_i and dividing their respective sums by the sum

148   of all z_i's by year (3). The $CG_{lat,long}$ was plotted by year for selected species. The value of

149   dispersion I is basically the same as the variance for all weighted positions around the $CG_{lat,long}$

150   (4) and ΔCG was calculated for each pairwise comparison of years using spherical geometry (5).

151   3) $CG_{lat} = \dfrac{\sum\limits_{i=1}^{n} lat_i z_i}{\sum\limits_{i=1}^{n} z_i}$ $CG_{long} = \dfrac{\sum\limits_{i=1}^{n} long_i z_i}{\sum\limits_{i=1}^{n} z_i}$

152

153   4) $I = \dfrac{\sum\limits_{i=1}^{n} (\Delta CG)^2 z_i}{\sum\limits_{i=1}^{n} z_i}$

154

155   5) $\Delta CG = \arccos(\sin(CG_{lat_1}) * \sin(CG_{lat_2}) + \cos(CG_{lat_1}) * \cos(CG_{lat_2}) * \cos(CG_{long_1} - CG_{long_2}))$

156

157   *2.2 Surveys*

158   Since 1982, the NMFS eastern Bering Sea shelf standardized bottom trawl survey has

159   been conducted annually using chartered commercial fishing vessels to sample stations within a

160   systematic grid design consisting of ten strata and 356 fixed stations (Fig. 1). In 1987, an

161   additional two strata with 20 fixed stations were added to the northwestern most part of the shelf.

162   The inner, middle, and outer shelf strata are delineated by the 50, 100, and 200 -m isobaths, and

163   the line drawn diagonally across the middle of the shelf separate two geographic strata. Strata in

164   the vicinity of St. Matthew Island and the Pribilof Islands are sampled at a higher density than

165   the other strata. All bottom trawl surveys were conducted within the same 3-month time period

166   (May-August) using standardized gear and methods (Stauffer, 2004). Survey catch data were

167   standardized to catch per unit of effort (CPUE) for each station by dividing total catch weight

168   (kg) by the area-swept for each survey trawl haul (km^2). The mean CPUE for each stratum was

169   weighted by the proportion of the total stratum area and then summed for all strata to obtain

170   population abundance (*ABUND*) for each year. Methods for collecting survey bottom

171   temperatures and calculating mean annual bottom temperature are described in Stevenson and

172   Lauth (2012). ArcMap v9.3 was used to plot trawl station bottom temperatures for by year and

173   to generate isotherms in one degree intervals within the standard survey area using the inverse

174   distance weighted interpolation method. An Albers Equal Area Conic projection was used to

175   calculate the area within the polygons generated from the 0°, 1°, and 2°C isotherms.

176   The primary criterion for selecting the taxa used in the analysis (Table 1) was that bottom

177   trawl abundance had to be a credible index of abundance over time. Excluded taxa (Table 2)

178   failed to meet this criterion for a variety of reasons: 1) pelagic species, 2) historical changes in

179   the specificity and consistency of field identifications (Stevenson and Hoff, 2009), 3) historical

180   changes in the consistency of subsampling rare or singular species from large catches, and 4) rare

181   or patchily distributed species with insufficient data for analyses. Accordingly, Alaska skate

182   (*Bathyraja parmifera*) and northern rock sole (*Lepidopsetta polyxystra*) were combined into the

183   broader taxonomic groups *Bathyraja* spp. and *Lepidopsetta* spp., respectively. In both cases,

184   other species combined into these taxonomic groups had overlapping spatial distributions but

185   comprised only a small percentage of the total abundance within that group in any given year

186   (<5%). Flathead sole (*Hippoglossoides elassodon*) and Bering flounder (*H. robustus*) are

187   difficult to differentiate, however, their zoogeography differs (Mecklenburg et al., 2002) and

188   there was a concerted effort to separate the two species since 1982, so the two species were

189   analyzed separately. Two other similar species, arrowtooth flounder (*Atheresthes stomias*) and

190   Kamchatcka flounder (*A. evermanni*) were not identified separately in the survey until 1992, so

191   the analysis for arrowtooth flounder was confined to the 1992-2011 time period. A separate

192   analysis for Kamchatka flounder was not conducted due to insufficient data.

193

194   *2.3   Model*

195   A GAM was used to investigate how the *GIC* and the *LIC* responded to the between-year

196   differences in the areal extent (km^2) of the cold pool (*CPA_T*) at a threshold temperature T (°C),

197   the difference in population abundance ($\Delta ABUND$), and the time lag ($\Delta YEARS$) by taxon. The

198   time lag factor accounted for autocorrelation of any temporal trends that may be present in the

199   survey time series. The GAMs were run using the "mgcv" package in R (Wood, 2006) with the

200   smoothing spline protocol (Wood, 2003). The basic form of the GAM used in the analysis was:

201

202   *LIC or GIC ~ s(CPA_ T) + s(ΔABUND) + s(ΔYEARS) + factor(VESSEL) + factor(YEAR1)*

203

204   To investigate more specific responses to a range of cold pool bottom temperatures, backward

205   variable selection was performed for three different temperature thresholds: *CPA_ 0°C*, *CPA_*

206   *1°C*, and *CPA_ 2°C*, where a temperature threshold defines the two dimensional boundary within

207   the cold pool. Factors representing survey *VESSEL* and the first year of the comparison pair

208   (*YEAR1*) were included in the model to account for the random or systematic errors that were not

209   biologically significant but considered to be artifacts of sampling methodology such as vessel or

210   skipper effects (Munro, 1998; von Szalay and Brown, 2001), survey timing, and technology

211   creep (Zimmerman et al., 2003).

212   Because the data used in the modeling were not completely independent (e.g. the *LIC*

213   derived from a comparison between 1982 and 1983 was not independent of the *LIC* derived from

214   a comparison between 1982 and 1984), we could not use the p-values provided by the mgcv

215   package. Instead we derived p-values from the delete-d jackknife variance estimates around

216   predictions, which is preferable to the delete-one jackknife because it produces a consistent

217   variance estimate (Shao, 1989). A backward variable elimination was performed using

218   jackknife-derived p-values by eliminating one variable at a time. The variable with the largest p-

219   value was eliminated first and the jackknife was then repeated to estimate new p-values for the

220   reduced model. This process was continued until remaining p-values for all variables were $P <$

221   0.01. A more stringent $P < 0.01$ was chosen instead of $P < 0.05$ to minimize the possibility of a

222   Type II error. Confidence bounds around predictions were also estimated using model

223   predictions from the jackknife. Among the different temperature models the final one was chosen

224   based on the lowest generalized cross-validation (GVC) score (Wood, 2006).

225   Our null hypothesis was that there is no relationship between the interannual differences

226   observed in an animal's spatial distribution and the interannual differences observed in the

227   predictor variables. Rejection of the null hypothesis implies that a predictor variable has an effect

228   on the spatial index, and thus affects the spatial distribution of a species. For example, if the

229   magnitude of the difference in $\Delta ABUND$ is negatively correlated with a spatial index (i.e. greater

230    $\Delta ABUND$ corresponds to decreasing similarity of the spatial index) then the population

231   abundance influences the spatial distribution.

232   A more detailed examination of spatial analyses was done for three species of particular

233   interest to Bering Sea Integrated Ecosystem Research Program (BSIERP) researchers because of

234   their important role in the eastern Bering Sea ecosystem: arrowthooth flounder, Pacific cod

235   (*Gadus macrocephalus*), and walleye pollock (*Theragra chalcogramma*). To illustrate effects on

236   the *LIC*, plots of spatial distribution by species were made for ΔCPA_T, $\Delta ABUND$ and $\Delta YEARS$

237   if they were significant. As a proxy for each significant effect, median values among all years

238   for each of the predictor variables by species were used as cut-off values to categorize the catch

239   data into "cold" and "warm" years (ΔCPA_T), "high" and "low" abundance years ($\Delta ABUND$),

240   and "early" and "recent" years ($\Delta YEARS$). An IDW plot of the spatial distribution of mean

241   CPUE for the pooled data was made for all three species and an additional IDW plot of the mean

242   coefficient of variation was made for arrowtooth flounder. For predictor variables which had a

243   significant effect on the *GIC*, the same methodology as above was used for delineating cold and

244   warm years, high and low abundance years, and early and recent years. A mean *CG* was taken

245   for each pooled set of data by species and a distance and bearing for the ΔCG within each set

246   was calculated using spherical geometry. The relative ΔCG distance and bearing of all taxa was

247   plotted for each significant predictor variable to compare their relative effects on the global

248   spatial distribution.

249

250   **3.   Results**

251   *3.1   Survey bottom temperatures and extent of cold pool*

252   Mean survey bottom temperatures and areal extent of the cold pool on the eastern Bering

253   Sea shelf showed considerable interannual variability from 1982-2011 (Fig. 3). Deviations from

254   the survey 30-year mean bottom temperature started to become more extreme in 1993. The

255   largest deviation occurred in 1999, resulting in the coldest year and the largest areal extent of

256   cold pool in the time series (393,595 km^2). This extremely cold year was followed by a five-year

257   warm period (2001-2005) during which the average survey bottom temperature on the eastern

258   Bering Sea shelf was the warmest (2003) and the areal extent of cold pool reached its minimum

259   size (48,000 km^2). The *CPA_0°C* was generally absent or small during years when the mean

260   survey bottom temperature was above the long term mean (Fig. 3). From 2005 to 2006, the

261   warm trend reversed and there was a sharp decline in the mean bottom temperature, coinciding

262   with a cold period that lasted for five years (2006-2010). In 2011, the cold pool decreased in

263   size, especially the *CPA_0°C*, resulting in a mean survey bottom temperature that was slightly

264   above the 30-year mean.

265

266   *3.2   Model results*

267   The *LIC*'s generally had lower similarities and greater variability than *GIC*'s for all

268   species (Table 3). The mean *LIC* ranged from 0.32 to 0.78 compared to the mean *GIC* which

269   ranged from 0.83 to 0.98, and standard deviations were on average 2.5 times greater for *LIC* than

270   *GIC*. Also, the highest *GIC* for every species was 1.0, compared to the highest *LIC* values which

271   varied from 0.67 – 1.0.

272   As expected, we observed a significant *YEAR1* effect for all species and *VESSEL* effects

273   for most of the species, which together accounted for the differences in the survey catchability

274   between vessels and years. A closer examination of results or a discussion for the *YEAR1* and

275   *VESSEL* effects was omitted because they were sampling artifacts without biological relevance

276   to the primary purpose of this study.

277   The Δ*YEARS* was a significant effect for a majority of both the *LIC* (86%) and *GIC*

278   (82%) with the dominant trend being decreasing similarity in spatial indices with increasing

279   Δ*YEARS* (Table 1). The *LIC* was significantly affected by the areal extent of the cold pool for a

280   majority of taxa (77%), compared to about half (55%) for the *GIC* (Table 1). The Δ*CPA_ 1°C*

281   most frequently affected both *LIC* and *GIC* (61%), followed by Δ*CPA_ 0°C* (23%) and Δ*CPA_*

282   *2°C* (16%). The Δ*ABUND* was a significant effect for a greater percentage of the *LIC* models

283   (59%) than for the *GIC* models (41%), with most species showing decreasing similarity with the

284   *LIC* and variable trends in similarity with the *GIC* (Table 1).

285   The *GIC* for all species except longhead dab showed a significant response to at least one

286   of the predictor variables (Table 1), indicating a community-wide shift in the global distribution

287   of demersal fauna on the eastern Bering Sea shelf. The Δ*YEARS* was significant for a majority of

288   taxa (82%), and compared to the temperature and abundance effects, the Δ*CG* for early relative

289   to recent years showed the largest magnitude of displacement (mean = 45 km) and the broadest

290   range of directional shifts with the largest percentage of species undergoing a shift to the north

291   (Table 4; Fig. 4a). The cold pool effect on Δ*CG* was generally less pronounced (mean = 34 km),

292   and directional shifts ranged from ESE (116°) to WSW (262°) with the exception of the wattled

293   eelpout which shifted to the northwest with the increasing size of the cold pool (Fig. 4b).

294   Changes in abundance had the smallest effect on Δ*CG*, with a mean displacement of 23 km along

295   a relatively narrow southeast-northwest axis (Fig. 4c).

296

297   *3.3   Selected species*

298   *Walleye pollock*: Distributions of pollock on the global scale decreased in similarity with

299   both an increase in Δ*CPA_ 0°C* and Δ*YEARS* (Table 1). The cold year *CG*'s were generally west

300   of warm year *CG*'s along a southeast-northwest axis (Fig. 5) resulting in a mean *CG* for cold

301   years that shifted 42 km toward the shelf edge (262°; Table 4). Among the eight years with the

302   most northerly distribution (latitude > 58°05' N), four of those years, 1999 and 2008-2010, were

303   the coldest in the survey time series (Fig. 5). The pollock population had a mostly southeastern

304   distribution during early years, but switched to a more northwestern distribution during recent

305   years, shifting 50 km to the northwest (309°; Table 4; Fig. 5). For pollock, there was not a

306   significant relationship between the *LIC* and Δ*CPA_ T* at any temperature, but there was

307   decreasing similarity with increasing Δ*ABUND* (Table 1; Fig. 6). During high abundance years,

308   there were larger aggregations and higher densities of pollock along the northwest outer eastern

309   Bering Sea shelf east of Zemchung Canyon, in the vicinity of the Pribilof Islands, and north of

310   Unimak Island and the Alaska Peninsula (Fig. 5).

311   *Pacific cod*: The spatial distribution of Pacific cod was significantly affected by

312   Δ*ABUND* and Δ*YEARS* on a global scale but not Δ*CPA_T* (Table 1). There was a decreasing

313   similarity in the *GIC* with increasing Δ*YEARS*, and the years 2000 -2008 generally had a lower

314   abundance and more northwestern *CG*'s than other years (Fig. 7). With the increasing

315   abundance of Pacific cod starting in 2009, the *CG*'s shifted southeast (Fig. 7). The direction of

316   the Δ*CG* was similar between high and low abundance years and between early and recent years

317   (Table 4; Fig. 7). The *LIC* was significantly affected by all three predictors: Δ*CPA_ 1°C*,

318   Δ*ABUND*, and Δ*YEARS* (Table 1). On the local scale, the similarity between spatial distributions

319   decreased with increased differences in both Δ*CPA_ 1°C* and Δ*ABUND* (Fig. 7). There was also

320   a decrease in similarity with Δ*YEARS* up to 10 years after which similarity generally increased,

321   but not consistently. During both cold and warm years, CPUE above 40 kg/km^2 remained

322   outside the 1°C isotherm. Localized pockets of higher CPUE were apparent and more numerous

323   in the cold, high abundance, and early years, but were less apparent and more dispersed in the

324   warm, low abundance, and late years. A large pocket of higher CPUE in the vicinity of St.

325   Matthew Island was present in all cases except during the cold years, and during the warm years,

326   the dense aggregation remained outside the 1°C isotherm (Fig. 7). Also, during the cold, high

327   abundance, and early years, CPUE was higher in northern Bristol Bay compared to the warm,

328   low abundance, and recent years.

329   *Arrowtooth flounder*: Both the *GIC* and *LIC* indices decreased significantly with an

330   increase in $\Delta CPA\_\ 1°C$, and the *LIC* also decreased with an increase in $\Delta ABUND$ (Table 1). The

331   ΔCG from warm to cold years shifted 36 km to the southeast (Table 4; Fig. 9). Arrowtooth

332   flounder were absent or densities were generally below 1 kg/km^2 inside the 1°C isotherm

333   boundary (Fig. 10). During the cold and high abundance years, densities were higher on the

334   outer shelf south of Pribilof Canyon and during the warm and high abundance years, arrowtooth

335   flounder distribution expanded across the middle shelf and onto the inner coastal shelf where

336   higher densities extended into Bristol Bay (Fig. 10). The coefficient of variation of CPUE for

337   the combined years was relatively low where the spatial distribution of arrowtooth flounder was

338   more persistent through time and relatively high where changes in the spatial distribution were

339   affected by $CPA\_\ 1°C$ and $\Delta ABUND$ (Fig. 10).

340

341   **4.   Discussion**

342   *4.1   Summary*

343   Here we present a modeling framework for detecting temporal trends and

344   environmentally driven changes in the spatial distributions of bottom fish and crab populations

345   by analyzing how between-year differences in spatial distribution, quantified by global and local

346   indices of collocation, are affected by corresponding differences in three predictor values derived

347   from a 30-year time series on the eastern Bering Sea shelf. This study evaluates and presents

348   partial support to the BSIERP hypothesis that trophic relationships are structured by ocean

349   conditions. Our results suggest that northward temporal shifts in the distribution of populations

350   are associated with a reduction in the areal extent of cold pool on the eastern Bering Sea shelf as

351   observed in earlier studies (Meuter and Litzow, 2008; Spencer, 2008). However, the temporal

352   northward displacement of populations is still apparent after accounting for the increased size of

353   the cold pool during the major cold period lasting from 2006-2010. Given that a temporal lag in

354   the survey time series and the changes in abundance were also significant responses for a

355   majority of species on both local and global spatial scales suggests that other density-

356   independent and density-dependent mechanisms are driving the temporal northward shift rather

357   that a warming climate.

358   There are several aspects to the approach and model that we believe make it robust. The

359   model incorporated more variability than previous studies by comparing similarities between the

360   predictor and response variables for all possible survey year combinations rather than directly

361   comparing the similarity over a 30-year linear time period. To address the issue of an

362   appropriate spatial scale (Levin, 1992), the same predictor variables were used to model the

363   response of indices representing two contrasting spatial scales, a local spatial index incorporating

364   spatially explicit analysis data, and a global spatial index that considered broad scale spatio-

365   temporal displacement of populations in all directions. All three predictor variables were under

366   the same modeling framework and included a time lag effect that also compensated for the

367   temporal autocorrelation in the eastern Bering Sea time series. Finally, rigorous criteria were

368   used for selecting species to analyze, and for each species, the model iteratively selected among

369   three cold pool temperature levels for the one with the best fit.

370

371   *4.2 Choice of predictors*

372   The three predictors chosen for investigating global and local spatial patterns were: 1) the

373   areal extent of the cold pool at three different temperature levels, 2) population abundance, and

374   3) time lag in survey years. These variables were chosen because other studies have suggested

375 that they effect spatial distribution (Kotwicki et al. 2005; Mueter and Litzow, 2008; Spencer,

376 2008) and because data for all three were available from the eastern Bering Sea time series. The

377 first two factors are most often cited by other researchers as important in determining species

378 distribution (e.g. Ciannelli et al. 2008, Spencer, 2008). However, the third, time lag in survey

379 years, is also very important because it incorporates temporal trends about other density-

380 independent factors in the eastern Bering Sea marine ecosystem (see below) that are dynamic

381 and unrelated to temperature or population abundance. We also used spatial indices that

382 measured general similarity in the distribution, but did not require assumptions about the

383 direction of the temporal displacement (e.g., Mueter and Litzow, 2008).

384   In contrast to the previous studies, we incorporated three different temperature levels to

385 model temperature effects on bottom fish and crab distributions. Past studies have used mean

386 temperature over eastern Bering Sea shelf area (Mueter and Litzow, 2008), or the proportion of

387 the area that was covered by the cold pool defined as the area where bottom temperature was

388 below a single threshold (e.g., < 2ºC; Spencer, 2008). Although both of these metrics are

389 adequate indicators of the general bottom temperature conditions over the eastern Bering Sea

390 shelf, neither provides a direct measure the extent of the cold pool. Moreover, different fish

391 species have different temperature preferences (Scott, 1982) and an arbitrary choice of one

392 temperature level may not be adequate to assess the effect of the cold pool on specific fish

393 distributions.   Thus, we chose a more explicit model that was allowed to choose a best fit to the

394 data using three different temperature levels.

395

396 *4.3 Community level effects*

397   Studies have shown that both density-independent and density-dependent factors can

398 affect bottom fish distribution (Cianelli et al., 2008; Spencer, 2008). A host of density-

399 independent factors other than temperature are integrated within the time lag variable in our

400 model and it was significant for all but a few species at both global and local spatial scales. The

401 prevalence of the time lag variable suggests that the density-independent factors (other than

402 temperature) that it represents may have more influence on the spatial distribution of species than

403 does changes in the cold pool or population abundance. Density-independent factors have often

404 been limited to the effects of climate approximated by water temperature (e.g. Mountain and

405 Murawski, 1992; Swain, 1999; Spencer, 2008). However, distribution shifts can also result from

406 changes in other density-independent factors such as food availability (Swain, 1999), *in situ* light

407 conditions (Kotwicki et al., 2009), primary production patterns, competition between species,

408 predation, or fishing pressure (Ciannelli et al., 2008; Zador et al., 2011). Migrations involving

409 ontogeny, spawning, and feeding are other density-independent factors that can cause temporal

410 changes in the global or local spatial patterns of bottom fish (Nichol, 1998; Kotwicki et al. 2005;

411 Sohn et al., 2010) and crab (Ernst et al. 2005) distribution on the eastern Bering Sea shelf.

412 Second to the time lag variable, the area occupied by the cold pool was the next most

413 common significant effect on both local and global scales, suggesting that, by itself, it is a major

414 environmental feature affecting spatial patterns of distribution on the eastern Bering Sea shelf.

415 The cold pool affected a much higher percentage of taxa on the local scale (77%) than global

416 scale (55%) indicating that distributional changes due to the cold pool are more prevalent on

417 spatial scales smaller than the eastern Bering Sea shelf. The cold pool area enclosed by the 1°C

418 isotherm was the temperature threshold most commonly affecting spatial indices on both scales,

419 suggesting it is an important boundary for describing temperature preferences of eastern Bering

420 Sea demersal fauna.

421 Fluctuations in population abundance also affected distribution patterns on both scales,

422 but it was more apparent with taxa locally (59%) than globally (41%). Density-dependent

423   factors are important because population growth creates greater competition for resources,

424   forcing animals within a population to spread more into outlying areas (Swain and Wade, 1993;

425   Atkinson et al., 1997). In the 1980's there was rapid growth in the populations of several eastern

426   Bering Sea flatfish species, which corresponded to significant increases in the dispersion of those

427   species (McConnaughey, 1995). Increases in the population abundance of "arrowtooth

428   flounder" (combined *Atherethes stomias* and *A. evermanni*) and rock sole (*Lepidopsetta* spp.) on

429   the eastern Bering Sea shelf have been strongly related to increased spatial coverage of their

430   populations, while increases in the area occupied by the cold pool have been associated with

431   decreased spatial coverage of the same species (Spencer 2008).

432   An additional consideration with the effect of fluctuating population size on spatial

433   distribution patterns for some species is immigration and emigration to and from the survey area.

434   During a northward extension of the Bering Sea shelf bottom trawl survey in 2010, it was

435   discovered that some species had a contiguous northern distribution with large percentages of

436   their total survey biomass outside the standard sampling survey area, including 64% of snow

437   crab (*Chionoecetes opilio*), 51% of the Bering flounder, 38% of the Alaska plaice (*Pleuronectes*

438   *quadrituberculatus*), 15% of yellowfin sole (*Limanda aspera*), and 10% of Pacific halibut

439   (*Hippoglossus stenolepis*; Lauth, 2010). Deep water species such as arrowtooth flounder and

440   Greenland turbot (*Reinhardtius hippoglossoides*) occupy the shelf as juveniles, but older ages

441   occupy both the shelf and the upper continental slope (Alton et al., 1988, Spies et al. 2011).

442   Changes in spatial distribution of many fish populations have been attributed to climate

443   change (Perry et al., 2005; Nye et al., 2009). Similar to a previous study (Mueter and Litzow,

444   2008), our analysis shows a broad scale community-wide northward shift in the eastern Bering

445   Sea over the last three decades; however, the temporal trend continued despite the recent cold

446   period suggesting something other than a warming climate as the mechanism. We took the

447   analysis a step further by carefully selecting species that provide a meaningful index of

448   abundance, and we looked at the spatio-temporal displacement in all directions rather than just a

449   northward direction. Twelve of the 13 species that were found to have a northern displacement in

450   the Mueter and Litzow (2008) study were also found to have a northern displacement in our

451   study, and four species that were found to have a southern displacement also were also found to

452   have a southern displacement in our study. Despite the similarities, directional vectors

453   representing temporal shifts in populations varied considerably among species and vectors for

454   some species were greater in magnitude to the east or west than to the north. The cross shelf

455   shifts in populations of pollock and arrowtooth flounder in response to the size of the cold pool

456   was more noticeable than northerly latitudinal shifts. Population shifts along different axes for

457   the different species suggest a variety of species-specific biological or environmental

458   mechanisms or perhaps different responses to the same mechanism.

459   The observation of a northward community-wide distributional shift on the eastern

460   Bering Sea shelf came following a protracted warm period lasting from 2001 to 2005, when

461   summer bottom temperatures were increasing and the extent of the summer cold pool was

462   decreasing. This observation made it easy to associate changes in fish distributions within the

463   same temporal framework as a warming climate. However, the northward shift persisted

464   following an extended cold period lasting from 2006-2010. This cold period had a greater

465   duration and intensity than anything previously observed on eastern Bering Sea shelf during the

466   30-year survey time series. There is a compelling argument that mechanisms other than a

467   warming climate are causing the temporal shift in distribution given that the cold pool size is

468   partly driving the short-term interannual variability in the spatial distributions and that the

469   temporal northward trend continues despite the inclusion of the survey data from the cold period.

470   It is now generally believed that the persistence of winter ice cover on the eastern Bering Sea

471 shelf will result in cold near-bottom water temperatures during summer that will continue as a

472 barrier to northward migration of subarctic species (Sigler er al., 2011; Stabeno et al., in press).

473 Another explanation for the northern displacement could be disproportional fishing effort

474 across the eastern Bering Sea shelf. Commercial fisheries can impact fish distribution and can

475 change community structure (Garrison and Link, 2000). Of the thirteen species that showed

476 northward displacement in this study, eight have been targeted by a commercial fishery during

477 the last 30 years including walleye pollock, Pacific cod, Pacific halibut, Pribilof Island Bristol

478 Bay red king crab (*Paralithodes camtschaticus*) , Pribilof Island blue king crab (*P. platypus*),

479 Tanner crab (*Chionoecetes bairdi*) , flathead sole, and Greenland turbot. The southeastern Bering

480 Sea is in close proximity to a major fishing port and it is where the two biggest flatfish trawl

481 fisheries in the world operate and catch a majority of their total annual quota (Wilderbuer, 2011a;

482 2011b). Thus, it is conceivable that disproportional fishing effort in the southeastern Bering Sea

483 shelf during the last 30 years may be contributing to this apparent northward shift.

484

485 *4.4 Implication for studies of spatial dynamics in the eastern Bering Sea ecosystem*

486 Spatial relationships in relation to environmental factors are key components in

487 constructing models of marine ecosystems (Rose et al., 2010). Accounting for environmental

488 factors in spatial dynamics studies can be challenging, especially in cases like the eastern Bering

489 Sea, where spatial data for many stocks is limited to summer months when feeding migrations

490 predominate. Spatial data from winter or early spring, when many bottom fishes are spawning

491 (e.g., Nichol, 1998) might show entirely different trends in relation to environmental factors.

492 Although this study lacks data on intra-annual or seasonal variability, we have attempted to

493 capture more interannual variability by quantifying similarities in summer fish distribution

494 between all possible survey year combinations.

495   This study presents a method of detecting temporal trends and environmentally driven

496   changes in the spatial distribution of bottom fish and crab populations. There are many different

497   ways to extend such a modeling framework to address more specific questions regarding the

498   spatial dynamics of the eastern Bering Sea shelf ecosystem such as detecting differences in the

499   spatial distribution between different age groups (Woillez et al., 2007) or investigating the

500   overlap between the daily egg production and fish abundance (Petitgas et al., 2009). The eastern

501   Bering Sea survey data could be used for developing indices for comparing the abundance of

502   new recruits or specific age groups to environmental variables such as bottom type

503   (McConnaughey and Smith, 2000) or temperature. Indices of spatial overlap between different

504   species or different age groups of the same species could also be used to investigate

505   environmental responses to cannibalism, predator-prey relationships, or interspecies competition.

506

515

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650 **Figure captions**

651 Figure 1. Variation in the extent of the summer cold pool during a warm year (2003) and a cold

652   year (2009) on the eastern Bering Sea shelf as measured during bottom trawl surveys

653   (modified from Lauth, 2010). Also shown are the 50-m, 100-m, and 200-m isobaths,

654   survey stratum boundaries, and sampling stations for each year (dots).

655 Figure 2. Hypothetical grid depicting the influence of spatial scale on an investigation of

656   distributional change. Numbers inside the grid cells represent animal abundance or

657   bottom temperature. Grid cells that are ≤ 2.0 are white to illustrate an arbitrary

658   environmental feature. Regardless of the obvious heterogeneity within the grid cells, all

659   four years have an identical center of gravity (*CG*).

660 Figure 3. Annual variation in the average survey bottom temperature, the 30-year mean survey

661   bottom temperature, and the area (km^2) of the cold pool (*CPA_T*) for three different

662   temperature thresholds, 0°, 1°, and 2°C.

663 Figure 4. Relative shifts in the centers of gravity for species that had statistically significant

664   effects in the GAM models for a) time lag (*Y*; early relative to recent years), b) cold pool

665   area by temperature level *T* in C° (*T0*, *T1*, or *T2*; warm relative to cold years), and c)

666   abundance (*A*; high relative to low abundance years).

667 Figure 5. On top are GAM results for walleye pollock showing decreasing trend for Δ*CPA_ 0°C*

668   and Δ*YEARS* against the global index of collocation (*GIC*) in relation to a decreasing.

669   Red lines are the 99% confidence intervals. Below is a plot of the center of gravity (*CG*)

670   for walleye pollock by year and the mean *CG*'s for cold and warm years and for early and

671   recent years.

672 Figure 6. Spatial distribution of walleye pollock during the high and low abundance years

673   illustrating the decreasing similarity of the local index of collocation (*LIC*) associated

674   with an increased change in abundance (Δ*ABUND*). Red lines are the 99% confidence

675   intervals.

676   Figure 7. On top are GAM results for Pacific cod showing decreasing trends of Δ*ABUND* and

677   Δ*YEARS* against the global index of collocation (*GIC*). Red lines are the 99% confidence

678   interval. Below is a plot of the center of gravity (*CG*) for Pacific cod by year and the

679   mean *CG*'s for high and low abundance years and for early and recent years.

680   Figure 8. Spatial distribution of Pacific cod during cold and warm years and the high and

681   low abundance years to illustrate the decreasing similarity of the local index of

682   collocation (*LIC*) to the effects of increasing Δ*CPA_ 1°C* and Δ*ABUND*. Red lines are the

683   99% confidence interval.

684   Figure 9. On top are GAM results for arrowtooth flounder showing a decreasing trend of

685   Δ*CPA_ 1°C* against the global index of collocation (*GIC*). Red lines are the 99%

686   confidence interval. Below is a plot of the center of gravity (*CG*) for arrowtooth flounder

687   for cold and warm years.

688   Figure 10. Spatial distribution of arrowtooth flounder during cold and warm years and the

689   high and low abundance years to illustrate the decreasing similarity of the local index of

690   collocation (*LIC*) to the effects of increasing Δ*CPA_ 1°C* and Δ*ABUND*. Red lines are the

691   99% confidence interval. At bottom is the coefficient of variation of arrowtooth flounder

692   catch per unit of effort for the combined years 1992 - 2011. Low values indicate areas

693   where the distribution was persistent, while high values indicate where the distribution of

694   arrowtooth flounder is affected by temperature and abundance.

Table 1.-- General additive model results of local (*LIC*) and global (*GIC*) indices of collocation selected taxa from the eastern Bering Sea shelf. Predictor variables include pairwise interannual comparisons of survey cold pool area at temperatures (ΔCPA_T) 0°, 1°, and 2°C, abundance ($\Delta ABUND$), and survey time lag ($\Delta YEARS$). The level of signifcance for listed predictor variables is either $P < 0.01$ or $P < 0.001$. Dashes indicate that the variable dropped out from the model during the selection process, and "d", "n", and "i" indicate whether trend in the response variable was decreasing, neutral or increasing, respectively.

| Common name | Scientific name | LIC | | | | | GIC | | | | |
		ΔCPA_T	Trend	Trend with $\Delta ABUND$	Trend with $\Delta YEARS$	Deviance explained (%)	ΔCPA_T	Trend	Trend with $\Delta ABUND$	Trend with $\Delta YEARS$	Deviance explained (%)
Skates	*Bathyraja* spp.	1°	d	d	d	69.6	1°	n	-	d	76.6
Arrowtooth flounder	*Atheresthes stomias*	1°	d	d	-	56.6	1°	d	-	-	39.7
Greenland turbot	*Reinhardtius hippoglossoides*	1°	d	-	d	48.1	-	-	n	d	67.2
Pacific halibut	*Hippoglossus stenolepis*	2°	d	d	d	41.9	1°	n	-	i	66.9
Flathead sole	*Hippoglossoides elassodon*	-	-	d	d	67.3	-	-	d	d	30.6
Bering flounder	*Hippoglossoides robustus*	0°	d	-	d	48	2°	d	d	n	48.5
Rex sole	*Glyptocephalus zachirus*	0°	d	-	d	60.4	0°	i	i	i	52.6
Yellowfin sole	*Limanda aspera*	2°	d	i	d	58.3	-	-	-	d	51.6
Longhead dab	*Limanda proboscidea*	-	-	d	d	41.7	-	-	-	-	64.4
Starry flounder	*Platichthys stellatus*	0°	d	-	n	55.9	1°	d	-	n	76.9
Rock sole	*Lepidopsetta* spp.	1°	d	d	d	62.7	1°	n	-	n	87.4
Alaska plaice	*Pleuronectes quadrituberculatus*	2°	d	-	d	43.7	-	-	-	d	23.1
Sturgeon poacher	*Podothecus accipenserinus*	-	-	-	d	61.9	1°	d	-	d	65.2
Buterfky sculpin	*Hemilepidotus papillio*	1°	n	-	-	43.8	-	-	i	-	49.4
Pacific cod	*Gadus macrocephalus*	1°	d	d	n	54.8	-	-	i	d	58.3
Walleye pollock	*Theragra chalcogramma*	-	-	d	-	37	0°	d	-	d	36.8
Wattled eelpout	*Lycodes palearis*	0°	d	-	d	53.4	1°	n	i	n	39
Shortfin eelpout	*Lycodes brevipes*	1°	d	d	d	62.1	1°	n	-	-	66.3
Tanner crab	*Chionoecetes bairdi*	1°	d	i	d	55.3	-	-	i	n	81.1
Snow crab	*Chionoecetes opilio*	1°	i	d	d	47.5	-	-	-	n	48.5
Red king crab	*Paralithodes camtschaticus*	2°	d	d	d	53.4	0°	d	-	n	61.6
Blue king crab	*Paralithodes platypus*	-	-	-	d	54.9	-	-	n	d	51.2

Table 2. Species omitted from analysis with rationale for exclusion.

Common name	Scientific name	Rationale
Kamchatka flounder	*Atheresthes evermanni*	1,4
Arctic cod	*Boreogadus saida*	1,2
Saffron cod	*Eleginus gracilis*	4
Pacific herring	*Clupea pallasi*	1
Yellow Irish lord	*Hemilepidotus jordani*	4
Bigmouth sculpin	*Hemitripterus bolini*	3
Sakhalin sole	*Limanda sakhalinensis*	4
Marbled eelpout	*Lycodes raridens*	2,4
Capelin	*Mallotus villosus*	1
Plain sculpin	*Myoxocephalus jaok*	2
Great sculpin	*Myoxocephalus polyacanthocephalus*	2
Warty sculpin	*Myoxocephalus verrucosus*	2
Eulachon	*Thaleichthys pacificus*	1
Bering poacher	*Occella dodecahedron*	4
Pacific sand lance	*Ammodytes hexapterus*	1
Pacific sandfish	*Trichodon trichodon*	4
Rainbow smelt	*Osmerus mordax*	1
Sawback poacher	*Leptagonus frenatus*	2,3
Searcher	*Bathymaster signatus*	3,4
Spinyhead sculpin	*Dasycottus setiger*	3,4
Whitespotted greenling	*Hexgrammos stelleri*	3,4
Decorator crab	*Oregonia gracilis*	2
Horsehair crab	*Erimacrus isenbeckii*	4
Helmet crab	*Telmessus cheiragonus*	4

1. Bottom trawl not designed for quantative sampling of pelagic species.
2. Historical changes in the specificity and consistency of field identifications.
3. Historical changes in the consistency of subsampling rare or singular species.
4. Rare or patchily distributed species with insufficient data for spatial analyses.

Table 3. Range, average, and standard deviation of local (*LIC*) and global (*GIC*) collocation indices by species.

Species	LIC				GIC			
	Min.	Max.	Avg.	SD	Min.	Max.	Avg.	SD
Skates	0.19	0.72	0.49	0.11	0.79	1.00	0.97	0.03
Arrowthooth flounder	0.27	0.84	0.64	0.13	0.88	1.00	0.98	0.02
Greenland turbot	0.26	0.83	0.54	0.11	0.60	1.00	0.93	0.08
Pacific halibut	0.23	0.71	0.46	0.09	0.80	1.00	0.97	0.03
Flathead sole	0.08	0.85	0.44	0.16	0.85	1.00	0.97	0.04
Bering flounder	0.04	0.84	0.46	0.15	0.71	1.00	0.92	0.06
Rex sole	0.38	0.99	0.78	0.13	0.84	1.00	0.97	0.03
Yellowfin sole	0.35	0.87	0.59	0.09	0.88	1.00	0.98	0.02
Longhead dab	0.09	0.92	0.57	0.16	0.58	1.00	0.93	0.08
Starry flounder	0.03	0.84	0.37	0.18	0.44	1.00	0.90	0.12
Rock sole	0.28	0.91	0.57	0.12	0.69	1.00	0.96	0.05
Alaska plaice	0.21	0.82	0.53	0.13	0.83	1.00	0.97	0.03
Sturgeon poacher	0.07	0.89	0.46	0.17	0.51	1.00	0.91	0.09
Buterfly sculpin	0.01	1.00	0.46	0.25	0.47	1.00	0.84	0.13
Pacific cod	0.12	0.80	0.37	0.12	0.81	1.00	0.97	0.03
Walley pollock	0.08	0.67	0.32	0.10	0.74	1.00	0.95	0.05
Wattled eelpout	0.08	0.71	0.38	0.13	0.56	1.00	0.90	0.10
Shortfin eelpout	0.00	0.85	0.48	0.19	0.09	1.00	0.85	0.21
Tanner crab	0.09	0.89	0.36	0.17	0.55	1.00	0.92	0.08
Snow crab	0.08	0.73	0.43	0.11	0.66	1.00	0.95	0.06
Red king crab	0.03	0.95	0.38	0.19	0.45	1.00	0.91	0.10
Blue king crab	0.03	0.97	0.44	0.22	0.31	1.00	0.83	0.18

Table 4. The distance and bearing associated with a change in the center of gravity (ΔCG) by species for warm relative to cold years, high relative to low abundance years, and early relative to recent years for illustrating the magnitude and direction of the predictor variables ΔCPA_T (cold pool area at threshold temperature T), $\Delta ABUND$ (change in abundnace), and $\Delta YEARS$ which had a significant effect on the global index of collocation (GIC).

Species	Approximated predictor variable	ΔCG Distance (km)	ΔCG Bearing (degrees)
Skates	$\Delta CPA \leq 1°$	30	196
	$\Delta YEARS$	61	28
Arrowtooth flounder	$\Delta CPA \leq 1°$	36	136
Greenland turbot	$\Delta ABUND$	16	147
	$\Delta YEARS$	24	336
Pacific halibut	$\Delta CPA\_1°$	35	119
	$\Delta YEARS$	54	306
Flathead sole	$\Delta ABUND$	33	131
	$\Delta YEARS$	90	301
Bering flounder	$\Delta CPA\_2°$	37	205
	$\Delta ABUND$	20	135
	$\Delta YEARS$	21	45
Rex sole	$\Delta CPA\_0°$	6	264
	$\Delta ABUND$	17	294
	$\Delta YEARS$	22	132
Yellowfin sole	$\Delta YEARS$	19	85
Starry flounder	$\Delta CPA\_1°$	21	116
	$\Delta YEARS$	35	20
Rock sole	$\Delta CPA\_1°$	31	161
	$\Delta YEARS$	42	316
Alaska plaice	$\Delta YEARS$	21	52
Sturgeon poacher	$\Delta CPA\_1°$	5	244
	$\Delta YEARS$	36	230
Butterfly sculpin	$\Delta ABUND$	13	334
Pacific cod	$\Delta ABUND$	32	292
	$\Delta YEARS$	40	303
Walleye pollock	$\Delta CPA\_0°$	42	262
	$\Delta YEARS$	50	309
Wattled eelpout	$\Delta CPA\_1°$	79	296
	$\Delta ABUND$	16	296
	$\Delta YEARS$	113	112
Shortfin eelpout	$\Delta CPA\_1°$	54	128
Tanner crab	$\Delta YEARS$	42	211
Snow crab	$\Delta ABUND$	35	152
	$\Delta YEARS$	57	303
Red king crab	$\Delta CPA\_0°$	31	240
	$\Delta YEARS$	11	90
Blue king crab	$\Delta YEARS$	68	337

Year 1

3.0	3.0	3.0
3.0	3.0	3.0
3.0	3.0	3.0
3.0	3.0	3.0

mean = 3.0

Year 2

2.0	1.0	6.0
5.0	0.0	4.0
4.0	0.0	5.0
6.0	1.0	2.0

mean = 3.0

Year 3

4.0	1.0	4.0
4.0	1.0	4.0
4.0	1.0	4.0
4.0	1.0	4.0

mean = 3.0

Year 4

3.5	2.5	4.0
3.0	2.0	3.0
3.0	2.0	3.0
4.0	2.5	3.5

mean = 3.0

X = Center of gravity

Figure 1.

Fig. 2

Fig. 3

a)

N
100 km

W ——————————— E
100 km   100 km

100 km
S

b)

N
100 km

W ——————————— E
100 km   100 km

100 km
S

c)

N
100 km

W ——————————— E
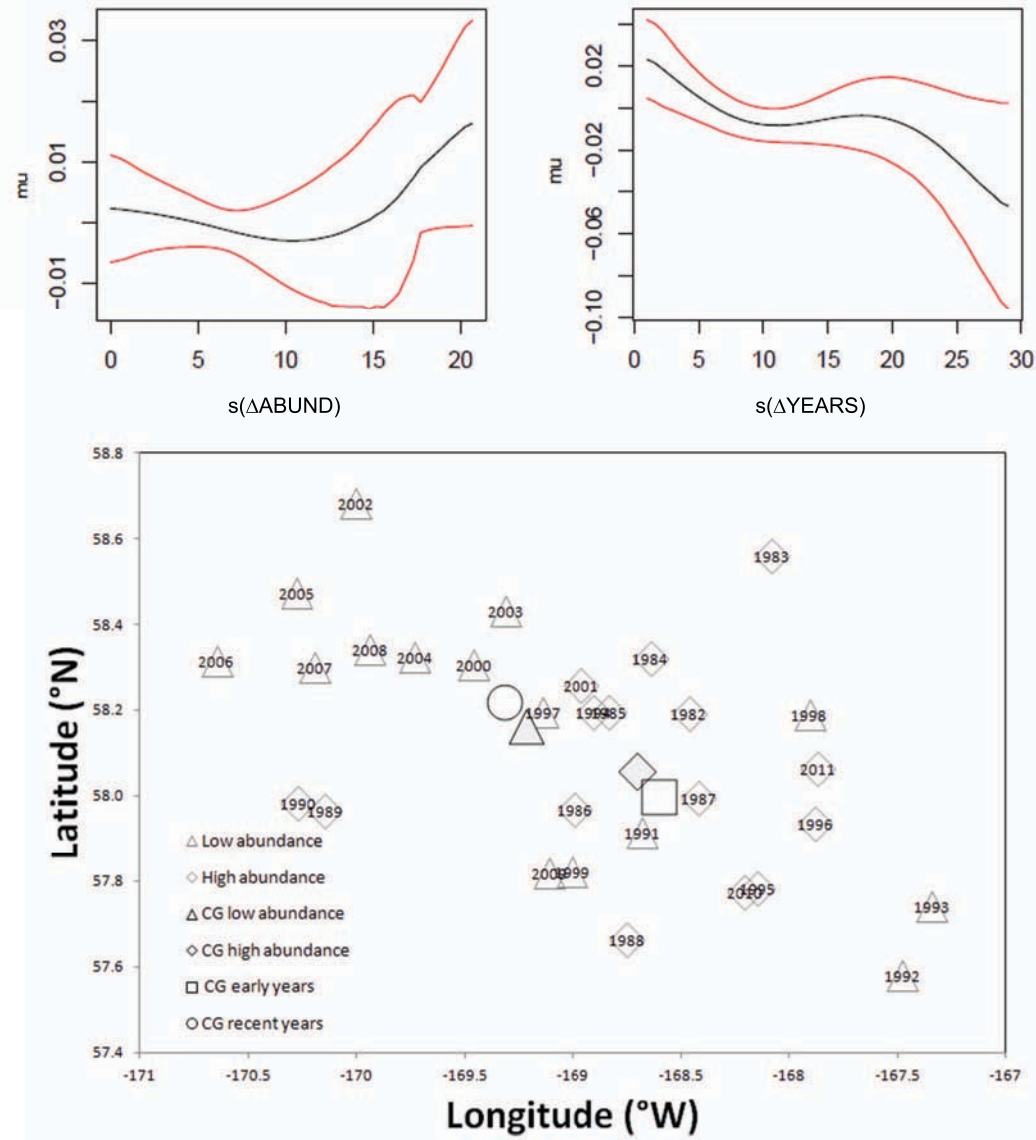100 km   100 km

100 km
S
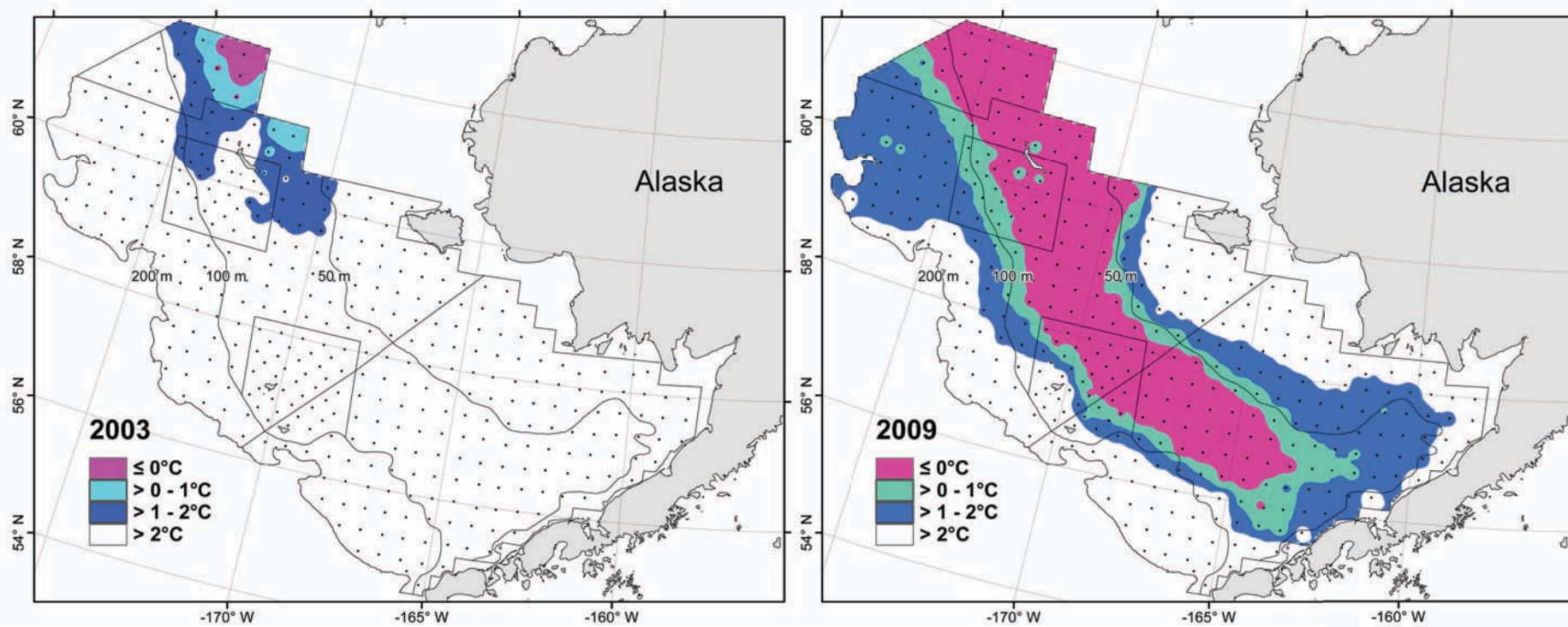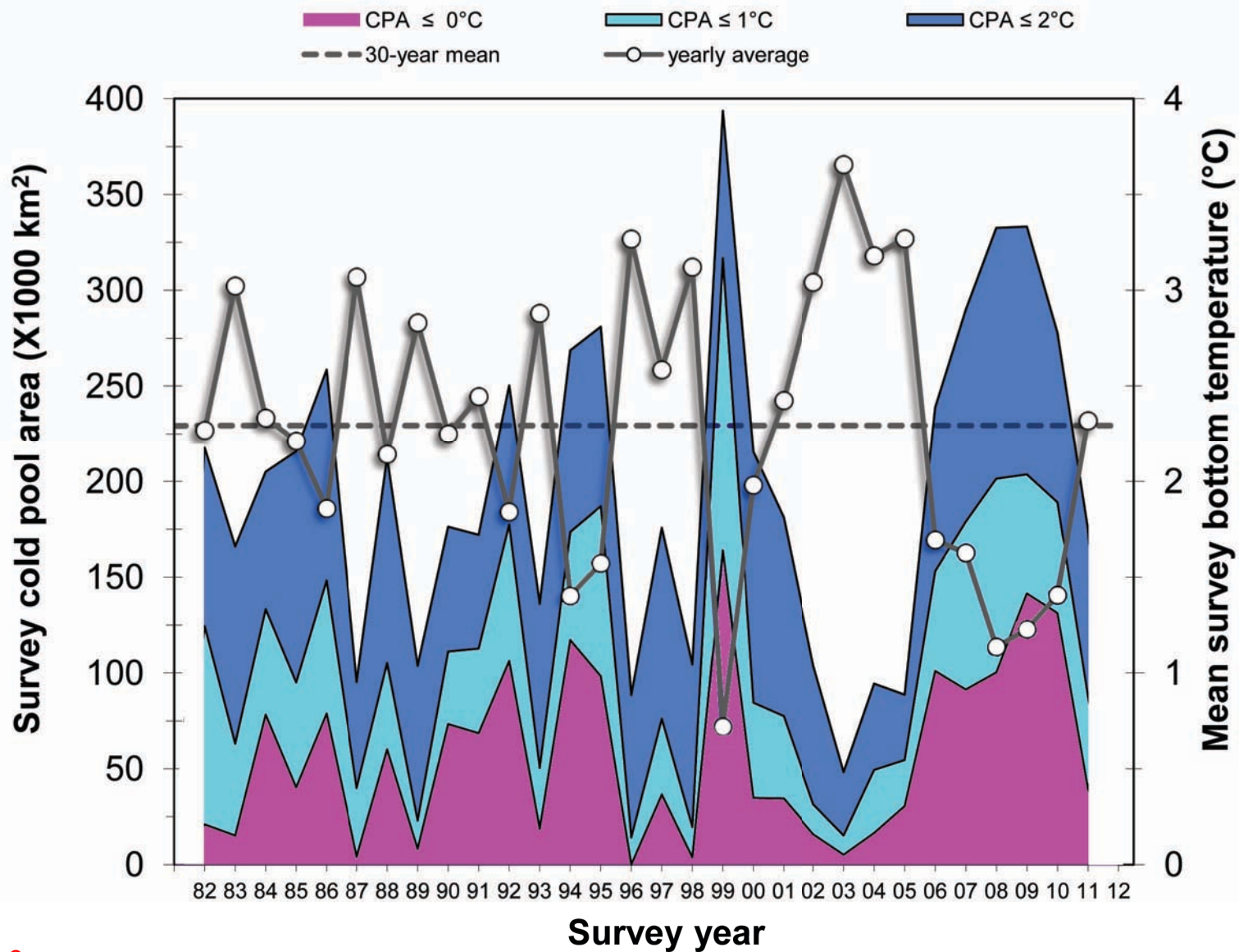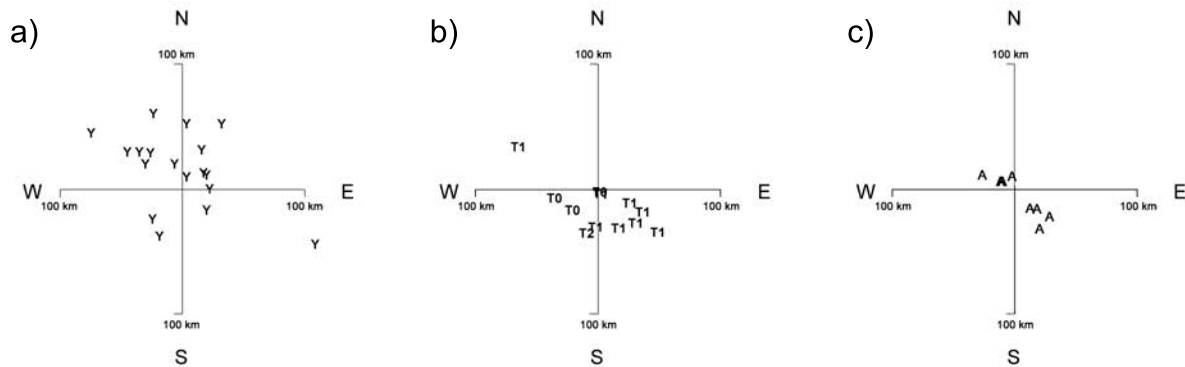
Fig. 4

Walleye pollock

Fig. 5

Fig. 6

Pacific cod

s(ΔABUND)

s(ΔYEARS)

Fig. 7

Fig. 8

Pacific cod
— 1°C isotherm

Cold years

Warm years

St. Matthew Island

Bristol Bay

s(ΔCPA≤ 1°C)

High abundance

Low abundance

kg/km²

0
> 0 - 10
> 10- 20
> 20 - 30
> 30 - 40
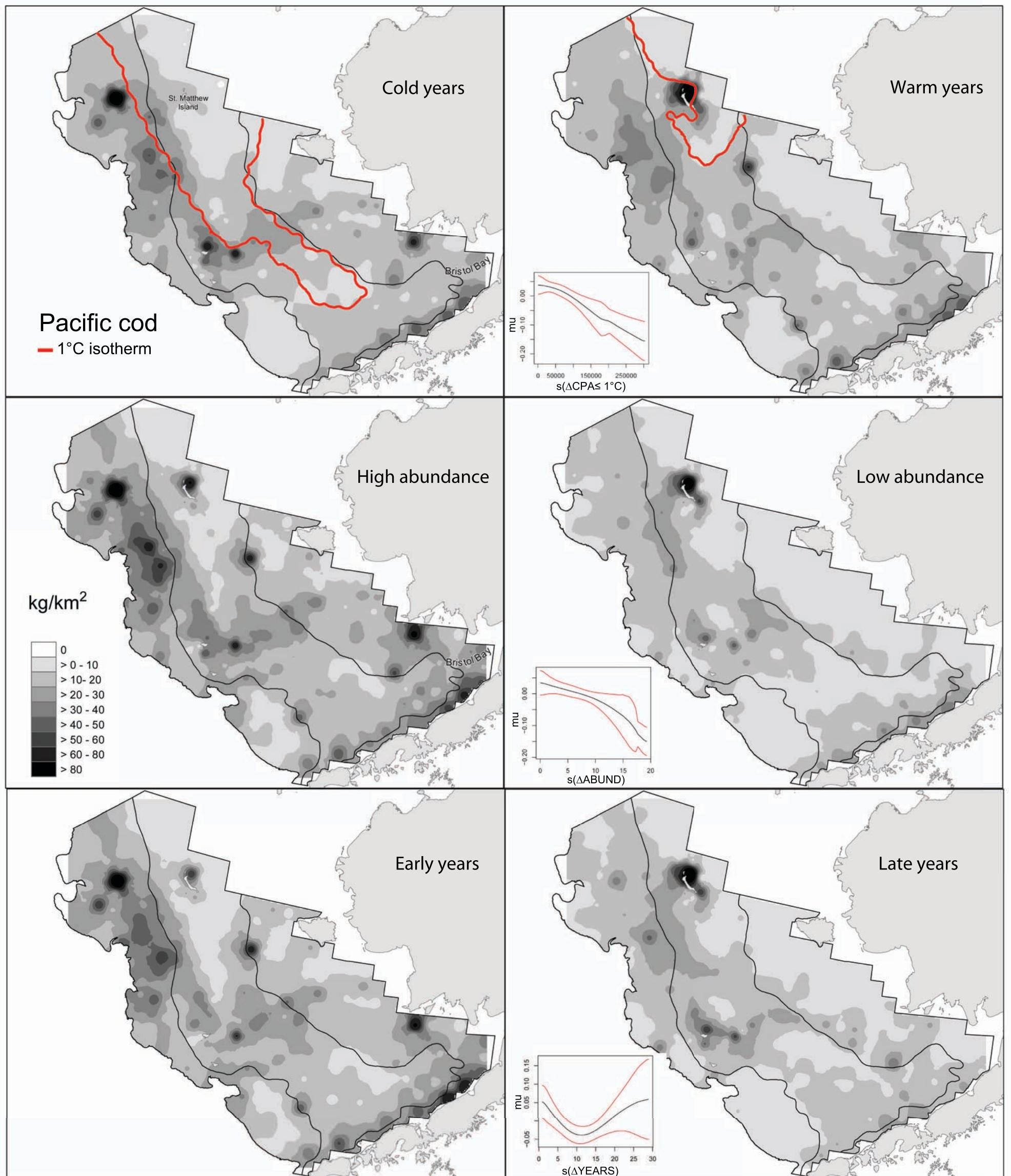> 40 - 50
> 50 - 60
> 60 - 80
> 80

Bristol Bay

s(ΔABUND)

Early years

Late years

s(ΔYEARS)
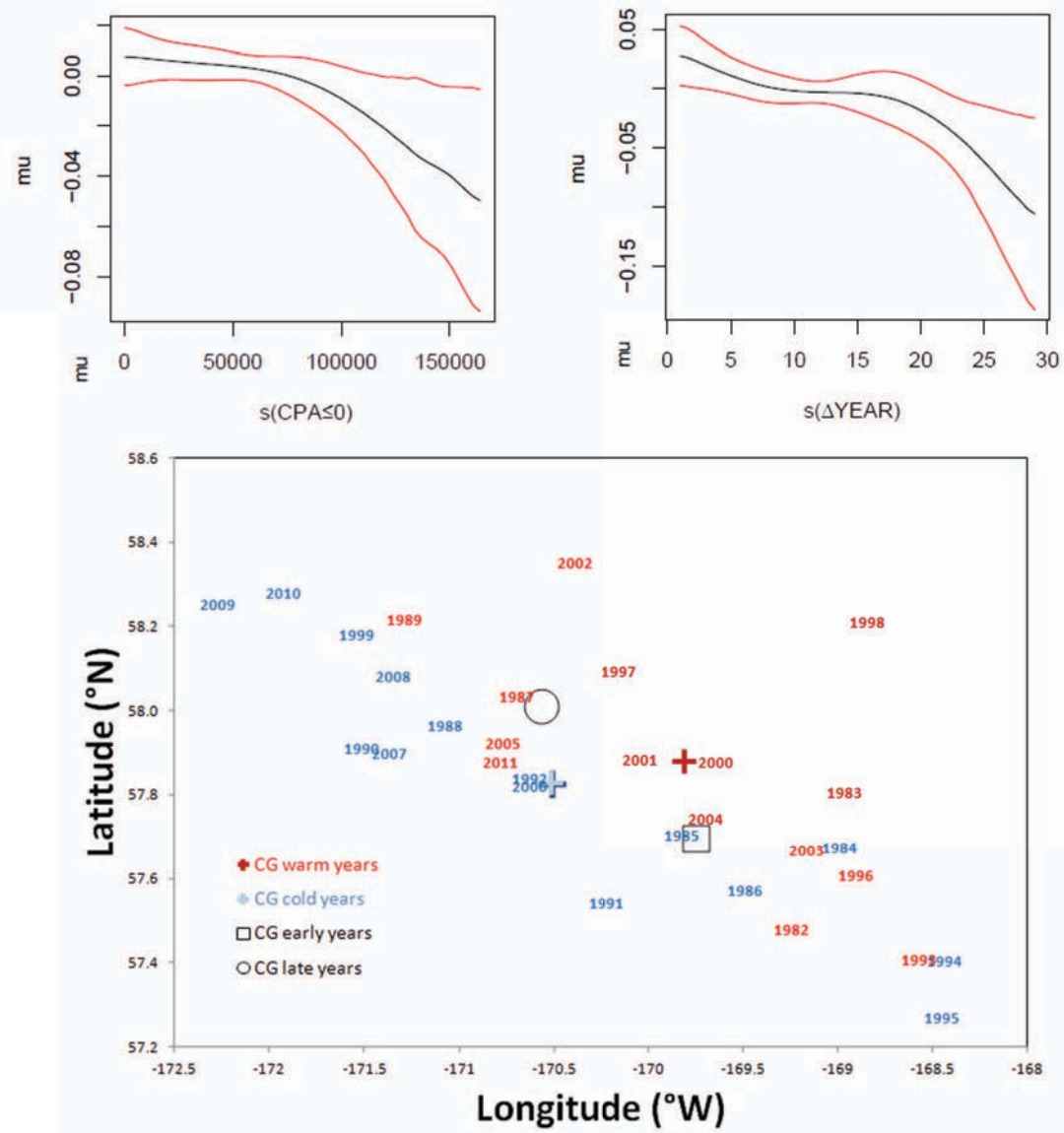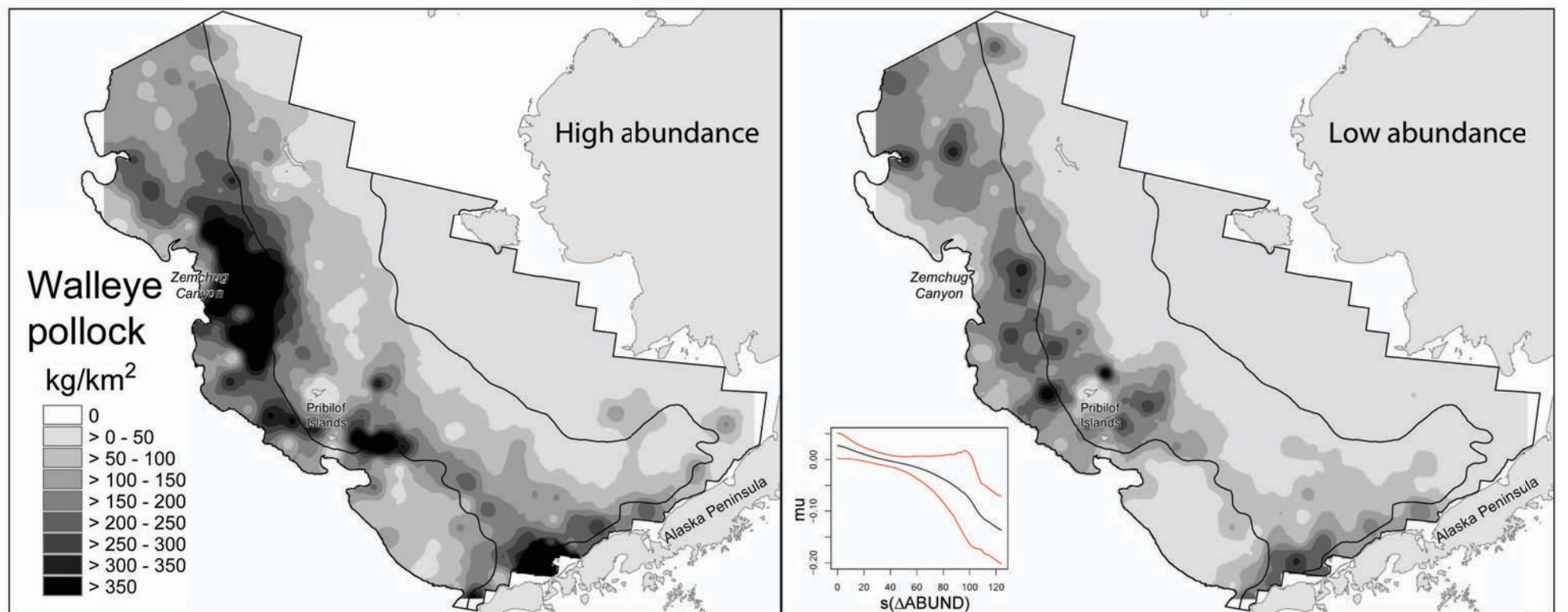
Arrowtooth flounder

Fig. 9

Fig. 10