

1 **Biogeography of seabirds within a high-latitude ecosystem: use of a data-**  
2 **assimilative ocean model to assess impacts of mesoscale oceanography**

3 Jarrod A. Santora<sup>1</sup>, Lisa B. Eisner<sup>2</sup>, Kathy J. Kuletz<sup>3</sup>, Carol Ladd<sup>4</sup>, Martin Renner<sup>5</sup>, George L. Hunt,  
4 Jr<sup>6</sup>

5 <sup>1</sup>University of California Santa Cruz, Department of Applied Mathematics and Statistics, Center  
6 for Stock Assessment Research, Santa Cruz, CA, 95060

7 <sup>2</sup>Alaska Fisheries Science Center, NOAA, 7600 Sand Point Way NE, Seattle, WA, 98115 USA

8 <sup>3</sup>U.S. Fish and Wildlife Service, Anchorage, AK, 99503 USA

9 <sup>4</sup>NOAA, Pacific Marine Environmental Laboratory, 7600 Sand Point Way NE, Seattle, WA 98115

10 <sup>5</sup>Tern Again Consulting, 811 Ocean Drive Loop, Homer, AK 99603 USA

11 <sup>6</sup>School of Aquatic and Fishery Sciences, University of Washington, Seattle WA 98195 USA

12 Email: jsantora@ucsc.edu

13

14

15

16

17

18

19

20

21

22

23

24 **Abstract:** We assessed the biogeography of seabirds within the Bering Sea Large Marine  
25 Ecosystem (LME), a highly productive and extensive continental shelf system that supports  
26 important fishing grounds. Our objective was to investigate how physical ocean conditions  
27 impact distribution of seabirds along latitudinal gradients. We tested the hypothesis that  
28 seabird biogeographic patterns reflect differences in ocean conditions relating to the boundary  
29 between northern and southern shelf ecosystems. We used a grid-based approach to develop  
30 spatial means (1975-2014) of summertime seabird species' abundance, species' richness, and a  
31 multivariate seabird assemblage index to examine species composition. Seabird indices were  
32 linked to ocean conditions derived from a data-assimilative oceanographic model to quantify  
33 relationships between physics (e.g., temperature, salinity, and current velocity), bathymetry  
34 and seabirds along latitudinal gradients. Species assemblages reflected two main sources of  
35 variation, a mode for elevated richness and abundance, and a mode related to partitioning of  
36 inner/middle shelf species from outer shelf-slope species. Overall, species richness and  
37 abundance increased markedly at higher latitudes. We found that latitudinal changes in species  
38 assemblages, richness and abundance indicates a major shift around 59–60°N within inner and  
39 middle shelf regions, but not in the outer shelf. Within the middle shelf, latitudinal shifts in  
40 seabird assemblages strongly related to hydrographic structure, as opposed to the inner and  
41 outer shelf waters. As expected, elevated species richness and abundance was associated with  
42 major breeding colonies and within important coastal foraging areas. Our study also indicates  
43 that seabird observations supported the conclusion that the oceanographic model captured  
44 mesoscale variability of ocean conditions important for understanding seabird distributions and  
45 represents an important step for evaluating modeling and empirical studies. Biogeographic  
46 assessments of LMEs that integrate top predator distributions resolve critical habitat  
47 requirements and will benefit assessment of climate change impacts (e.g., sea-ice loss)  
48 predicted to affect high-latitude marine ecosystems.

49 **Key words:** Bering Sea; biodiversity; macroecology; large marine ecosystem; species richness;  
50 structural realism

52 **1.0 Introduction**

53 Macroecology provides a framework for assessing relationships between marine organisms and  
54 ocean-climate conditions to understand the biogeography of Large Marine Ecosystems (LMEs;  
55 Sherman 1991). As global climate change is predicted to impact marine biodiversity patterns  
56 and food web interactions in LMEs (Willig et al., 2003; Tittensor et al., 2011), investigating the  
57 biogeography of potential indicator species and how they reflect latitudinal gradients in the  
58 physical and biological components of the coastal ocean will improve our ability to predict  
59 future range shifts of species and key ecosystem services (e.g., fisheries; Meuter and Litzow,  
60 2008). This is especially important in high-latitude, sea-ice-dominated ecosystems, where  
61 conditions are predicted to change rapidly, thereby possibly denying presently resident species  
62 of habitat qualities essential for survival (Arrigo et al., 2008; Wang et al., 2012). However, to  
63 reveal key processes underlying the spatial organization of LMEs, macroecological investigations  
64 require large, long-term data sets of species distributions and climatic conditions. Upper trophic  
65 level predators (i.e. seabirds and marine mammals) integrate the influences of hydrography and  
66 lower trophic levels (i.e., zooplankton and fish) via changes in their distribution, abundance or  
67 species composition.

68 Large data sets of seabird species' distribution and abundance patterns are available for  
69 assessing seabird biogeography in the eastern Bering Sea (e.g., Renner et al., 2013; Hunt et al.,  
70 2014). Living at the interface between land, sea and air, seabirds are highly mobile and  
71 conspicuous in marine ecosystems, and may be useful indicators of ocean-climate conditions  
72 and fishery resources (Piatt et al., 2007). In this study, we investigated the biogeography of  
73 seabird species' abundance, richness, and assemblages using a 40-year dataset of pelagic  
74 seabird distribution and abundance. We assessed the co-occurrence of seabird assemblages  
75 and hydrographic features of the eastern Bering Sea and tested hypotheses about the  
76 differences in seabird responses to hydrographic clines vs. fronts. Through this approach, we  
77 also assessed the utility of seabirds as indicators of the macroecology of a high-latitude LME,  
78 the eastern Bering Sea shelf region.

79 The eastern Bering Sea shelf ecosystem is a vast and highly productive ecosystem that sustains  
80 a diverse array of micronekton, fish, shellfish, seabirds and marine mammals (Piatt and  
81 Springer, 2003), and is one of the most important fishing grounds in the world (Mueter and  
82 Litzow, 2008; Baker and Hollowed, 2014). Stretching from the Alaska Peninsula to Bering Strait  
83 (Fig.1), the Bering Sea represents a 1200 km gradient of sub-Arctic to Arctic environmental  
84 conditions within a 600K km<sup>2</sup> continental shelf that is 500 km wide (Stabeno et al., 1995; Piatt  
85 and Springer, 2007; Danielson et al., 2011). Biological productivity and its fate in this marine  
86 ecosystem are strongly influenced by the latitudinal extent, concentration, and timing of retreat  
87 of seasonal sea-ice cover (Stabeno et al., 2012). Substantial environmental gradients in ocean  
88 conditions and bathymetry exist in both the cross-shelf and along-shelf directions, and interact  
89 to influence the structure of benthic, mid-water and surface biological communities (Coachman  
90 1986; Danielson et al., 2014; Stabeno et al., 2016; Sigler et al., 2011, 2017). Environmental  
91 gradients in the cross-shelf direction are similar to many continental shelf ecosystems (Levin  
92 and Dayton, 2009), with well-mixed coastal waters inshore, stratified waters offshore, and a  
93 hydrographic front marking the boundary between oceanic and shelf waters (Schumacher et  
94 al., 1986; Kachel et al., 2002; Ladd and Stabeno, 2012). The spatial structure of the  
95 southeastern Bering Sea shelf ecosystem is organized according to hydrographic conditions  
96 related to the bathymetry of the inner (<50 m), middle (50-100 m) and outer shelf regions (100-  
97 200 m), each separated by fronts (Coachman 1986), along with centers of rich biological  
98 productivity associated with sub-marine canyon systems and islands (Hunt et al., 2008). In the  
99 southeastern Bering Sea, the southern extent of cold bottom temperatures (i.e., cold pool)  
100 within the middle shelf is a defining characteristic of the ecosystem's biogeography and impacts  
101 regional fisheries (Mueter and Litzow, 2008; Baker and Hollowed, 2014).

102

103 At about 59 - 60 degrees north, there is a transition between the northern (Arctic) and southern  
104 (sub-Arctic) shelf ecosystems (Sigler et al., 2011; Stabeno et al. 2012). The hydrographic  
105 differences north and south of this transition zone are influenced by winter sea ice conditions  
106 (e.g., approximate location of the maximum sea ice extent in March), and persist throughout  
107 the summer (Danielson et al., 2011a, b). North of the transition zone, there are major

108 differences in the hydrography of the inner (< 40-50 m) and middle (50-100 m) shelf regions  
109 compared to the southeastern shelf (Ladd and Stabeno, 2012). In winter the inner and middle  
110 shelf regions are well mixed from the Alaska Peninsula to Bering Strait (Stabeno et al., 2012). In  
111 summer in the southeastern Bering Sea (south of the transition zone), the inner shelf remains  
112 well mixed due to the interaction of wind and tidal mixing (Danielson et al., 2014), while, the  
113 middle shelf is stratified by solar heating (Ladd and Stabeno, 2012). The pycnocline of the  
114 summer southern middle shelf is thin and subsurface blooms are uncommon (Stabeno et al.,  
115 2012). In contrast, north of the transition zone, summer stratification occurs in both the middle  
116 shelf and the inner shelf regions (Ladd and Stabeno, 2012). This northern stratification is based  
117 on both temperature and salinity with summer heating, sea-ice formation and melting, and  
118 river input all playing a role (Danielson et al. 2011; Stabeno et al., 2012; Ladd and Stabeno,  
119 2012). On the northern middle shelf, the pycnocline is thicker and subsurface phytoplankton  
120 blooms are common (Stabeno et al., 2012). There is growing evidence that food webs of the  
121 middle shelf differ north and south of this zonal boundary (Aydin and Meuter, 2007; Sigler et  
122 al., 2011) and that they support different communities of zooplankton, groundfish, seabirds and  
123 marine mammals (Piatt and Springer, 2003; Sigler et al., 2011; Baker and Hollowed, 2014;  
124 Eisner et al., 2014). In contrast to the sluggish flow of the inner and middle shelf regions, along  
125 the shelf edge and over much of the outer shelf, northward flowing waters can carry abundant  
126 large crustacean zooplankton from the southern shelf-slope and basin northward through  
127 Anadyr Strait into the western Chirikov Basin and Bering Strait (Springer et al., 1996). These  
128 northward flowing waters transport nutrients and phytoplankton as well as zooplankton, and  
129 support a rich fauna of seabird planktivores in the central and western Chirikov Basin and  
130 Chukchi Sea (Piatt and Springer, 2003; Sigler et al., 2017). Because of this continuous northward  
131 flow, there is no abrupt shift in either the physical or biological oceanography of the outer and  
132 shelf-slope regions until one reaches St. Lawrence Island and the input of Anadyr Water  
133 (Springer et al., 1996; Piatt and Springer, 2003; Eisner et al., 2014).

134

135 Our overarching objective was to assess how physical ocean conditions impact the  
136 biogeography of seabird species' abundance, richness, and assemblages, along latitudinal

137 gradients within the inner, middle and outer shelf regions of the eastern Bering Sea shelf.  
138 Specifically, we tested the hypothesis that seabird biogeographic patterns reflect differences  
139 relating to the boundary (59 – 60 °N) between northern and southern shelf ecosystems. We  
140 predicted that there would be significant changes in the seabird fauna where the hydrographic  
141 structure of the inner and middle shelf regions change, but in the outer shelf, where there is  
142 only a gradual, clinal shift with increasing latitude, the seabird fauna would show no abrupt  
143 shifts south of the input of Anadyr Water. To test our hypothesis, we used data from the North  
144 Pacific Pelagic Seabird Database (NPPSD) to develop spatial climatologies (1975-2014) of  
145 summertime pelagic seabird biogeography patterns within the eastern Bering Sea shelf LME.  
146 We evaluated relationships between seabird distributions and the physical environment using a  
147 data-assimilative oceanographic model to assess the role of ocean conditions on seabird  
148 biogeography. In doing so, we also assessed the utility of seabird observations for evaluating  
149 the structural realism of the oceanographic model (Santora et al., 2013; Schroeder et al., 2014),  
150 thereby providing insight on how seabirds may inform the efficacy of physical models to  
151 identify the mesoscale ecosystem oceanography of upper trophic level species in an LME. We  
152 discuss the implications of our results for applying seabird biogeography and oceanographic  
153 models to understand the zonal boundaries of shelf ecosystems and the potential impacts of  
154 climate change.

## 155 **2.0 Methods**

### 156 ***2.1 Synthesis of seabird assemblages***

157 The geographic scope and scale of our biogeographic assessment of seabird assemblages  
158 focused on climatological summer spatial distribution patterns, covering the geographic domain  
159 shown in Figs. 1-2. The study domain was bounded to the east, shoreward to the 10 m isobath,  
160 to the west by the 1500 m isobath, south to the Alaska Peninsula and north to Bering Strait.  
161 Seabird distributions were derived from the NPPSD (U.S. Geological Survey, Drew et al., 2015)  
162 and the data used herein are reviewed in Renner et al., (2013, 2016) and Hunt et al., (2014).  
163 Although the data set provided a long-time series, there were limited data available across the  
164 entire study domain to assess seasonal and long-term changes (Hunt et al., 2014). Therefore,

165 this study focused on the macro perspective of seabird biogeographic patterns based on  
166 climatological spatial averages.

167 As in previous studies of seabird species assemblages and distribution patterns in the Bering  
168 Sea (Sigler et al., 2011; Renner et al., 2013; Hunt et al., 2014; Kuletz et al., 2014), we established  
169 a grid of cells 50x50 km based on the extent and continuity of the seabird surveys contained  
170 within the NPPSD to summarize survey effort (# 3 km transect segments). First, survey data  
171 were extracted from 1975-2014 for the months of May through September. To estimate  
172 comparable long-term spatial means of seabird species richness (mean number of all species  
173 observed; n=67 taxa) and abundance per grid cell, we applied an effort cutoff (cells had to have  
174 >50 3-km transect segments; Fig. 1). Due to the inconsistency in species identification of  
175 *Ardenna spp.* shearwaters across years, shearwater observations (primarily short-tailed  
176 shearwaters) were pooled into a 'dark shearwater' category (as per Renner et al., 2016). We  
177 also included a *Brachyramphus* murrelet species group to avoid difficulties regarding species  
178 identification in this genus. For consistency over the large temporal scope of this study, we  
179 excluded all other un-identified taxa from our total taxa list (n=67 taxa), but included sea ducks,  
180 loons and grebes. The latter species may not forage in the study area, but are important  
181 migratory species during summer and early fall (Hunt et al., 2014). Second, we determined a  
182 subset of species with occurrences in greater than 10% of grid cells (i.e., removed rare or less  
183 frequently sighted species), resulting in a group of 34 species to assess biogeographic patterns  
184 of seabird assemblages. These species represent a variety of life histories and have different  
185 feeding, breeding and migratory behaviors. Regarding feeding behavior, this group of seabirds  
186 is generally categorized as pursuit-diving (e.g., alcids and cormorants) and surface feeders (e.g.,  
187 albatrosses, gulls and storm-petrels), or a combination of both feeding types (e.g.,  
188 shearwaters). See Hunt et al. 2014 and Renner et al. 2016 for a further description of the  
189 feeding behavior and occurrence of seabirds derived from the NPPSD.

190 We predicted that a spatial analysis of the most frequently encountered and abundant species  
191 would show the following major sources of spatial variation: (a) locations characterized by high  
192 species abundance (and species richness) associated with known breeding islands (Renner et

193 al., 2013) and key abundance hotspots (e.g., Unimak Pass and submarine canyons; Ladd et al.,  
194 2005), (b) an east – west division partitioning species with affinities for the outer shelf-slope  
195 and those with inshore shelf preferences (Hunt et al., 2014), and c) a north-south division in the  
196 middle shelf that reflected the abrupt shift in the physical environment at about 60° N (Sigler et  
197 al., 2011), but no such division in the outer shelf.

198 The spatial mean of species relative abundance (n=34 taxa) per grid cell (over 40 years) was  
199 transformed (ln+1) and inputted into a Principal Component Analysis (PCA) to assess coherence  
200 among species. Determined by eigenvalues (e.g., >3) and percent variance explained, the major  
201 PC axes (i.e., PC1 and PC2) were then mapped onto grid cells to provide a spatially-explicit  
202 multivariate species assemblage index, enabling further evaluation of the latitudinal variability  
203 of species assemblages and the location of distinct biogeographic zonal boundaries. Moreover,  
204 to assess their coherence with the leading modes derived from the PCA and to determine  
205 potential geographic indicator species, a randomization test was used to evaluate the  
206 correlation between species abundance and PC loadings. To complement the PCA and to  
207 visualize seabird species assemblages, we calculated a similarity matrix (based on species  
208 abundance per grid cell) for a cluster analysis to derive a dendrogram to visualize species  
209 assemblages. The resulting seabird species assemblage index (index by PC1 and PC2) was then  
210 compared to climatological physical oceanographic conditions to assess biogeographic patterns  
211 on the eastern Bering Sea shelf.

## 212 **2.2 Oceanographic conditions**

213 Bathymetry data were derived from the GEBCO satellite altimetry data product  
214 ([https://www.bodc.ac.uk/data/online\\_delivery/gebco/](https://www.bodc.ac.uk/data/online_delivery/gebco/)), which was specifically designed for the  
215 Bering Sea (AlaskaREgionBathymetricDEMv1.04, provided by the Alaska Ocean Observing  
216 System). We calculated the slope of sea depth (ln of percent rise) as an index of the  
217 heterogeneity of bathymetry. Since our objective was to assess regional drivers of the  
218 climatological biogeography of seabird assemblages, we used the results of a data assimilative  
219 model of climatological ocean conditions (Panteleev et al., 2011). The model was tuned to  
220 climatological ocean conditions for the Bering Sea using observational data such as



221 hydrographic casts, moorings and drifter buoys; the model has an 18 km resolution, and  
222 assimilated observations from 1932-2004 (see Panteleev et al., 2011 for a review of the model;  
223 <http://beringsea.eol.ucar.edu/models/panteleev-approach.html>). Specifically, we extracted the  
224 modeled summertime climatology data on sea surface height (SSH; cm), and current velocities  
225 ( $\text{cm s}^{-1}$ ) at 7.5 m, and temperature ( $^{\circ}\text{C}$ ) and salinity averaged over 10-35 m. Bathymetric and  
226 oceanographic model output was spatially averaged onto the seabird grid cells for geospatial  
227 modeling (Figs. 1-2).

228 Depth integration ranges were chosen to reflect generalized mesoscale ocean conditions for  
229 surface-feeding and pursuit-diving seabirds (Schneider et al., 1987; Schneider 1990; Russell et  
230 al., 1999; Jahncke et al., 2008) and to delineate frontal boundaries between the inner, middle  
231 and outer shelf (Coachman 1986). Furthermore, the bathymetric and hydrographic variables  
232 were selected to characterize the ecosystem oceanography for assessing seabird biogeographic  
233 hotspot concentration patterns (Santora et al., 2017a, b), which often interact to influence the  
234 mesoscale spatial organization of seabird abundance and biodiversity hotspots at sea (Piatt et  
235 al., 2006; Hyrenbach et al., 2007, Renner et al., 2013, Santora et al. 2017a, b). We did not  
236 consider evaluating relationships between seabird distribution patterns with satellite remotely-  
237 sensed conditions (e.g., Chlorophyll-*a*) because we were interested in assessing ocean  
238 conditions from particular water-column depths. Further, evaluation of seabird biogeographic  
239 patterns with modeled ocean conditions provided an independent assessment of model  
240 performance and may advance the discipline of ecosystem oceanography (Cury et al., 2008).

### 241 **2.3 Geospatial models**

242 To test our hypothesis that the along-shelf latitudinal variability of seabird species richness,  
243 total abundance, and species assemblages reflects the zonal boundary at approximately 59 – 60  
244  $^{\circ}\text{N}$  for the inner and middle shelf areas, but not for the outer shelf, we extracted geographic  
245 slices of grid cells containing seabird indices (e.g., species richness, total abundance and  
246 principal components, PC1 and PC2) and oceanographic conditions (contingent with isobaths  
247 selections) within the inner, middle and outer shelf regions (Coachman 1986; see Fig.1 for the  
248 boundaries of geographic slices). The inner shelf geographic slice was selected based on

249 centering grid cells inshore of the 50 m isobath, ranging from the inner coastal waters of the  
250 Alaskan Peninsula to the Bering Strait (n=79 cells). The waters to the east of Unimak Pass along  
251 the 50 m isobath ('Slime Bank') were excluded from this analysis. The geographic slice for the  
252 middle shelf was selected from grid cells seaward of the 50 m to the 100 m isobath (n=117  
253 cells), and the outer shelf and shelf-slope from 100 m to 1500 m depth (n=74 cells). Our  
254 reasoning behind examining the along-shelf variability of the inner and middle shelf is that they  
255 are separated by hydrographic fronts occurring in proximity to the 50 and 100 m isobaths, and  
256 the inner shelf during summer is well mixed and weakly stratified, compared to the strongly  
257 stratified middle shelf (e.g., warm wind-mixed surface and cooler bottom temperature)  
258 (Coachman 1986). Furthermore, these cross-shelf gradients also display latitudinal variability  
259 owing to circulation of water and the position of hydrographic fronts in the northern middle  
260 shelf (Stabeno et al., 2012).

261 We used Generalized Additive Models (GAMs) to investigate the along-shelf variability of the  
262 seabird species richness, total seabird abundance and species assemblage index (PC1 and PC2),  
263 per grid cell within the inner, middle and outer shelf regions (Fig. 1) relative to latitude,  
264 bathymetric slope, temperature, salinity, SSH, and current speed. Due to collinearity issues that  
265 may impact model fitting, the variable 'distance to land' (Fig. 2) was omitted from models  
266 because it was highly correlated (e.g.,  $r > 0.8$ ) with other physical oceanographic variables.  
267 Furthermore, we examined the relationship among other physical variables within each shelf  
268 region and determined that SSH was highly correlated ( $r > 0.7$ ) with some variables (e.g., salinity)  
269 within the inner and outer shelf regions. Therefore, it was removed from those models to avoid  
270 overfitting (Zuur et al. 2009). However, SSH was included in the middle shelf models because it  
271 was not correlated with other model variables. No other significant correlations were detected  
272 among environmental variables.

273 The GAM (e.g., for middle shelf) was specified as Seabird Variable =  $s(\text{latitude}) + s(\text{slope}) +$   
274  $s(\text{temperature}) + s(\text{salinity}) + s(\text{SSH}) + s(\text{current speed})$ ; where  $s$  is a smooth regression spline.  
275 GAMs for seabird species richness and total abundance were specified with a quasi-Poisson  
276 distribution and a log-link function, whereas the seabird assemblage index (PC1 and PC2) was

277 specified as a Gaussian distribution and identity link function (Wood 2011). GAMs were  
278 implemented using the *mgcv* package in the R statistical program (R Development Core Team,  
279 2016) using generalized cross-validation to estimate smoothness parameters (Zuur et al. 2009).  
280 Adjusted pseudo  $R^2$  and percent deviance explained were used to evaluate model performance.  
281 The effect of each covariate included in each GAM was plotted to inspect visually the  
282 functional form and assess potential biogeographic breaks in seabirds assemblage indices,  
283 species richness and abundance relative to latitude, and to determine specific range values  
284 associated with changes in environmental variables within each shelf region (Dormann et al.,  
285 2007; Zuur et al., 2009).

## 286 **3.0 Results**

### 287 ***3.1 Biogeography of seabird assemblages***

288 Maps of the climatological spatial means of total seabird abundance and species richness .  
289 showed that mean seabird abundance and species richness were elevated near island breeding  
290 colonies (e.g., Pribilof Islands, St. Matthew and St. Lawrence Islands) and along the Alaska  
291 Peninsula (Fig. 3a-b). Additional high abundance and richness areas were associated with  
292 Unimak Pass and along the shelf-slope in association with Bering, Pribilof and Zhemchug  
293 submarine canyons (Figs. 1 and 3). Total seabird abundance was also high within the southeast  
294 Bering Sea shelf, in association with the inner and middle shelf regions. North of the Pribilof  
295 Islands, between Nunivak and St. Matthew Islands, there was an area of relatively low total  
296 seabird abundance and species richness that extended to the waters south and east of St.  
297 Lawrence Island. To the north of St. Lawrence Island within the Anadyr Water, total seabird  
298 abundance and richness was high from the southern Chirikov Basin to the Bering Strait (Fig. 3a-  
299 b).

300 The PCA applied to the abundance of 34 taxa partitioned the variance of species associations,  
301 resolving two principal components, explaining 11.3% and 10.4% (Eigenvalues >3) of the total  
302 variance, respectively (Table S.1; Fig. 4a-b, Fig. S.1). Similarly, the cluster analysis of species  
303 abundance complemented the biogeographic breaks informed by the PCA (Fig. S.1) and  
304 provided additional detail on associations among specific species (Fig. 4c). The first principal

305 component ('seabird PC1') indicated locations of high species' richness and total seabird  
306 abundance (Figs. 3 and 4a), highlighting locations associated with seabird colonies at the  
307 Pribilof, St. Matthew, and Nunivak islands, as well as waters north of St. Lawrence Island within  
308 the Chirikov Basin associated with the Anadyr Water (Figs. 1 and 4a). Species whose abundance  
309 is positively correlated ( $p < 0.05$ ) and are associated with PC1 (Table S.1, Fig. S.1)) are black-  
310 legged kittiwake (*Rissa tridactyla*), common murre (*Uria aalge*), crested auklet (*Aethia*  
311 *cristatella*), herring gull (*Larus argentatus*), horned puffin (*Fratercula corniculata*), Kittlitz's  
312 murrelet (*Brachyramphus brevirostris*), parakeet auklet (*Aethia psittacula*), pelagic cormorant  
313 (*Phalacrocorax pelagicus*), pigeon guillemot (*Cephus columbia*), red phalarope (*Phalaropus*  
314 *fulicarius*), red-faced cormorant (*Phalacrocorax urile*), red-legged kittiwake (*Rissa brevirostris*),  
315 red-necked phalarope (*Phalaropus*), thick-billed murre (*Uria lomvia*), and tufted puffin  
316 (*Fratercula cirrhata*).

317 The second component ('seabird PC2') indicated a geographic break in seabird assemblages  
318 that separated the inner and middle shelf from the outer shelf-slope area (e.g., species with  
319 either on-shore/offshore affinity; Table S.1, Fig. 4b-c, Fig. S.1). For PC2, positive values indicate  
320 increased abundance of inner and middle shelf species (i.e., shoreward species), while negative  
321 values are associated with increased abundance of outer shelf and shelf-slope species. Inner  
322 and middle shelf indicator species associated with PC2 are arctic tern (*Sterna paradisaea*),  
323 black-legged kittiwake, ancient (*Synthliboramphus antiquus*), Kittlitz's, marbled (*B. marmoratus*)  
324 and murrelet spp. (*Brachyramphus spp.*), Cassin's auklet (*Ptychoramphus aleuticus*), common  
325 murre, glaucous winged-gull (*Larus glaucescens*), Pacific loon (*Gavia pacifica*), Sabine's gull  
326 (*Xema sabini*), and shearwater (*Ardrenna spp.*). Outer shelf and slope indicator species are fork-  
327 tailed storm petrel (*Oceanodroma furcata*), Laysan albatross (*Phoebastria immutabilis*), least  
328 auklet (*Aethia pusilla*), northern fulmar (*Fulmarus glacialis*), red-legged kittiwake and thick-  
329 billed murre. Within PC2, there was an apparent north-south geographic break in shoreward  
330 species assemblages around 59 – 60° N from Nunivak Island extending west-northwest towards  
331 St. Matthews Island.

### 332 **3.2 Latitudinal variability of seabird biogeographic patterns**

333 We found oceanographic conditions and latitudinal variability were important for explaining the  
334 biogeographic patterns of seabird species richness, species assemblages and total abundance  
335 (Table 1a-c). Overall, all seabird variables revealed a strong response to increasing latitude  
336 within the inner and middle shelf, indicating potential biogeographic zonal boundaries in  
337 avifauna (Fig. 5-6). Along the inner shelf, the multivariate seabird assemblage indices (seabird  
338 PC1 and PC2) displayed contrasting functional relationships relative to latitude, with seabird  
339 PC1 (i.e., variance associated with increased abundance and richness associated with islands)  
340 increased in magnitude abruptly around 63° N, near St. Lawrence Island and where Anadyr  
341 water dominates, while PC2 (i.e., variance associated with shoreward species) displayed a  
342 decrease in response to latitude between ~59° and 61°N (Fig. 5a-b). Within the middle shelf  
343 (50-100 m isobaths), both seabird PC1 and PC2 displayed abrupt increases around 59 – 60° N,  
344 and this change is partly attributable to the location of St. Matthew Island (Figs. 4 and 5c-d). In  
345 the outer shelf, we found no effect of latitude for either the seabird assemblage index (P1 and  
346 P2) or total seabird abundance (Table 1c).

347 The GAM analysis showed that species richness within the inner shelf increased around 63° N  
348 (near St. Lawrence Island), while species richness within the middle shelf increased around 59–  
349 60° N (south of St. Matthew Island) (Fig. 6a, c). However, in the outer shelf, species richness  
350 declined with increasing latitude and displayed a geographic break around 59° N in the outer  
351 shelf, possibly associated with Zemchug Canyon (Fig.6e). There was a decline in total seabird  
352 abundance around 59° N and an increase around 63° N within the inner shelf. In contrast, total  
353 seabird abundance within the middle shelf displayed a steep decline with increasing latitude,  
354 with a leveling off occurring around 58° N (Fig. 6b, d).

### 355 ***3.3 Environmental determinants of seabird biogeographic patterns***

356 Along the inner shelf, seabird PC1 was positively and linearly related to current speed and  
357 displayed a positive asymptotic relationship with bottom slope (Table 1a; Fig. 7a, Fig. S.2).  
358 Species richness within waters < 50 m deep was related to current speed owing to increased  
359 current speed and richness at higher latitudes associated with the productive waters of the

360 Anadyr Current and Bering Strait regions (Figs. 1, and S.2). There were no significant  
361 relationships between seabird PC2 and environmental variables within the inner shelf.

362 Overall, our models indicate there were more significant relationships between seabirds and  
363 environmental variables within the middle shelf compared to the inner and outer shelf regions  
364 (Table 1a-c), which may be attributed to more complex physical ocean conditions within the  
365 highly stratified waters of the middle shelf. Bathymetric slope, temperature, salinity, current  
366 speed and SSH were important for relating changes in seabird variables relative to  
367 environmental gradients within the middle shelf (Figs 7-8 and Figs. S.2-4). Seabird PC1  
368 displayed a peak at moderate levels of slope, while PC2 and total abundance were linearly  
369 related to slope within the middle shelf (Fig. 7a-b). Seabird PC1 was negatively related to  
370 current speed (Fig. S.2). Seabird PC1, PC2 and species richness were positively and linearly  
371 related to temperature (averaged over 10-35 m), while total abundance was non-linearly  
372 related to temperature, with a sensitivity to temperatures around 5.5° C within the middle shelf  
373 (Figs. 2d, 8a-b). In the middle shelf, seabird PC1, species richness, and total abundance were  
374 strongly related to salinity (averaged over 10-35 m), with sensitivity around 31.4 to 31.8 (PSU)  
375 (Fig. 2e, Fig. S.3). Further, seabird PC1, species richness and total abundance were non-linearly  
376 related to SSH, indicating a strong effect for SSH values of 16 to 18 cm (Fig. S.4).

377 In the outer shelf, seabird PC1 was negatively related to temperature (Figs. 8). Seabird PC2,  
378 which relates to abundance of outer shelf species (e.g., fork-tailed storm-petrel and Laysan  
379 albatross), was positively related to temperature, with a strong response to temperatures  
380 greater than 7.0° C (Fig. 8). PC1 was also associated with bottom slope (Fig. 7), especially within  
381 steep regions of the outer shelf. Species richness in the outer shelf was negatively and linearly  
382 related to temperature and current speed, and positively associated with higher values of  
383 salinity (Table 1c; Figs. 7-8 and Fig. S.3).

#### 384 **4.0 Discussion**

385 Biogeographic assessments of high-latitude marine systems are critical for understanding the  
386 structure and function of ecosystems and evaluating future climate change impacts on the

387 distributions of species. In particular, quantifying latitudinal gradients of species diversity and  
388 composition along with environmental drivers is important for assessing the spatial  
389 organization of marine ecosystems. In this paper, we used the output of a data-assimilative  
390 oceanographic model to determine the relationships between seabird distribution and  
391 abundance and oceanographic variables descriptive of the Bering Sea LME. We found evidence  
392 supporting our hypothesis regarding a change in seabird species assemblages, richness and  
393 abundance that indicates a major shift around latitude 59 – 60° N within both the inner and  
394 middle shelf regions, but not in the outer shelf regions. Further, our biogeographic assessment  
395 indicated two major macro-scale (1000s km) sources of variation for seabird assemblages  
396 within Bering Sea LME: (a) areas of high species richness and abundance associated with  
397 breeding colonies and feeding hotspots, and (b) partitions reflecting both north-south  
398 (separated at ~60°N) and east-west divisions of species abundance associated with the inner  
399 and middle shelf regions from those in the outer shelf and shelf-slope regions. The latter  
400 partition suggests that seabird assemblages are strongly related to the physical and biological  
401 structure of the Bering Sea shelf, which is organized by bathymetry (e.g., bottom slope), water  
402 column structure (e.g., stratification and mixing) and location of frontal zones, all of which  
403 interact to generate seabird foraging habitats (Hunt et al., 2014; Renner et al., 2016). Our  
404 results on seabird biogeography support previous biogeographic assessments of fish and  
405 shellfish that also found evidence for the separation of northern and southern shelf ecosystems  
406 (Meuter and Litzow, 2008; Sigler et al., 2011; Baker and Hollowed, 2014) and changes  
407 associated with sub-Arctic to Arctic ecosystems (Sigler et al., 2017).

408 Our synthesis is dependent on at least two important caveats. First, due to data limitations at  
409 the scale of the study area, we were unable to examine temporal variability of seabird  
410 distributions to assess the presence of trends, cycles (e.g., seasonality and inter-decadal  
411 variability), or long-term range shifts for species richness and abundance. It would be useful for  
412 future efforts to examine subsets of the data set to assess temporal patterns. For example, in  
413 the southeast Bering Sea, where surveys were more frequent, Renner et al. (2016)  
414 demonstrated that the cross-shelf distribution of seabirds is altered by timing of sea ice retreat  
415 in spring and the summer abundance of zooplankton and forage fish. Furthermore, Suryan et

416 al., (2016) indicated that spatial relationships among seabirds and forage species (e.g.,  
417 zooplankton and forage fish) are also seasonally-dependent on seabird migration patterns and  
418 prey availability. Examination of these effects on seabirds in the along-shelf direction is of  
419 interest because seabird response may differ between the northern and southern shelf as a  
420 result of differences in hydrography (Stabeno et al., 2012). Second, we did not explicitly assess  
421 physical ocean processes within ecoregions that may offer a mechanistic explanation of the  
422 observed differences in seabird assemblages that we found. Important physical processes may  
423 include sub-mesoscale variability of currents and frontal development (i.e., indicators of  
424 retention and advective processes) which are known influences on productivity hotspots  
425 (Santora et al., 2017b), and associated with islands or submarine canyon systems in the Bering  
426 Sea (Moore et al., 2002; Sigler et al., 2017).

#### 427 ***4.1 Northern and southern biogeographic regions***

428 Seabird biogeography in the Bering Sea LME reflects oceanographic conditions along both  
429 cross-shelf and along-shelf gradients. Our study corroborates the results of others that  
430 identified three biogeographic regions: the area associated with the Chirikov Basin and Bering  
431 Strait, and a partition between the northern and southern shelf areas, with a major geographic  
432 shift around 59 – 60° N in both the inner and middle shelf regions (Piatt and Springer, 2003;  
433 Sigler et al., 2011). The latitudinal increase in species richness and abundance (i.e., PC1) at the  
434 northern extent of the inner shelf region (63 – 64° N) is related to the swift, turbulent, and  
435 productive Anadyr Water west of St. Lawrence Island and extends into Bering Strait, and  
436 represents a region of enhanced eddy activity and concentration of biological productivity (Piatt  
437 and Springer, 2003; Grebmeier et al., 2006). As a result, the shallow shelf region north and  
438 west of St. Lawrence Island contains dense concentrations of crustacean zooplankton (e.g.,  
439 copepods and euphausiids), and supports ~ 5 million seabirds during summer, most of which  
440 are planktivorous auklets, whose breeding colonies are located on the north shore of St.  
441 Lawrence Island and on King Island (Springer et al., 1987, 1989; Elphic and Hunt, 1993; Russell  
442 et al., 1999; Piatt and Springer, 2003).



443 The Alaska Coastal Current, which enters the Bering Sea through Unimak and Samalga Passes,  
444 flows eastward along the Alaska Peninsula and northward within the inner and middle shelf  
445 regions (Schumacher et al., 1982; Stabeno et al., 2002; Ladd et al., 2005). Freshwater input  
446 from rivers also interacts with the Alaska Coastal Current to influence the position of  
447 hydrographic fronts between the inner shelf and the middle shelf (Danielson et al., 2014). The  
448 waters of the inner shelf (<40 m) north of 60°N are stratified in summer due to brine rejection  
449 in winter, which creates a cold dense bottom layer, and ice melting in spring that creates a  
450 buoyant surface layer (Eisner et al., 2014). Moreover, stratification in the inner shelf in the  
451 north is likely due to higher freshwater input and weaker tides than farther south (Ladd and  
452 Stabeno, 2012). South of 60 °N, the waters of the inner shelf are well mixed by a combination  
453 of tidal stirring at the bottom and wind mixing at the surface (Danielson et al. 2011b, 2014).  
454 Collectively, these hydrography patterns influence the cross-shelf and along-shelf distribution  
455 and abundance of forage fish and piscivorous seabird species within the inner shelf (Schneider  
456 et al., 1987; Parker-Setter et al., 2013; Hunt et al., 2014; Renner et al., 2016). Our seabird  
457 assemblage index, PC2 (abundance of shoreward species) indicates a distinct grouping of high  
458 values within Bristol Bay that extends north to Nunivak Island, and then declines abruptly with  
459 increasing latitude (i.e., north-south boundary). Presumably, the decline in the seabird  
460 assemblage index is in part due to lack of breeding colonies along the mainland coast. The  
461 seabird fauna of the inner shelf is mostly composed of sub-surface (diving) seabirds, including  
462 alcids and large concentrations of shearwaters (Schneider et al., 1986; Hunt et al., 2014; Suryan  
463 et al., 2016) that depend on variety of crustacean zooplankton and forage fish species (Eisner et  
464 al., 2014, 2015).

465 Within the middle shelf, we also detected shifts in seabird assemblages, and richness at 59 –  
466 60° N and a shift in total seabird abundance at 59° N. Forage fish and mesozooplankton  
467 communities also display a biogeographic shift at this latitude (Eisner et al., 2015). Both seabird  
468 assemblage indices (PC1 and PC2) and species richness increased at this boundary, indicating a  
469 positive change in species richness and assemblage of middle shelf species with increasing  
470 latitude. This shift is attributed to the presence of St. Matthew Island, which is located within  
471 the middle shelf just north of 60° N, and contains many species of breeding seabirds (Piatt and

472 Springer, 2007). However, total seabird abundance within the middle shelf displayed a decline  
473 around 59° N, and we attribute this to a decrease in shearwater abundance, the most abundant  
474 species in the southern shelf region (Hunt et al., 2014; Suryan et al., 2016).

475 Owing to the oceanographic complexity (e.g., more mixing, frontal development) of the middle  
476 shelf and greater cross-shelf area, we found a higher number of significant relationships  
477 between seabirds and environmental variables. Increases in total seabird abundance and  
478 seabird PC1 and PC2 coincided with areas with the steepest bottom slope, highest  
479 temperatures and lowest salinity values. Part of this variability is attributable to increased  
480 species richness and abundance associated with island locations in the middle shelf (e.g.,  
481 Pribilof and St. Matthews Islands), which are also regions of elevated Chl-a concentration  
482 (Eisner et al., 2016). However, most of the variability is related to the position of hydrographic  
483 fronts that separate the 3 shelf regions, which are effective in concentrating zooplankton,  
484 forage fish and seabirds (Schneider et al., 1987; Jahncke et al., 2008; Hunt et al., 2008; Eisner et  
485 al., 2014). Seabird species assemblages also changed from the inner shelf to the middle and  
486 outer shelf, with an increase in the abundance of surface foragers (i.e., storm-petrels and  
487 albatrosses) farther offshore (Sigler et al., 2011; Hunt et al., 2014; Kuletz et al., 2014).

488 In the outer shelf, we found species richness declined with increasing latitude and that there  
489 were no abrupt changes of seabird assemblage indices. In the region around 59° N at the  
490 northern edge of Zemchug Canyon, there was an area of increased abundance. As other studies  
491 have noted (Piatt and Springer, 2003), there was an increase in species richness and abundance  
492 in the northern outer shelf where these waters converge with the Anadyr current and move  
493 eastward onto the middle and inner shelf. Aside from bottom slope and temperature, our  
494 models found fewer environmental relationships with seabird variables in the outer shelf  
495 compared to the middle shelf. This could be attributed to the more homogenous physical  
496 conditions in the alongshore direction of the outer shelf (Springer et al., 1996; Danielson et al.,  
497 2011a), at least from the perspective of the physical variables we investigated. Mesoscale  
498 processes, such as eddy recirculation associated with the interaction of currents and the  
499 location of submarine canyon systems, were more important for understanding the regional

500 variability of seabird assemblage and abundance patterns within the outer shelf (Sigler et al.,  
501 2011; Renner et al., 2013, Kuletz et al., 2014, Paredes et al., 2014).

#### 502 ***4.2 Seabirds as indicators of modeled ocean conditions***

503 To best of our knowledge, our study is the first to investigate environmental drivers of seabird  
504 biogeography within an LME using a data-assimilative ocean model. Evaluating structural  
505 realism of ocean-ecosystem models by comparing independent observations that were not  
506 incorporated in the model may illuminate whether a model successfully captures important  
507 meso-scale ocean processes (e.g., eddies and frontal development) that influence the spatial  
508 organization of biological communities (Cury et al. 2008). Due to their relative ease in  
509 monitoring, seabird distribution and abundance at sea are useful for evaluating the structural  
510 realism of ocean-ecosystem models (Santora et al., 2013) and provide independent  
511 observations for assessing model performance. For these reasons, our synthesis of seabird  
512 biogeography used climatological oceanographic conditions from a data-assimilative model  
513 specifically tuned for the Bering Sea LME. We found that seabird assemblages, and species  
514 richness and abundance were significantly related to variability in modeled ocean conditions,  
515 especially along latitudinal gradients. In particular, our empirical models determined that  
516 seabird distributions were sensitive to spatial variability in modeled estimates of sub-surface  
517 temperature, salinity, and current speed, which indicates that the ocean model captures meso-  
518 to macro-scale variability of ocean conditions in the Bering Sea important for seabirds.  
519 Evaluation of other Bering Sea regional ocean models with observed biological time series also  
520 indicate models capture important modes of physical and biological variability (Danielson et al.,  
521 2011a). Data-assimilative oceanographic models enable assessment of ocean conditions  
522 throughout the water column and backwards through time to assess phenology and pre-  
523 conditioning effects on marine biological patterns (Schroeder et al. 2014). Therefore, relating  
524 seabird distributions and other biological observations to oceanographic model output can be a  
525 powerful tool for exploring biogeographic patterns and will also benefit the assessment and  
526 development of ocean-ecosystem models to assure they capture ecologically relevant scales of  
527 marine ecosystems.

### 528 **4.3 Climate and ecosystem implications**

529 Biogeographic assessments of LMEs that integrate top predator distributions help resolve basic  
530 habitat requirements of top predators, and will benefit conservation planning, and assessment  
531 of climate change impacts (Tittensor et al., 2011; Sydeman et al., 2016). Our seabird  
532 biogeographic assessment provides critical information on how the Bering Sea LME is spatially  
533 organized according to along-shore variation in species richness, total abundance and species  
534 assemblages. Our results supports previous work on the classification of ecoregions of the  
535 Bering Sea LME (Piatt and Springer, 2007; Sigler et al., 2011), and provides evidence that  
536 seabird biogeography patterns clearly indicate a partitioning of the LME into northern and  
537 southern zones. This information will be useful for developing or revising Bering Sea ecosystem  
538 models that integrate ocean climate conditions, forage species and top predators to evaluate  
539 climate change and human-related stressors.

540 It is well known that basin-scale ocean climate conditions in the North Pacific and Arctic Oceans  
541 impact the development of sea ice and timing of sea ice retreat in the Bering Sea (Arrigo et al.,  
542 2008; Meuter and Litzow, 2008; Overland et al., 2012). As a result of this climate variability, the  
543 southeastern Bering Sea shelf ecosystem has recently been characterized as having stanzas of  
544 warm and cool sea temperature, with impacts on the distribution and abundance of key forage  
545 species and top predators (Eisner et al., 2015; Andrews et al., 2016; Renner et al., 2016). Future  
546 global warming scenarios in the Bering Sea predict possible reductions in sea ice duration and  
547 extent (Wang et al. 2012). Changes in the biogeography of the Bering Sea are already apparent.  
548 Decreasing sea ice impacts the range of Arctic and sub-Arctic species, and variability in the  
549 catch of some commercially-fished species is increasing (Meuter and Litzow, 2008), and the  
550 extent of the Bering Sea cold pool influenced the southern range Arctic species (Stevenson and  
551 Lauth, 2012; Baker and Hollowed, 2014). However, it's unclear whether this will impact the  
552 zonal boundaries of northern and southern shelf communities of zooplankton, fish and  
553 seabirds, because the cold pool may act as a barrier for the range expansion of some Arctic and  
554 sub-Arctic species (Meuter and Litzow, 2008; Baker and Hollowed, 2014; Sigler et al., 2017).  
555 Our study indicates that species richness increases with latitude (i.e., closer to the Arctic) and is

556 highest in proximity to island breeding colony locations. It is unlikely that most resident  
557 breeding species (e.g., murre) will undergo distribution shifts due to lack of suitable breeding  
558 habitat. However, migratory species (e.g., shearwaters) may be more adept at shifting their  
559 distributions as they are not tied to breeding colonies and may be more flexible to track  
560 seasonal foraging hotspots throughout the Bering Sea (Hunt et al. 2017). Although our  
561 synthesis did not incorporate temporal change (e.g., seasonal and interannual), the seabird  
562 biogeographic patterns quantified here provide a promising starting point for exploring how  
563 species assemblages and zonal boundaries may shift as a result of climate change projections.  
564 For example, simulations of the effect of climate change on the ecoregions of Bering Sea could  
565 be compared to seabird observations to evaluate the sensitivity of seabird richness and  
566 abundance hotspots to different climate change projections (Wang et al., 2012). Comparing the  
567 velocity of climate change within and across LMEs (Burrows et al., 2011) may also prove useful  
568 for understanding how seabird distributions may undergo range shifts.

569 **Acknowledgements:**

570 Funding for this work was provided by the North Pacific Research Board (NPRB project number  
571 1408). At sea surveys since 2006 were funded by grants to USFWS by NPRB (Projects 637 and  
572 B64, B67, B68) and BOEM (IA AK10-10). We greatly appreciate the effort and dedication of all  
573 the seabird observers who at collected data at sea and especially, G. Drew and J. Piatt for  
574 developing the NPPSD. We are also grateful for the BEST-BSIERP, G. Panteleev and other  
575 researchers for providing access to their ocean model. We appreciate the feedback from 2  
576 anonymous reviewers which greatly improved this paper. This research is contribution EcoFOCI-  
577 0891 to NOAA's Ecosystems and Fisheries-Oceanography Coordinated Investigations and PMEL  
578 contribution 4656.

579 **References:**

580 Arrigo, K.R., van Dijken, G., Pabi, S. 2008. Impact of a shrinking Arctic ice cover on marine  
581 primary production. *Geophysical Research Letters*, 35:L19603. doi: 10.1029/2008GL035028  
582  
583 Aydin, K., Meuter, F. 2007. The Bering Sea – a dynamic food web perspective. *Deep-Sea*  
584 *Research II*, 54, 2501-2525.  
585

586 Baker, M.R., Hollowed, A.B. 2014. Delineating ecological regions in marine systems: integrating  
587 physical structure and community composition to inform spatial management in the eastern  
588 Bering Sea. *Deep-Sea Research II*, 109, 215-240  
589

590 Ballance, L.T., Pitman, R.L., Reilly, S.B. 1997. Seabird community structure along a productivity  
591 gradient: importance of competition and energetic constraint. *Ecology*, 78, 1502–1518  
592

593 Burrows, M.T. *et al.* 2011. Velocity of climate change in terrestrial and marine ecosystems.  
594 *Science*, 334, 652-655.  
595

596 Coachman, L.K. 1986. Circulation, water masses and fluxes on the southeastern Bering Sea  
597 shelf. *Continental Shelf Research*, 5, 23-108.  
598

599 Cury, P., Shin, Y-J., Planaque, B., Durant, J.M., Fromentin, J., Kramer-Schadt, S., Stenseth, N.C.,  
600 Travers, M., Grimm, V. 2008. Ecosystem oceanography for global change in fisheries. *Trends in*  
601 *Ecology and Evolution*, 23, 338–346.  
602

603 Danielson, S., Churchister, E., Hedstrom, K., Weingartner, T., Stabeno, P. 2011a. On ocean and  
604 sea ice modes of variability in the Bering Sea. *Journal of Geophysical Research: Oceans*, 116  
605 C12034  
606

607 Danielson, S., Eisner, L., Weingartner, T.W., Aagard, L. 2011b. Thermal and haline variability  
608 over the central Bering Sea shelf: seasonal and interannual perspectives. *Continental Shelf*  
609 *Research*, 31, 539-554.  
610

611 Danielson, S., Weingartner, T.W., Hedstrom, K., Aagaard, K., Woodgate, R., Curchister, E.,  
612 Stabeno, P. 2014. Coupled wind-forced controls of the Bering-Chukchi shelf circulation and the  
613 Bering Strait through-flow: Ekman transport, continental shelf waves, and variations of the  
614 Pacific-Arctic sea surface height gradient. *Progress in Oceanography*,  
615 <http://dx.doi.org/10.1016/j.pocean.2014.04.006>  
616

617 Dormann, C.F., McPherson, J.M., Araújo, M.B., Bivand, R., *et al.* 2007. Methods to account for  
618 spatial autocorrelation in the analysis of species distributional data: a review. *Ecography*, 30,  
619 609-628.  
620

621 Durksi, S.M., Kurapov, Zhang, J., Pantellev, G.G. 2014. Circulation in the Eastern Bering Sea:  
622 inferences from a 2-km-resolution model. *Deep-Sea Research II*  
623

624 Eisner, L.B., Napp, J.M., Mier, K.L., Pinchuk, A.I., Andrews, A.G. 2014. Climate-mediated changes  
625 in zooplankton community structure for the eastern Bering Sea. *Deep-Sea Research II*, 109, 157-  
626 171.  
627

628 Eisner, L., Siddon, E., & Strasburger, W. 2015. Spatial and temporal changes in assemblage  
629 structure of zooplankton and pelagic fish across varying climate conditions in the eastern Bering  
630 Sea. *Izvestia TINRO*, vol 181, 141-160.

631

632 Eisner, L., Gann, J., Ladd, C., Ciciel, K., Mordy, C. 2016. Late summer/early fall phytoplankton  
633 biomass (chlorophyll a) in the eastern Bering Sea: Spatial and temporal variations and factors  
634 affecting chlorophyll a concentrations. *Deep-Sea Research II*, 134, 100-114.

635 Elphick, C.S., Hunt, G.L., Jr. 1993. Variations in the distributions of marine birds with water mass  
636 in the northern Bering Sea. *Condor*, 95, 33-44.

637 Grebmeier, J.M., Overland, J.E., Moore, S.E., Farley, E.V., Carmack, E.C., Cooper, L.W., Frey, K.E.,  
638 Helle, J.H., McLaughlin, F.A., McNutt, S.L. 2006. A major ecosystem shift in the northern Bering  
639 Sea. *Science*, 311, 1461–1464.

640

641 Hunt, G.L. Jr., Renner, M., Kuletz, K. 2014. Seasonal variation in the cross-shelf distribution of  
642 seabirds in the southeastern Bering Sea. *Deep-Sea Research II*, 109, 266-281.

643

644 Hunt, G.L. Jr., Stabeno, P.J., Strom, S., Napp, J.M. 2008. Patterns of spatial and temporal  
645 variation in the marine ecosystem of the southeastern Bering Sea, with special reference to the  
646 Pribilof Domain. *Deep-Sea Research Part II*, 49, 5821-5853.

647

648 Hunt, G.L. Jr., Stabeno, P., Walters, G., Sinclair, E., Brodeur, R.D., Napp, J.M., Bond, N.A. 2002.  
649 Climate change and control of the southeastern Bering Sea pelagic ecosystem. *Deep-Sea*  
650 *Research II*, 49, 5821–5853.

651

652 Hyrenbach, D.K., Veit, R.R., Weimerskirch, H., Metz, N., Hunt, G.L. Jr. 2007. Community  
653 structure across a large-scale ocean productivity gradient: marine bird assemblages of the  
654 Southern Indian Ocean. *Deep Sea Research I*, 54, 1129–1145.

655

656 Jahncke, J., Vlietstra, L.S., Decker, M.B., & Hunt, G.L. Jr. 2008. At-sea distributions of marine  
657 birds around the Pribilof Islands: a multi-year comparison of temporal and spatial trends. *Deep-*  
658 *Sea Research II*, 55, 1809-1826.

659

660 Kachel, N.B., Hunt, G.L., Salo, S.A., Schumacher, J.D., Stabeno, P.J., Whitley. 2002.  
661 Characteristics and variability of the inner front of the southeastern Bering Sea. *Deep-Sea*  
662 *Research Part II*, 49, 5889-5909

663

664 Kuletz, K.J., Renner, M., Labunski, E.A., Hunt, G.L. 2014. Changes in the distribution and  
665 abundance of albatrosses in the eastern Bering Sea: 1975-2010. *Deep-Sea Research II*, 109, 282-  
666 292.

667

668 Ladd, C., Stabeno, P.J. 2012. Stratification on the eastern Bering Sea shelf revisited. *Deep-Sea*  
669 *Research II*, 65-70, 72-83.

670  
671 Legendre, P., Legendre, L. 1998. Numerical Ecology, 2<sup>nd</sup> English ed. Elsevier, Amsterdam,  
672 Netherlands.  
673  
674 Levin, L.A., Dayton, P.K. 2009. Ecological theory and continental margins: where shallow meets  
675 deep. Trends in Ecology and Evolution, 24, 606-617.  
676  
677 Meuter, F., Litzow, M. 2008. Sea ice retreat alters the biogeography of the Bering Sea  
678 continental shelf. Ecological Applications, 18, 309-320.  
679  
680 Overland, J.E., Wang, M., Wood, K.R., Percival, D.B., Bond, N.A. 2012. Recent Bering Sea warm  
681 and cold events in a 95-year context. Deep-Sea Research II, 65-70, 6-13.  
682  
683 Panteleev, G., Yaremchuk, M., Stabeno, P.J., Luchin, V., Nechaev, D.A., Kikuchi, T. 2011.  
684 Dynamic topography of the Bering Sea. Journal of Geophysical Research, 116, C05017,  
685 doi:10.1029/2010JC006354.  
686  
687 Panteleev, G., Yaremchuk, M., Luchin, V., Nechaev, D., Kukuchi, T. 2012. Variability of the Bering  
688 Sea circulation in the period 1992-2010. Journal Physical Oceanography, 68, 485-496.  
689  
690 Paredes, R., Orben, R.A., Suryan, R.M., Irons, D.B., Roby, D.D., Harding, A.M.A., Young, R.C.,  
691 Benoit-Bird, K., Ladd, C., Renner, H., Heppell, S., Phillips, R.A., Kitaysky, A. 2014. Foraging  
692 responses of black-legged kittiwakes to prolonged food shortages around colonies in the Bering  
693 Sea shelf. PLoS ONE 9.  
694  
695 Parker-Stetter, S., Horne, J., Farley, E., Barbee, D., Andrews, A., Eisner, L., Nomura, J. 2013.  
696 Summer distributions of forage fish in the eastern Bering Sea. Deep Sea Research II, 94, 211-  
697 230.  
698  
699 Piatt, J.F., Springer, A.M. 2003. Advection, pelagic food webs and the biogeography of seabirds  
700 in Beringia. Marine Ornithology, 31, 141-154.  
701  
702 Piatt, J.F., Springer, A.M. 2007. Marine ecoregions of Alaska, In Spies RB (Ed.) Longterm  
703 Ecological Change in the Northern Gulf of Alaska. Elsevier, Amsterdam.  
704  
705 Piatt, J.F., Sydeman, W.J., Wiese, F. 2007. Introduction: a modern role for seabirds as indicators.  
706 Marine Ecology Progress Series, 352, 199–204.  
707  
708 Piatt, J.F., Wetzel, J., Bell, K., DeGange, A.R., Balogh, G.R., Drew, G.S., Geernaert, T., Ladd, C.,  
709 Byrd, G.V. 2006. Predictable hotspots and foraging habitat of the endangered short-tailed  
710 albatross (*Phoebastria albatrus*) in the North Pacific: Implications for conservation. Deep-Sea  
711 Research II, 53, 387–98.  
712



713 Russell, R.W., Harrison, N.M., Hunt, G.L. 1999. Foraging at a front: hydrography, zooplankton  
714 and avian planktivory in the northern Bering Sea. *Marine Ecology Progress Series*, 182, 77-93.  
715

716 Renner, M., Parrish, J.K., Piatt, J.F., Kuletz, K.J., Edwards, A.E., Hunt, G.L. Jr. 2013. Modeling the  
717 distribution and abundance of a pelagic seabird to disentangle the roles of climate change and  
718 commercial fisheries. *Marine Ecology Progress Series*.  
719

720 Renner, M., Salo, S., Eisner, L.B., Ressler, P.H., Ladd, C., Kuletz, K.J., Santora, J.A., Piatt, J.F.,  
721 Drew, G.S., Hunt, G.L. 2016. Timing of ice retreat alters seabird abundances and distributions in  
722 the southeast Bering Sea. *Biology Letters*, 12(9), 20160276.  
723

724 Santora, J.A., Sydeman, W.J., Messie, M., Chai, F., Chao, Y., Thompson, S.A., Wells, B.K., Chavez,  
725 F.P. 2013. Triple check: Observations verify structural realism of an ocean ecosystem model.  
726 *Geophysical Research Letters*, 40, 541–546, doi:10.1002/grl.50312.  
727

728 Santora, J.A., Veit, R.R. 2013. Spatio-temporal persistence of top predator hotspots near the  
729 Antarctic Peninsula. *Marine Ecology Progress Series*, 487, 287–304.  
730

731 Santora, J.A., Veit, R.R., Reiss, C.S., Schroeder, I.D., Mangel, M. 2017a. Ecosystem oceanography  
732 of seabird hotspots: environmental determinants and relationship with Antarctic krill in an  
733 important fishing ground. *Ecosystems*, DOI: 10.1007/s10021-016-0078-8  
734

735 Santora, J.A., Sydeman, W.J., Schroeder, I.D., Field, J.C., Miller, R.R., Wells, B.K. 2017b.  
736 Persistence of trophic hotspots and relation to human impacts within an upwelling marine  
737 ecosystem. *Ecological Applications*, DOI: 10.1002/eap.1466  
738

739 Schneider, D.C. 1990. Seabirds and fronts: a brief overview. *Polar Research*, 8, 17–21.  
740

741 Schneider, D.C., Hunt, G.L., Harrison, N.M. 1986. Mass and energy transfer to seabirds in the  
742 southeastern Bering Sea. *Continental Shelf Research*, 5, 241:257.

743 Schneider, D., Harrison, N., Hunt, G.L. 1987. Variation in attendance at fronts by marine birds in  
744 the Bering Sea. *Estuarine, Coastal and Shelf Science*, 25, 135-141.

745 Schroeder, I.D., Santora, J.A., Moore, A.M., Edwards, C.A. *et al.* 2014. Application of a data-  
746 assimilative regional ocean modeling system for assessing California Current System ocean  
747 conditions, krill, and juvenile rockfish interannual variability. *Geophysical Research Letters*, 41,  
748 5942–5950.  
749

750 Schumacher, J.D., Kinder, T.H., Pashinksi, D.J., Charnell, R.L. 1979. A structural front over the  
751 continental shelf of the eastern Bering Sea. *Continental Shelf Research*, 5, 241-257.  
752

753 Sherman, K. 1991. The large marine ecosystem concept: research and management strategy for  
754 living marine resources. *Ecological Applications*, 1, 350-360

755  
756 Sigler, M.F., Renner, M., Danielson, S.L., Eisner, L.B., Lauth, R.B., Kuletz, K.J., Logerwell, E.A., &  
757 Hunt, G.L. Jr. 2011. Fluxes, fins and feathers: relationships among the Bering, Chukchi and  
758 Beaufort Sea in a time of Climate Change. *Oceanography*, 24, 112-127.  
759  
760 Sigler, M., Kuletz, K.J., Ressler, R., Friday, N., Wilson, C., Zerbini, A. 2012. Apex predators and  
761 hotspot persistence in the southeast Bering Sea. *Deep-Sea Research Part II*, 65-70, 292-303  
762  
763 Sigler, M.F., Mueter, F.J., Bluhm, B.A., Busby, M.S., Cokelet, E.D., Danielson, S.L., De Roberties,  
764 A., Eisner, L.B., *et al.* (2017) Late summer zoogeography of the northern Bering and Chukchi  
765 seas. *Deep-Sea Research II*, 135, 168-189.  
766  
767 Springer, A.M., McRoy, C.P., Flint, M.V. 1996. The Bering Sea green belt: shelf-edge processes  
768 and ecosystem production. *Fisheries Oceanography*, 5, 205–223.  
769  
770 Springer, A.M., Murphy, E.C., Roseneau, G.G., Mcroy, C.P., Cooper, B.A. 1987. The paradox of  
771 pelagic food webs in the northern Bering Sea – I. Seabird food habits. *Continental Shelf*  
772 *Research*, 7, 895-911.  
773  
774 Springer, A.M., Mcroy, C.P., Turco, K.R. 1989. The paradox of pelagic food webs in the northern  
775 Bering Sea – II. Zooplankton communities. *Continental Shelf Research*, 9, 359-386.  
776  
777 Stabeno, P.J., Danielson, S., Kachel, D., Kachel, N.B., Mordy, C.W. 2016. Currents and transport  
778 on the Eastern Bering Sea Shelf. *Deep-Sea Research II*  
779  
780 Stabeno, P., Farley, E., Kachel, N., Moore, S., Mordy, C., Napp, J.M., Overland, J.E., Pinchuk, A.I.,  
781 Sigler, M.F. 2012. A comparison of the physics, chemistry and biology of the northeastern and  
782 southeastern Bering Sea shelf. *Deep-Sea Research Part II*  
783  
784 Stabeno, P.J., Reed, R.K., Schumacher, J.D. 1995. The Alaska Coastal Current: continuity of  
785 transport and forcing. *Journal of Geophysical Research*, 100, 2477-2485.  
786  
787 Stevenson, D., Lauth, R.R. 2012. Latitudinal trends and temporal shifts in the catch composition  
788 of bottom trawls conducted on the eastern Bering Sea shelf and southeastern Chukchi Sea.  
789 *Deep-Sea Research Part II*, 65-70, 251-259.  
790  
791 Suryan, R.M., Kuletz, K.J., Parker-Stetter, S., Ressler, P.H., Renner, M., Horne, J.K., Farlet, J.,  
792 Edward, V. *et al.* (2016) Temporal shifts in seabird population and spatial coherence with prey  
793 in the southeastern Bering Sea. *Marine Ecology Progress Series*  
794  
795 Tittensor *et al.* (2011) Global patterns and predictors of marine biodiversity across taxa. *Nature*,  
466, 1098-1101.

- 796 U.S. Geological Survey, Drew, G.S., Piatt, J.F., Renner, M. 2015. User's guide to the North Pacific  
797 Pelagic Seabird Database 2.0 Open-file report U.S. Geological Survey Reston VA  
798 doi:10.3133/ofr20151123
- 799 Wang, M., Overland, J.E., Stabeno, P. 2012. Future climate of the Bering and Chukchi Seas  
800 projected by global climate models. *Deep-Sea Research Part II*, 65, 46-57.
- 801 Willig, M.R., Kaufmann, D.M., Stevens, R.D. 2003. Latitudinal gradients of biodiversity: pattern,  
802 process, scale and synthesis. *Annual Review of Ecology and Systematics*, 34, 273–309.
- 803 Zuur, A.F., Leno, E.N., Walker, N.J., Saveliev, A.A., Smith, G.M. 2009. GLM and GAM for absence-  
804 presence and proportional data, *Mixed Effects Models and Extensions in Ecology with R*.  
805 *Statistics for Biology and Health*. Springer Verlag, pp. 1–15.

806 **Table 1a-c:** Generalized additive model results for assessing the spatial organizations of seabird assemblage indices (PC1 and PC2),  
 807 species richness and total seabird abundance within (a) inner (<50m), (b) middles (50-100m), and (c) outer shelf regions (100-200m);  
 808 SSH is sea-surface height, Edf is estimated degrees of freedom, Res.df is residual degrees of freedom, % Dev. is percent deviance  
 809 explained, GCV is generalized cross-validation score.

810 **(a) Inner shelf**

Seabird Variable	Latitude		Temperature		Salinity		Current Speed		Slope		% Dev., r <sup>2</sup> , GCV
	Edf., Res.df	F, p	Edf., Res.df	F, p	Edf., Res.df	F, p	Edf., Res.df	F, p	Edf., Res.df	F, p	
PC1	5.06	7.69	1.00	0.59	1.00	0.31	7.52	14.67	3.82	4.44	90.4, 0.87, 1.22
	6.14	<0.0001	1.00	0.44	1.00	0.58	8.31	<0.0001	4.76	0.002	
PC2	8.28	3.75	3.90	1.09	2.05	0.65	1.00	0.22	1.00	0.0009	65.6, 0.56, 3.34
	8.83	<0.0001	4.93	0.37	2.57	0.55	1.00	0.64	1.00	0.92	
Species Richness	8.41	8.41	1.00	1.94	1.00	0.833	5.35	3.61	4.90	1.86	75.3, 0.69, 0.16
	8.83	<0.0001	1.00	0.17	1.00	0.36	6.33	0.003	5.96	0.10	
Total Abundance	5.58	2.90	2.58	1.14	1.00	0.74	2.12	0.80	1.00	0.18	56.5, 0.34, 17.82
	6.67	0.01	3.27	0.34	1.00	0.39	2.58	0.47	1.00	0.67	

811

812

813

814

815

816 (b) Middle shelf

Seabird Variable	Latitude		Temperature		Salinity		Current Speed		SSH		Slope		% Dev., r <sup>2</sup> , GCV
	Edf., Res.df	F, p	Edf., Res.df	F, p	Edf., Res.df	F, p	Edf., Res.df	F, p	Edf., Res.df	F, p	Edf., Res.df	F, p	
PC1	6.06	5.63	4.59	7.32	6.95	4.59	1.12	7.66	6.31	6.41	6.51	3.23	69.8, 0.59, 3.12
	7.28	<0.0001	5.65	<0.0001	8.02	<0.0001	1.22	0.01	7.48	<0.0001	7.59	<0.0001	
PC2	6.22	5.93	1.9	3.29	6.31	1.51	1.00	2.1	1.6	1.95	2.12	2.81	74.6, 0.70, 0.22
	7.39	<0.0001	2.39	0.03	7.49	0.16	1.00	0.15	1.99	0.15	2.69	0.04	
Species Richness	7.6	11.25	1.00	18.95	7.23	3.82	1.93	1.52	4.91	6.57	2.14	1.32	77.2, 0.70, 0.13
	8.5	<0.0001	1.00	<0.0001	8.23	<0.0001	2.43	0.21	6.13	<0.0001	2.72	0.26	
Total Abundance	6.38	4.51	6.17	4.37	8.1	6.42	1.00	3.66	8.66	5.68	1.00	4.79	79, 0.73, 7.97
	7.57	<0.0001	7.33	<0.0001	8.76	<0.0001	1.00	0.05	8.95	<0.0001	1.00	0.03	

817 (c) Outer shelf

Seabird Variable	Latitude		Temperature		Salinity		Current Speed		Slope		% Dev., r <sup>2</sup> , GCV
	Edf., Res.df	F, p	Edf., Res.df	F, p	Edf., Res.df	F, p	Edf., Res.df	F, p	Edf., Res.df	F, p	
PC1	3.49	0.63	2.51	4.70	1.00	3.31	1.03	1.86	1.00	2.38	41.0, 0.34, 0.29
	4.43	0.65	3.17	0.003	1.00	0.07	1.06	0.17	1.00	0.12	
PC2	4.69	1.95	7.07	2.27	4.28	2.52	3.81	1.66	6.00	5.11	70.5, 0.58, 0.31
	5.78	0.08	8.08	0.03	5.25	0.03	4.67	0.15	7.07	<0.001	
Species Richness	2.87	10.62	3.21	4.44	2.47	3.89	1.00	4.07	4.43	1.14	57.4, 0.49, 0.11
	3.65	<0.0001	9.98	0.002	3.09	0.01	1.00	0.04	5.43	0.34	
Total Abundance	4.22	1.61	1.46	0.89	7.02	2.24	1.00	0.01	1.00	1.60	40.4, 28.7, 6.19
	5.25	0.16	1.78	0.39	8.09	0.03	1.00	0.90	1.00	0.21	

818 **Figures:**

819 **Figure 1:** Eastern Bering Sea shelf study domain, extent of the seabird grid (50x50 km) and  
820 summarized survey effort (# 3km survey segments); a cut off of 50 segments was applied (UTM  
821 2 map projection). Empty cells are effort <50. AS is Anadyr Strait, BB is Bristol Bay, BC is Bering  
822 Canyon, BS is Bering Strait, CN is Cape Newenham, NC is Navarin Canyon, NI is Nunivak  
823 Island, NS is Norton Sound, PC is Pribilof Canyon, PeC is Pervenets Canyon, PI is Pribilof Islands,  
824 SB is Slime Bank region, SL is St. Lawrence Island, SM is St. Matthews Island, SP is Samalga Pass,  
825 UP is Unimak Pass, ZC is Zhemchug Canyon. Depth contours correspond to the 50 m (black), 100  
826 m (light blue) and 200 m (red) isobaths. Black-dashed line is the approximate position of the 50  
827 m isobaths, yellow-dashed line is approximate position of the 100 m isobaths, which partitions  
828 the shelf into inner, middle and outer regions.

829 **Figure 2:** Eastern Bering Sea shelf study domain. Examples of environmental variables  
830 (displayed as heat maps) that are linked to the seabird grid (50x50 km) for assessing  
831 macroecology of seabird biogeography: (a) distance to land (km), (b) ocean temperature  
832 averaged over 10-35m (°C), (c) salinity averaged over 10-35m, (d) bathymetric slope (ln of  
833 percent rise), (e) current speed ( $\text{cm s}^{-1}$ ) at 7.5 m, and (f) sea-surface height (cm). Distance to  
834 land illustrates the presence of important seabird breeding islands in the Bering Sea: Pribilof  
835 Islands, St. Matthews Islands, St. Lawrence Islands. Data from b-f are derived from a  
836 climatological data assimilated model of ocean conditions during summertime (Panteleev et al.  
837 2011). Empty grid cells indicate locations with low seabird survey effort (see Fig. 1 for  
838 geographic details).

839 **Figure 3:** Spatial mean of (a) species richness and (b) total seabird abundance; averaged over  
840 1975-2014, May-September. Grid cells are 50x50 km; UTM Zone 2 projection. See Fig. 1 for  
841 geographic details.

842 **Figure 4:** Results of PCA for assessing seabird species assemblages and dominant modes of  
843 variation. PC loadings are mapped onto the grid as an index of seabird assemblages: (a) PC1,  
844 increased species abundance and richness associated with islands and the Anadyr Current  
845 (increase of PC1 indicates more species and/or higher abundances), and (b) PC2, a division

846 between the inner and middle shelf (positive values indicate high abundance of shoreward  
847 species) and the outer shelf-slope (negative values indicate higher abundance of offshore  
848 species). PC2 also indicates a change in seabird assemblages regarding a north – south division  
849 partitioning southern and northern shelf ecosystems of the eastern Bering Sea. (c) Cluster  
850 analysis of seabird assemblages indicates the grouping of species most likely to occur in similar  
851 abundance in geographic space. See Table S.1 and Fig. S.1 for additional details.

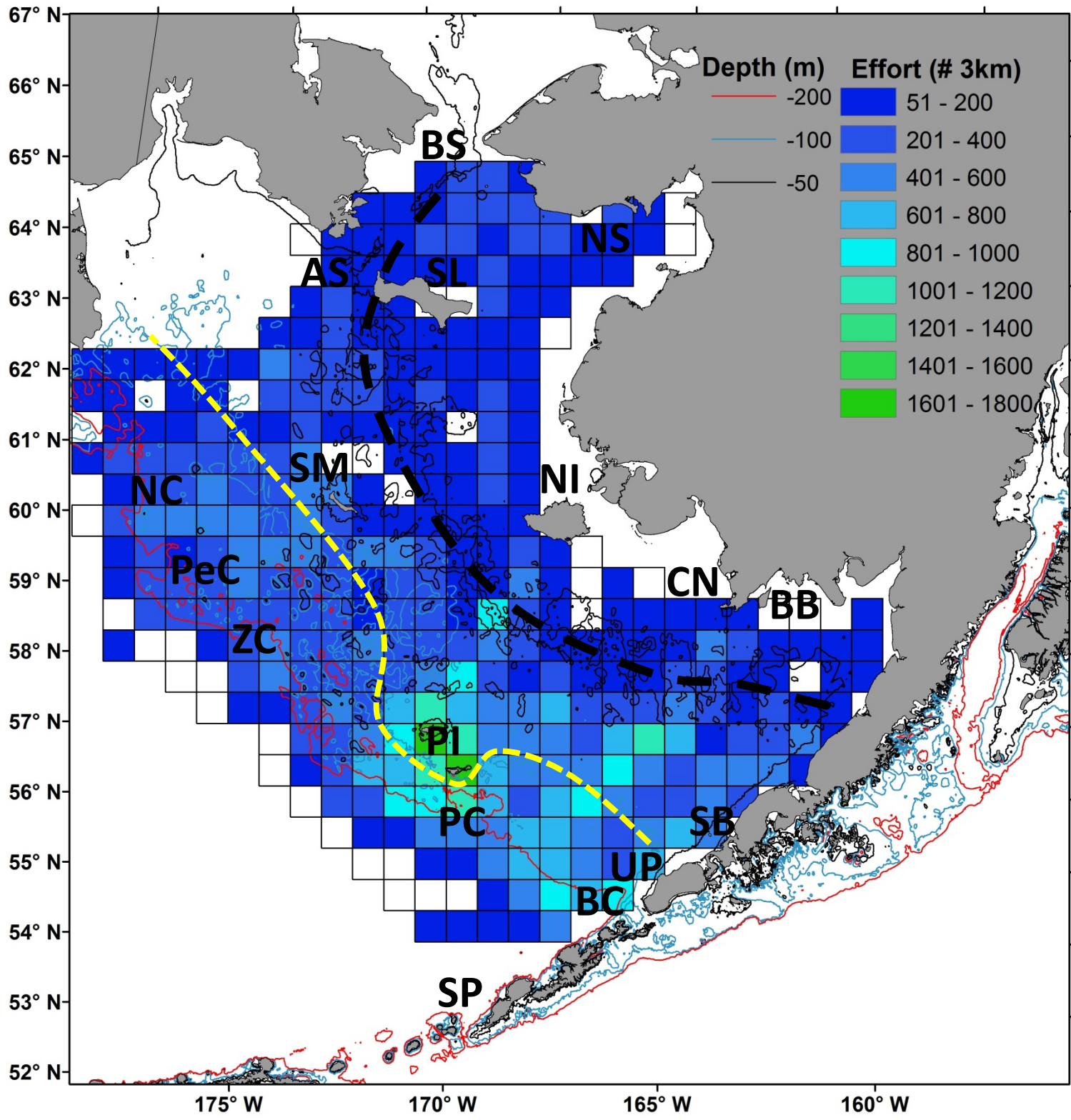
852 **Figure 5:** Results of GAMs for assessing the response of seabird assemblage index (PC1 and  
853 PC2) to latitude along the (a-b) inner shelf (depth  $\leq 50$  m isobath), and (c-d) middle shelf  
854 regions (50-100 m depth). Shaded areas are the 95% confidence intervals and tick marks on the  
855 x-axis indicate data availability.

856 **Figure 6:** Results of GAMs for assessing the response of the seabird species richness and  
857 abundance to increasing latitude along the (a-b) inner shelf (depth  $\leq 50$  m), and (c-d) middle  
858 shelf (50-100 m depth), and (e) richness in the outer shelf. Shaded areas are the 95%  
859 confidence intervals and tick marks on the x-axis indicate data availability.

860 **Figure 7:** Results of GAMs for assessing the response of the seabirds to bathymetric slope: (a)  
861 seabird assemblage index (PC1) within the inner shelf, (b-d) seabird PC1, PC2 and total seabird  
862 abundance within the middle shelf (50-100 m depth), (e) seabird PC2 within the outer shelf.  
863 Shaded areas are the 95% confidence intervals and tick marks on the x-axis indicate data  
864 availability.

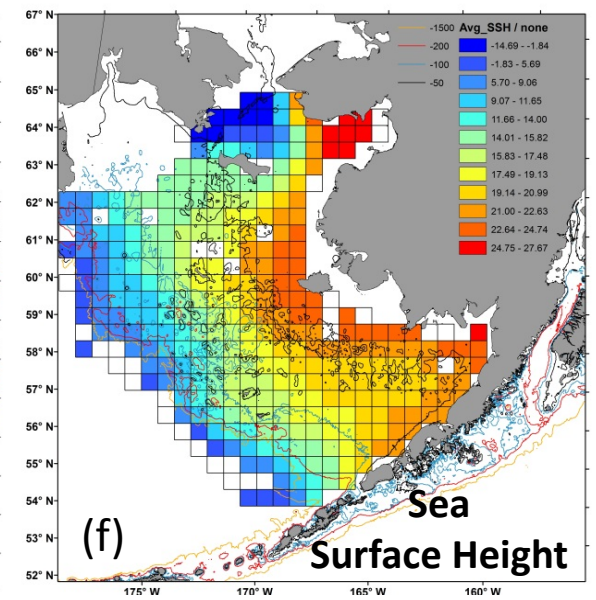
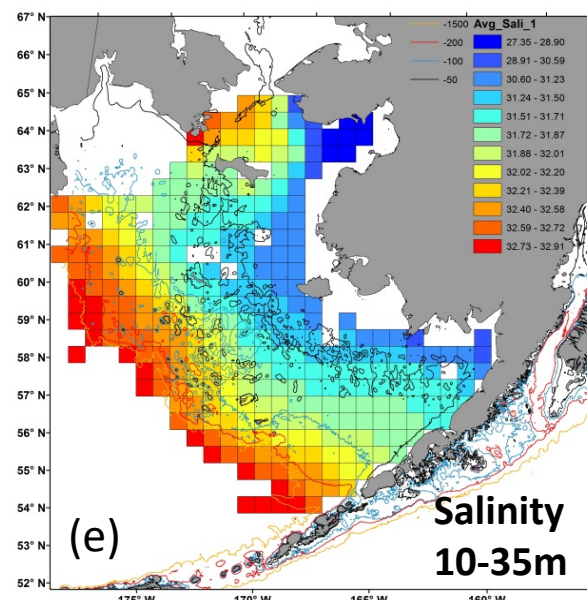
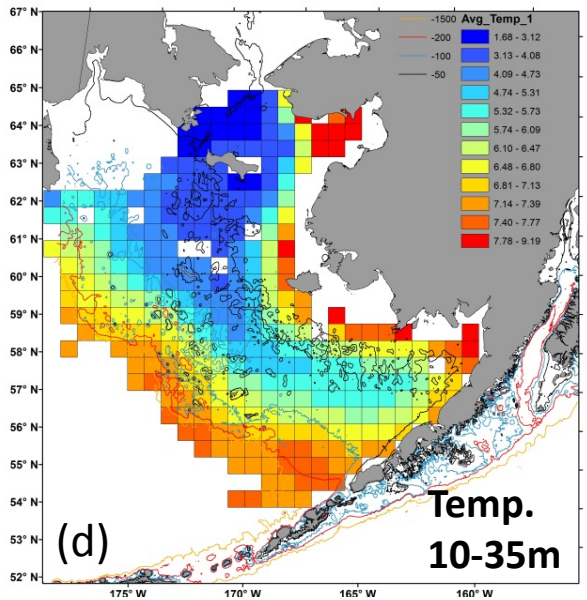
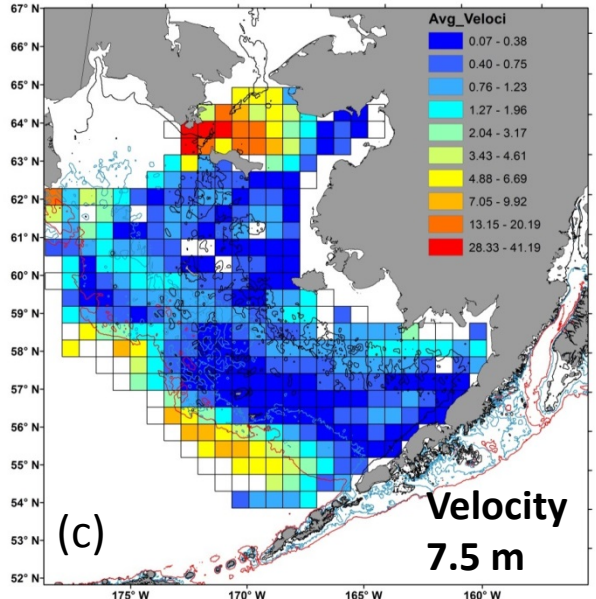
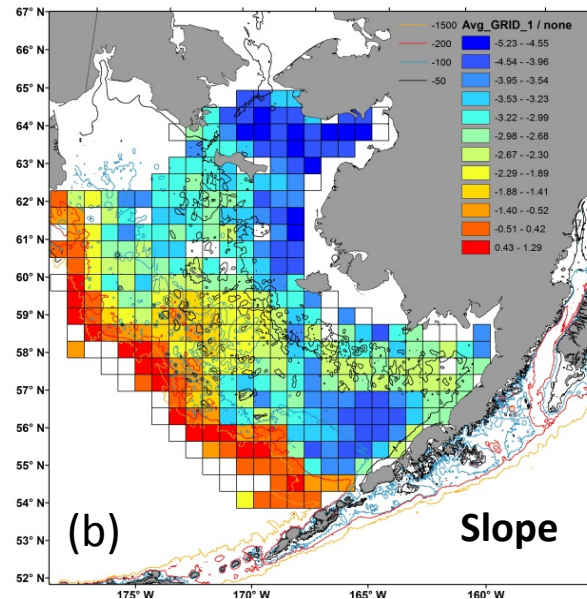
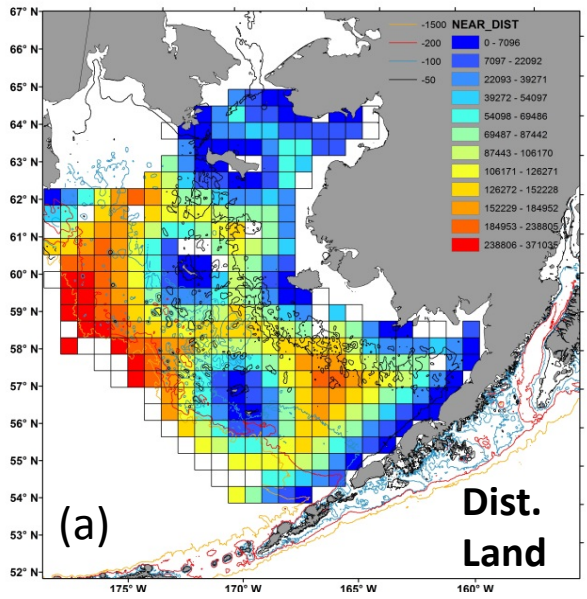
865 **Figure 8:** Results of GAMs for assessing the response of the seabirds to average sea  
866 temperature over 10-35m within the middle shelf (50-100 m depth): (a-b) seabird assemblage  
867 index (PC1 and PC2), (c) species richness, (d) total seabird abundance; and outer shelf (e) PC1,  
868 (f) seabird PC2 and (g) species richness. Shaded areas are the 95% confidence intervals and tick  
869 marks on the x-axis indicate data availability.

# FIGURE 1



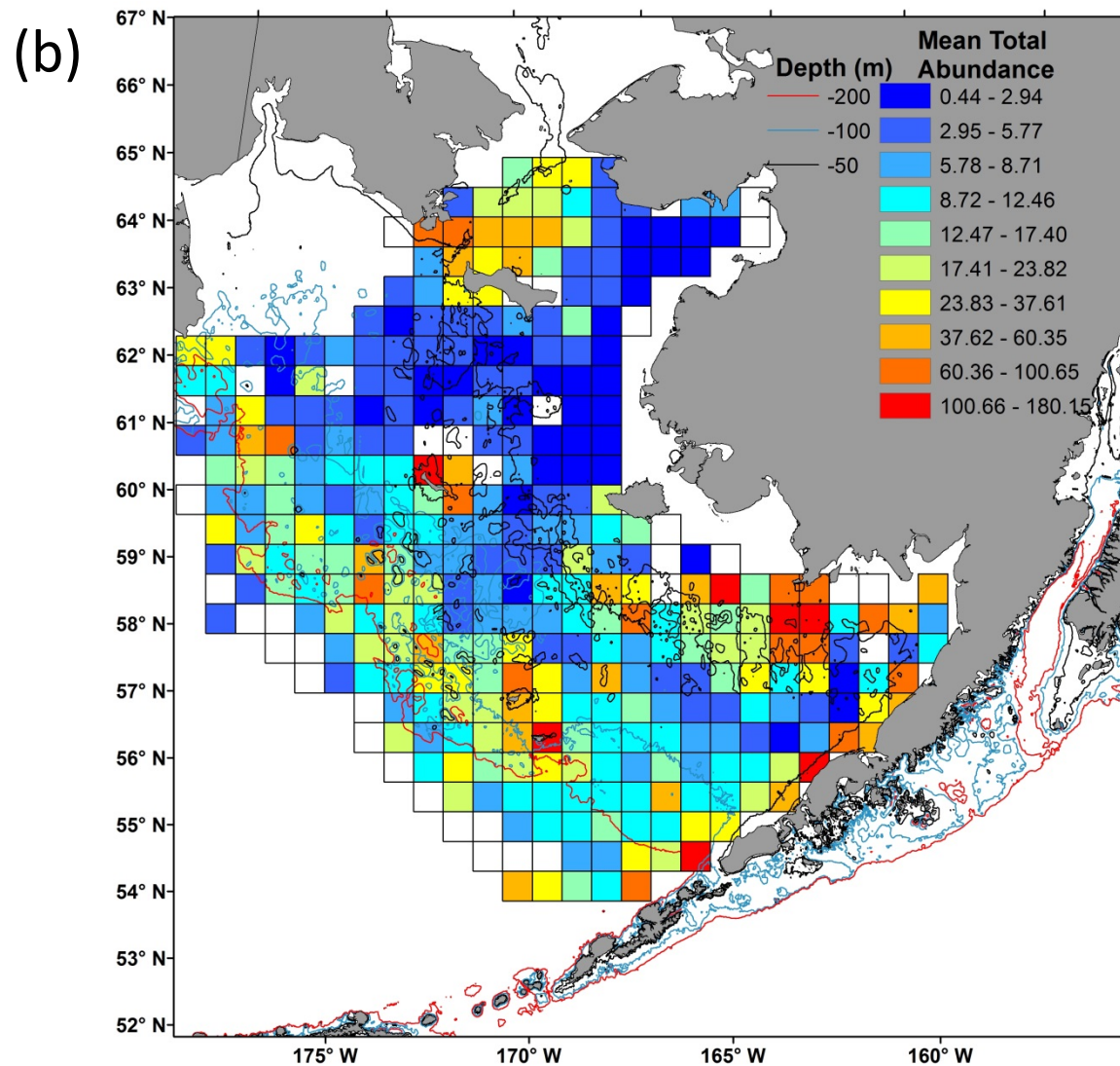
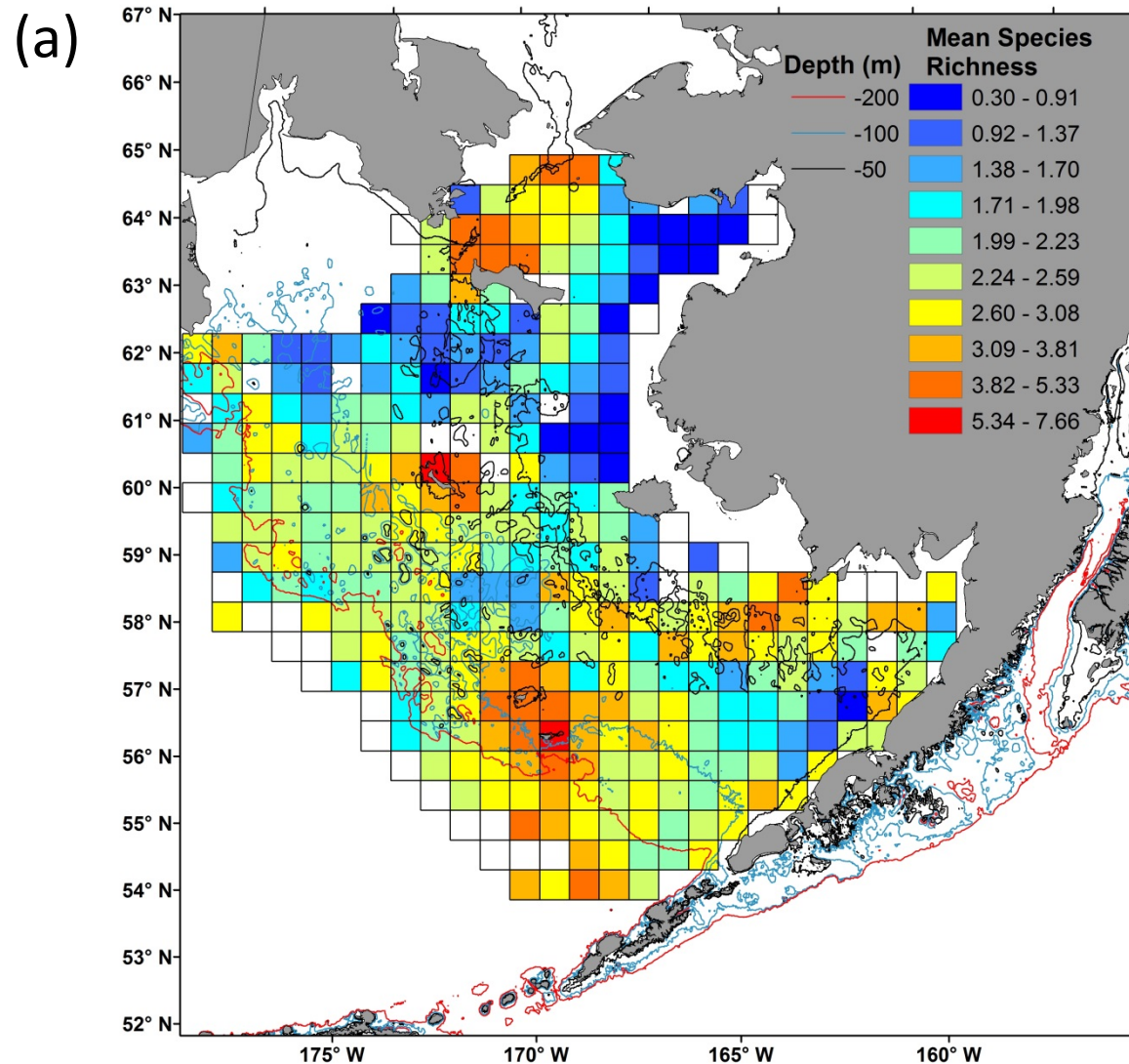


# FIGURE 2

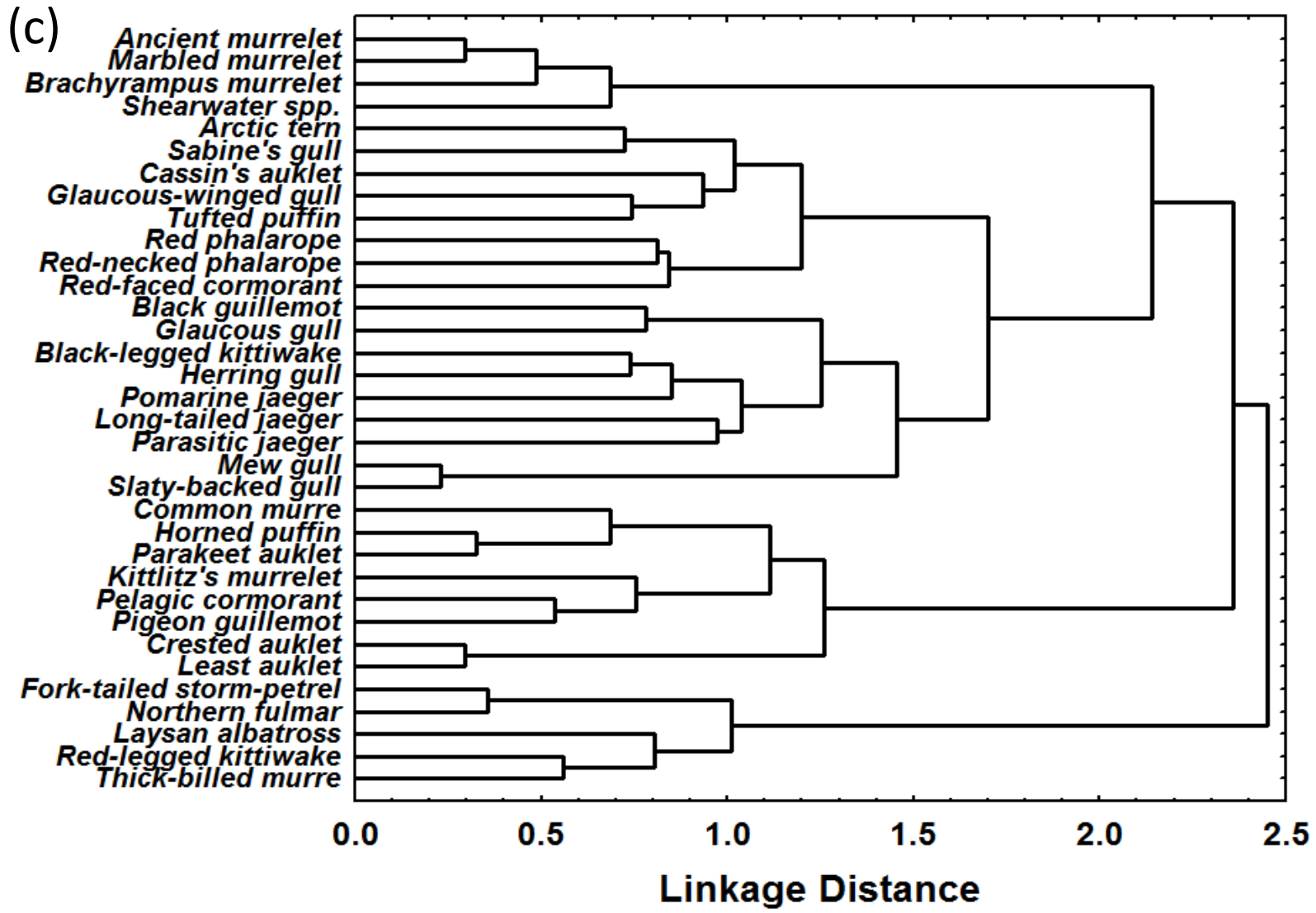
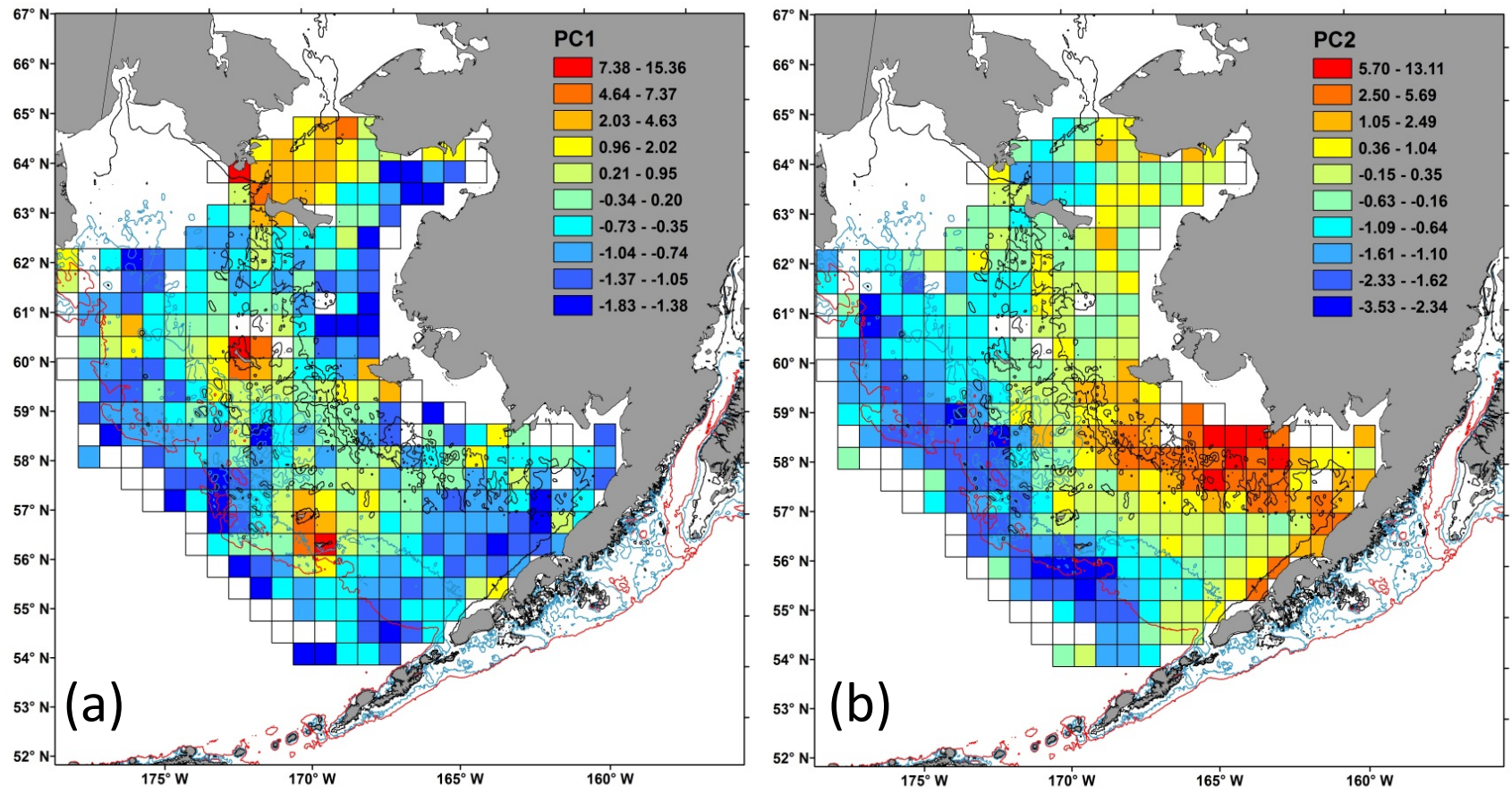




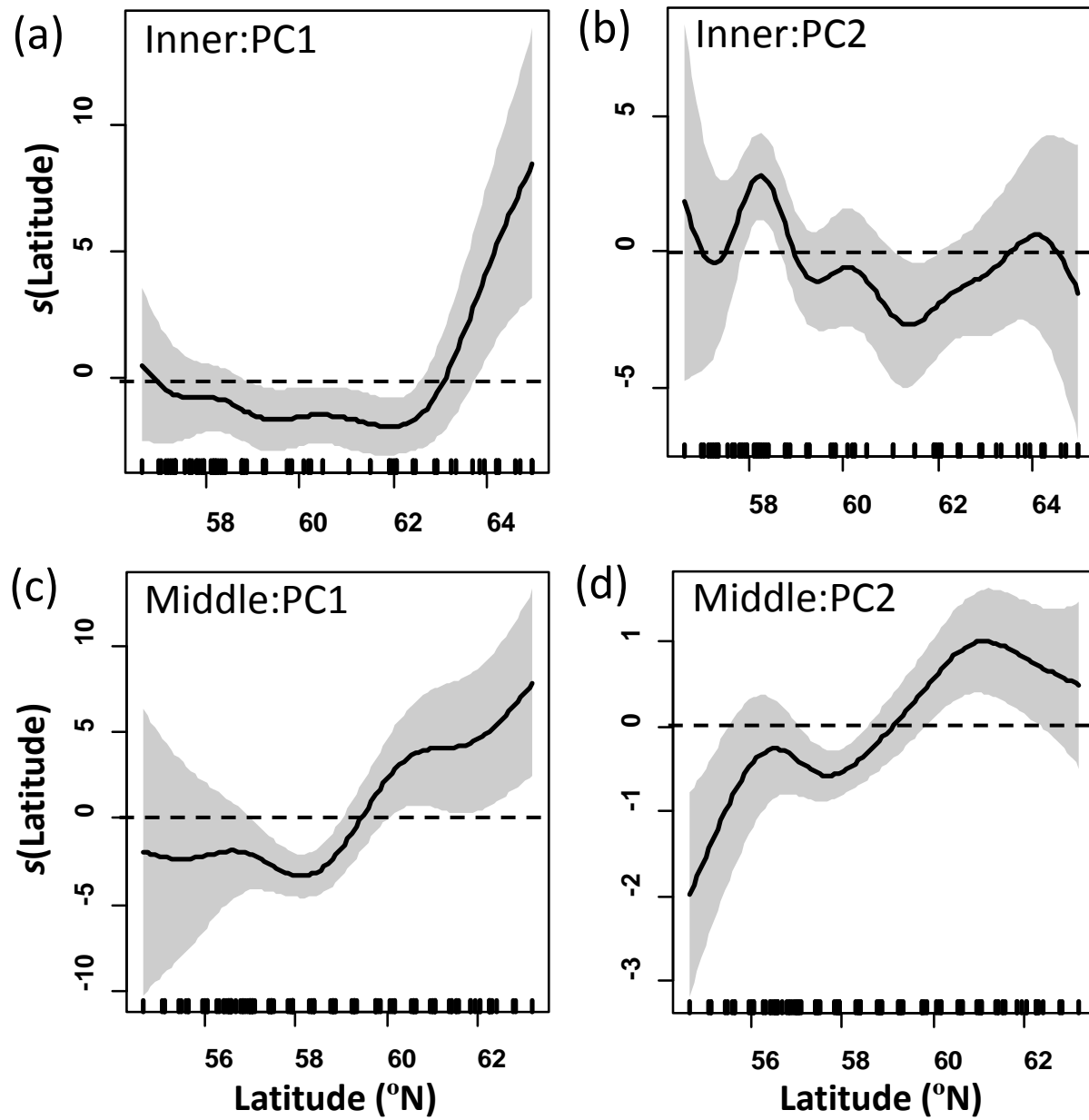
# FIGURE 3



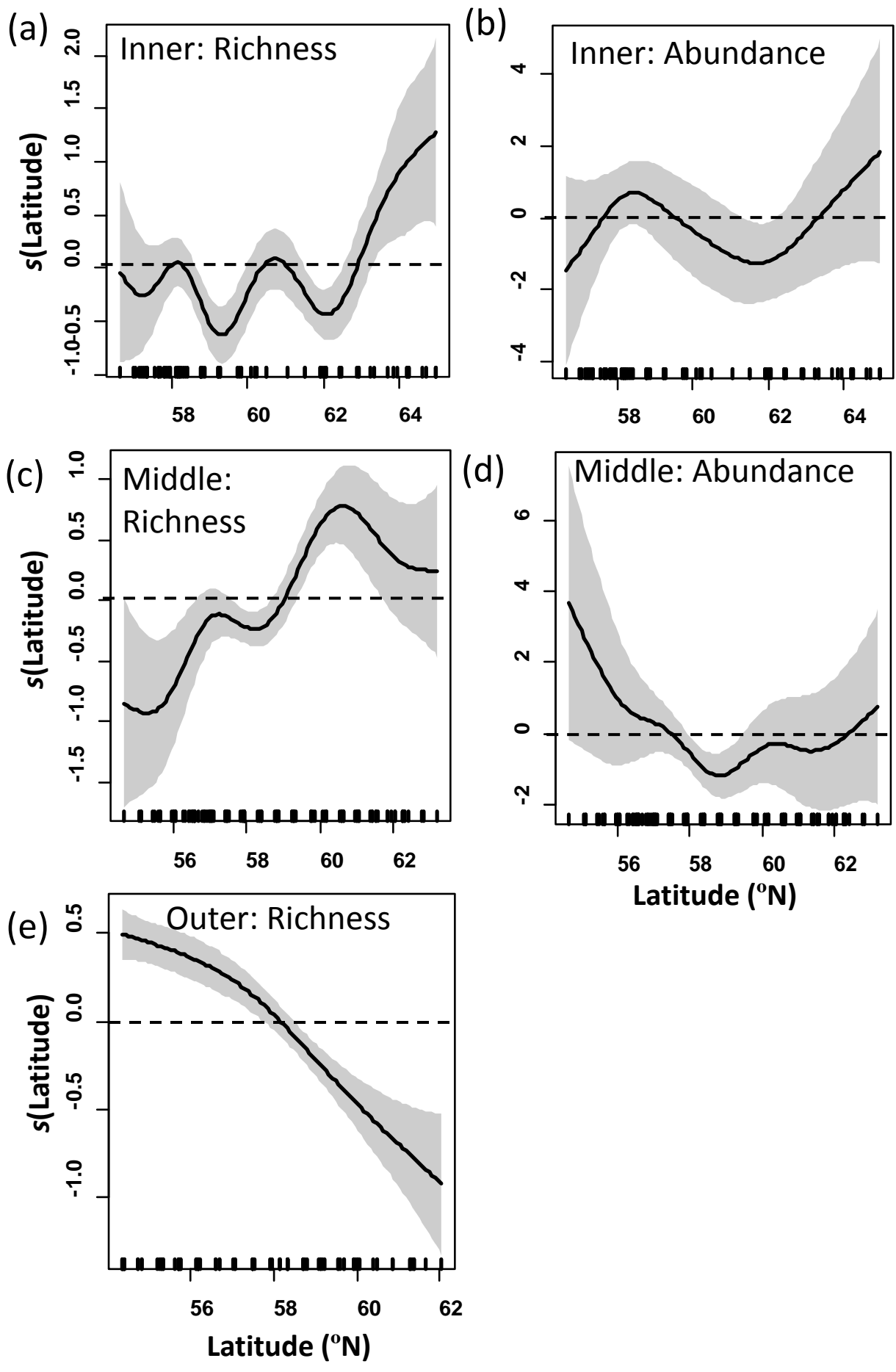
# FIGURE 4



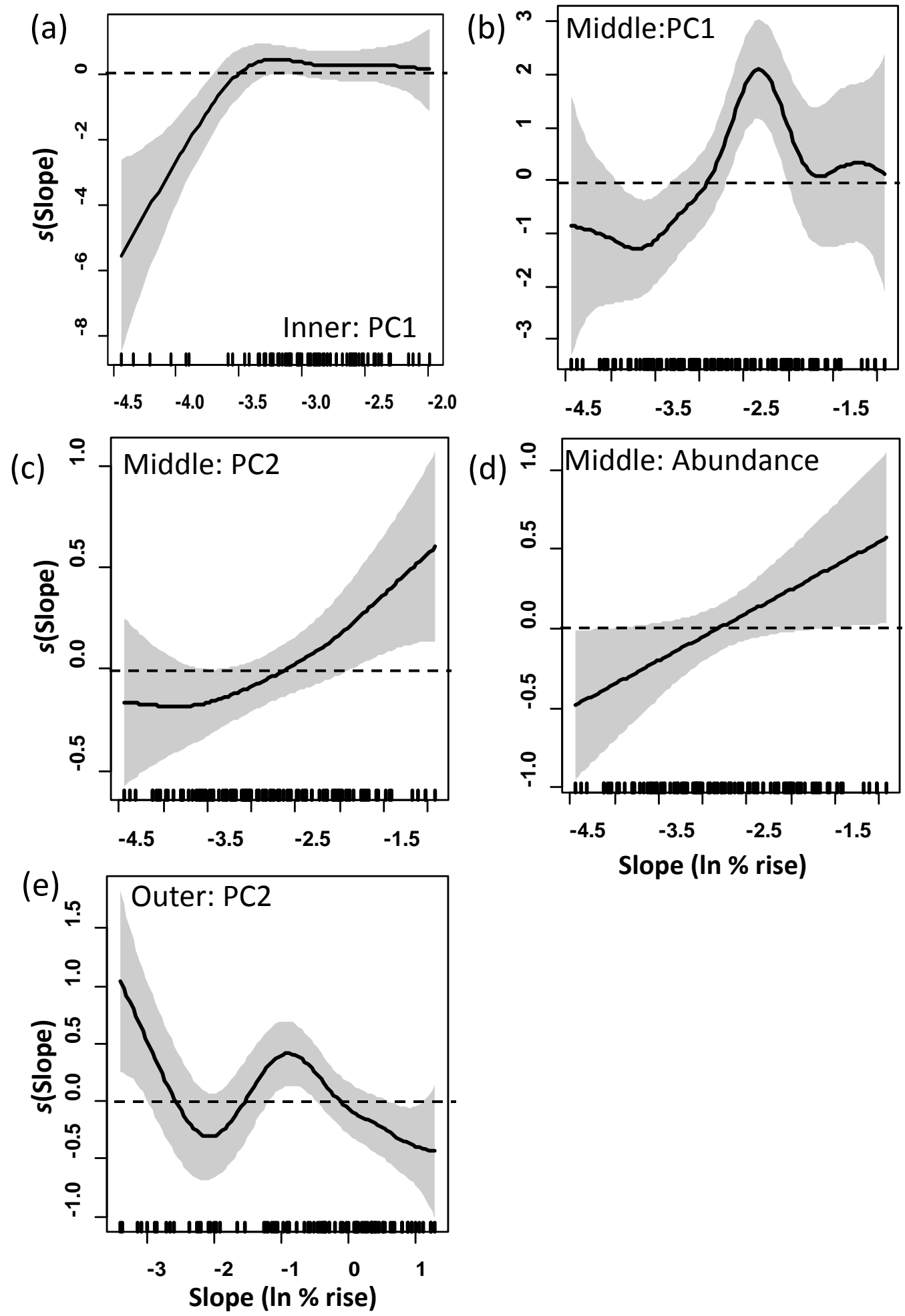
# FIGURE 5



# FIGURE 6

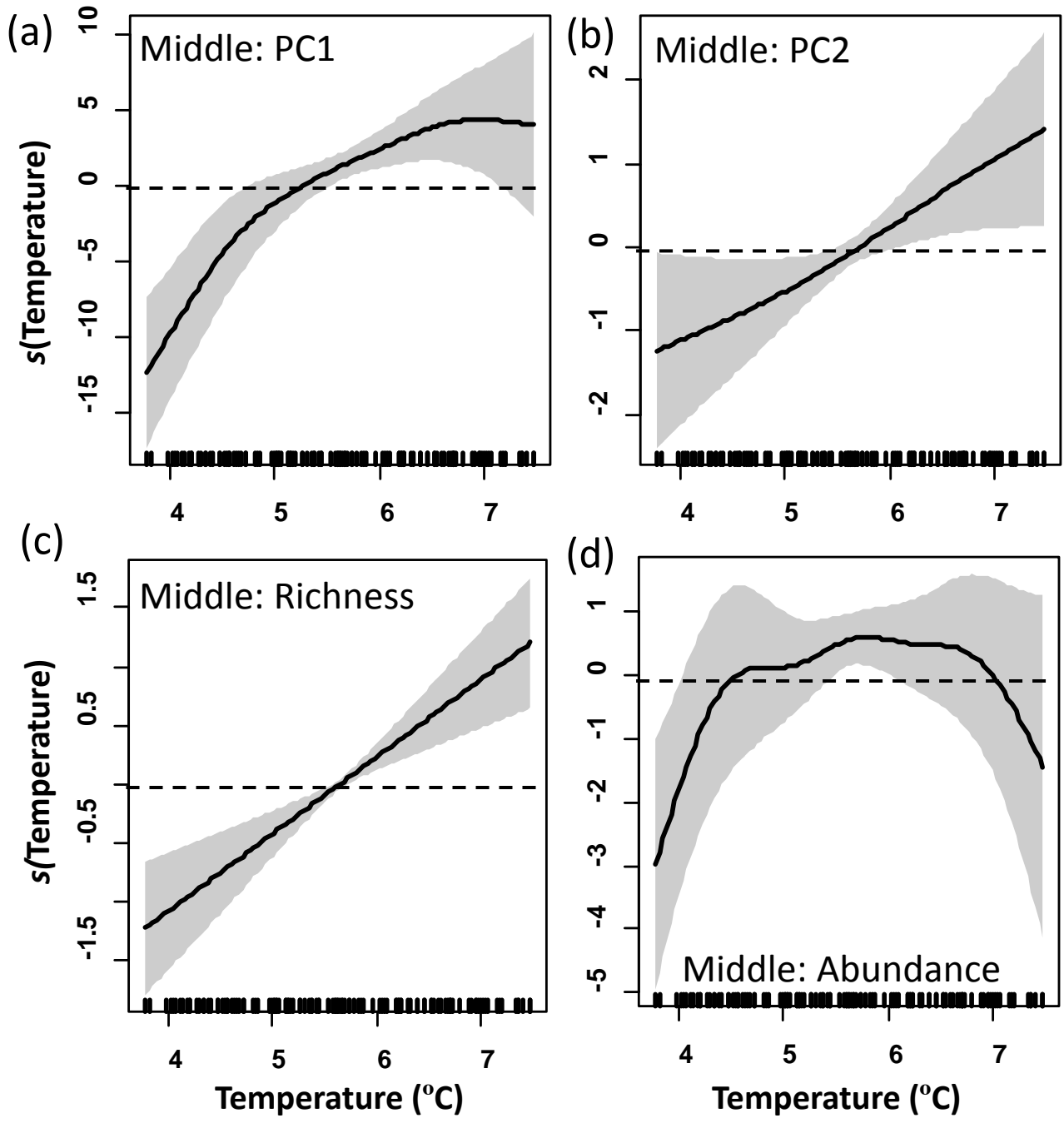


# FIGURE 7





# FIGURE 8



# FIGURE 8 cont'd

