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1 **Title**

2 Marine biodiversity refugia in a climate-sensitive subarctic shelf

3 **Running title**

4 Contemporary marine biodiversity refugia

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## Abstract

19 The subarctic shelf of the Eastern Bering Sea (EBS) is one of the world's most productive  
20 marine environments, exposed to drastic climate changes characterized by extreme fluctuations  
21 in temperature, sea ice concentration, timing, and duration. These climatic changes elicit  
22 profound responses in species distribution, abundance, and community composition. Here, we  
23 examined patterns of alpha- and temporal beta-diversity of 159 marine taxa (66 vertebrates and  
24 93 invertebrate species) from 29 years (1990-2018) of species observations from the NOAA  
25 bottom trawl surveys in the EBS. Based on these data, we identified geographically distinct  
26 refugial zones in the northern and southern regions of the middle shelf, defined by high species  
27 richness and similarity in the community species composition over time. These refugial zones  
28 harbor higher frequencies of occurrence for representative taxa relative to the regions outside  
29 of refugia. We also explored the primary environmental factors structuring marine biodiversity  
30 distributions, which underpinned the importance of the winter sea ice concentration to alpha-  
31 and temporal beta-diversity. The spatial biodiversity distributions between high and low winter  
32 sea ice regimes highlighted contrasting signals. In particular, the latter showed elevated species  
33 richness compare to the former. Further, the temporal beta-diversity between the high and low  
34 winter sea ice periods underpinned an overall increase in the compositional similarity of marine  
35 communities in the EBS. Despite these spatio-temporal differences in biodiversity distributions,  
36 the identified refugia are safe havens of marine biodiversity in the EBS, and distinguishing  
37 these areas can help facilitate conservation and management efforts under accelerated and on-  
38 going climatic changes.

39 **Key words:** Eastern Bering Sea, alpha diversity, biodiversity refugia, temporal beta-diversity,  
40 sea ice, Pacific Arctic region

## 41 **1. Introduction**

42 Marine biological diversity encompasses all levels of complexity of life in the ocean,  
43 assumes multiple ecosystem functions, and provides a plethora of valuable ecosystem services  
44 (Sala and Knowlton, 2006; Cavanagh et al., 2016; Barbier, 2017). Understanding the temporal  
45 trends, spatial patterns, and forces structuring biodiversity are critical to bolstering  
46 conservation and resource management efforts under multiple climatic and ecological  
47 disturbances (Sala and Knowlton, 2006; Tittensor et al., 2010; Selig et al., 2014). In particular,  
48 climate-driven changes in the abiotic environment combined with pervasive anthropogenic  
49 threats have caused unprecedented impacts on global marine biodiversity, as manifested  
50 through population declines, species extirpation, and community shifts (Sala and Knowlton,  
51 2006; Genner et al., 2010; Sydeman et al., 2015; Malhi et al., 2020).

52 The importance of conservation strategies and climate adaptation tools in reducing  
53 biodiversity losses along with their ecological and societal impacts is widely recognized. One  
54 of the increasingly proposed conservation approaches involves identification and protection of  
55 climate change refugia, which target regions that are resistant to on-going climatic changes  
56 relative to the surrounding environment (Keppel et al., 2012; Morelli et al., 2016). The concept  
57 of refugia was earlier introduced to explain species distributional patterns within the context of  
58 past climatic changes and characterized as locations where taxa may move to and persist during  
59 large-scale and long-term climatic changes (Keppel et al., 2012; Keppel et al., 2015). Hence,  
60 refugia provide a suite of spatio-temporal abiotic environments favorable for a given species  
61 and are especially crucial when the surrounding environmental conditions become inhospitable  
62 (Ashcroft, 2010; Stewart et al., 2010; Morelli et al., 2017). The identification of refugia over  
63 shorter, ecological time scales is being pursued within the perspective of biodiversity  
64 adaptation to recent anthropogenic climate changes (Morelli et al., 2017; Morelli et al., 2020).  
65 Within this context, climate change refugia are defined as habitats relatively buffered from the

66 contemporary climate change that permit the persistence of valuable physical, ecological, and  
67 socio-cultural resources (Morelli et al., 2016).

68 Multiple techniques to identify refugia have been explored and developed, often limited  
69 by the availability of climate and resource data. While most of these methods were  
70 predominantly applied to terrestrial and freshwater systems (Ashcroft et al., 2012; Isaak et al.,  
71 2016; Baumgartner et al., 2018), their use has been increasingly expanded to marine  
72 ecosystems. Earlier attempts to identify marine refugia were primarily focused on tropical coral  
73 reefs (Ban et al., 2012; Hooidonk et al., 2013). More recently, climate change refugia studies  
74 have progressed to accommodate broader ecological components of marine ecosystems. In  
75 particular, climate change refugia in both pelagic and shelf ecosystems have been identified  
76 based on the persistence of high genetic diversity (Provan, 2013; Assis et al., 2016), the  
77 resilience of diverse seascapes to environmental and climatic changes (Ban et al., 2016), and  
78 the occurrence of topographic features (Pinheiro et al., 2017; Kapsenberg and Cyronak, 2019)  
79 and oceanographic phenomena (Lourenço et al., 2016; Storlazzi et al., 2020). Another novel  
80 approach to identifying marine climate change refugia was through the use of in-situ species  
81 community observations in areas where long-term and consistent spatial biodiversity  
82 monitoring has been in place (Barceló et al., 2018). In this case, potential refugial zones are  
83 exemplified by regions that maintained high species richness and minimal change in the species  
84 composition over time. Invoking a multi-species community perspective to identifying refugia  
85 can further complement the limitation and trade-off of ecological niche models and taxon-  
86 specific approaches (Planque, 2016; Hollowed et al., 2000) for management applications and  
87 detecting potential locations of climate-resistant species communities (Barceló et al., 2018).

88 Here, we implemented a biodiversity-based approach (Barceló et al., 2018) for  
89 identifying biodiversity refugial zones in the EBS, which is among the most productive yet  
90 climatically-sensitive shelf ecosystems in the world (Overland and Stabeno, 2004). While

91 climate change refugia often represent biodiversity safe havens in the conservation planning  
92 literature (Keppel et al., 2012; Keppel et al., 2015), actual validation of whether these are  
93 indeed accrual areas for biodiversity is often overlooked (Barrows et al., 2020). Hence, we also  
94 compared biodiversity refugia to climatically stable areas (Ban et al., 2016) in the EBS shelf  
95 and examined their spatial correspondence, providing a potential independent validation of  
96 climate change refugia in this region (Barrows et al., 2020). We further examined the spatial  
97 and temporal patterns of alpha and beta diversity in the Eastern Bering Sea (EBS) in relation  
98 to environmental drivers between 1990 and 2018, a period characterized by large fluctuations  
99 in thermal and sea ice conditions. Over the past decades, the EBS has experienced pronounced  
100 environmental and climatic changes that elicited community-wide biological responses (Eisner  
101 et al., 2014; Duffy-Anderson et al., 2017; Stabeno et al., 2017). Thus, the primary objectives  
102 of this work are (1) to identify biodiversity refugial zones for marine species communities on  
103 the EBS shelf under contemporary climate changes; and (2) to examine recent spatio-temporal  
104 patterns of marine biodiversity and associated environmental drivers.

## 105 **2. Methods**

### 106 **2.1 Study area**

107 The study area is the Eastern Bering Sea shelf, situated in the Pacific sector of the Arctic (Fig.  
108 S1, inset map). This shallow continental shelf is one of the most fishery-productive and well-  
109 monitored marine areas in the world. The EBS is a wide (>500 km) continental shelf system,  
110 topographically classified by persistent fronts into the inner (<50 m water depth), middle (50–  
111 100 m), and outer (100–200 m) domains (Coachman, 1986). Each individual domain has its  
112 own unique hydrography, circulation, and species assemblages and food webs (Springer et al.,  
113 1996; Danielson et al., 2011; Hunt et al., 2011). The region further exhibits extremely high  
114 sensitivity and exposure to environmental and climatic changes (Stabeno et al., 2017; Stabeno  
115 and Bell, 2019). Particularly, the unprecedented warming and loss of seasonal sea ice cover on

116 the shelf over the recent decades have triggered pronounced impacts on productivity (Eisner et  
117 al., 2016; Duffy-Anderson et al., 2017) and on species abundances and distributions (Alabia et  
118 al., 2018; Stevenson and Lauth, 2019; Hirawake and Hunt, 2020).

## 119 **2.2 Marine fish and invertebrate data**

120 The biological data were sourced from the NOAA annual bottom trawl surveys between  
121 1990 and 2018. While bottom trawl surveys were conducted from 1982, we started our analyses  
122 from 1990 to minimize the uncertainty from species identification in earlier years (Stevenson  
123 and Hoff, 2009). Summer (late May-August) bottom trawl surveys were annually conducted  
124 and covered up to 376 standard stations (Table S1) distributed across the sampling strata (Fig.  
125 S1) (Stauffer, 2004). Standard-density sampling strata have fixed stations in the center of the  
126 20 x 20 nmi (37.04 x 37.04 km) cells while high-density strata encompass additional sites at  
127 the corners of the 20 x 20 nmi grids around the Pribilof and St. Matthew islands (Stauffer,  
128 2004). Only commonly sampled taxa, defined as those recorded at one or more stations for at  
129 least 20 of the 29 years comprising the study period, were included in the biodiversity analyses  
130 (Table S2). This was done to minimize the potential bias from the inclusion of rare species in  
131 the calculation of diversity measures. This resulted in a total of 159 taxa comprising 66 largely  
132 demersal fish and 93 benthic invertebrate taxa belonging to three major taxonomic groups (Fig.  
133 S2). We included several typically pelagic species (Table S2, e.g. Pacific herring, capelin, and  
134 chum salmon) that were regularly caught in the bottom trawl. Invertebrates belonging to less  
135 represented phyla ( $n = 10$ ) were combined into an ‘others’ group.

## 136 **2.3 Alpha and beta-diversity metrics**

137 Annual site-specific biodiversity metrics were calculated using species matrices based on  
138 presence-absence data derived from the raw species abundances (i.e., species presence records  
139 corresponding to abundances greater than zero). We used presence-absence species data over  
140 abundance-based species richness to reduce the confounding effect of density on compositional

141 similarity due to potential differences in sampling sizes (Jost et al., 2010). The annual alpha  
142 ( $\alpha$ ) diversity was then computed as the total number of species present at each survey site (i.e.,  
143 species richness). Temporal beta-diversity was computed based on the Sorensen dissimilarity  
144 index computed between consecutive years at each site. For consecutive years with unsurveyed  
145 stations, temporal beta-diversity metrics were also set to missing values to ensure consistent  
146 analysis throughout the study period and avoid potential interpretation bias. We also utilized  
147 the Sorensen index for our analysis as it weighs matches in species composition between site  
148 pairs more heavily than mismatches thus, is more suitable for evaluating similarity in species-  
149 rich communities where some taxa could be absent in a given sample (Krebs, 2014). These  
150 year-to-year changes in community composition were calculated to capture the documented  
151 species and community-wide responses to inter-annual fluctuations of seasonal processes in  
152 the EBS (Baker and Hollowed, 2014; Ortiz et al., 2016). These include environmental (e.g.  
153 extent and retreat of sea ice) and biological processes (e.g. population dynamics, species  
154 growth, and recruitment). All biodiversity metrics were calculated using the ‘betapart’ package  
155 (version 1.5.1) (Baselga and Orme, 2012) in the R open source software (version 4.0.3).

#### 156 **2.4 Identifying biodiversity refugia for the marine fish and invertebrate community**

157 Biodiversity refugia on the EBS shelf were identified as areas harboring high species richness  
158 and experiencing low compositional changes across the 29-year period (Barceló et al., 2018).  
159 Annual species richness data between 1990 and 2018 were averaged and standardized to range  
160 from 0 to 1. The compositional similarity was also computed as the inverse of the Sorensen  
161 index averaged over the period from 1991-2018. The refugia index was then computed as the  
162 product of the normalized alpha-diversity and compositional similarity measures (Barceló et  
163 al., 2018). The refugia index threshold for the identification of refugial zones was arbitrarily  
164 set to 0.31, representing the 90% quantile of the computed metric and the maximum cut-off  
165 value delineating the gradient between pixels of high and moderate refugia index.

## 166 **2.5 Local environmental data**

167 We compiled a preliminary pool of 14 environmental factors to explore their effects on marine  
168 biodiversity facets in the EBS (Table S3). The datasets comprised in-situ observations of  
169 bottom depth and bottom and surface temperatures collected during the bottom trawl surveys,  
170 spatially-interpolated at 25 x 25 km spatial resolution using a nearest-neighbor gridding  
171 algorithm implemented within the GMT software (Wessel et al., 2013). From the interpolated  
172 in-situ data, annual spatial gradients of summer temperatures were then calculated using a 9-  
173 pixel kernel neighbourhood with diagonal weighting (Burrows et al., 2011). The remaining  
174 parameters were derived from satellite-based measurements of distance to the nearest coast  
175 (<https://oceancolor.gsfc.nasa.gov/docs/distfromcoast/>, date accessed: 31 May 2018) at 0.04°  
176 spatial resolution, seasonal averages of sea surface temperature (SST) and sea ice concentration  
177 (SIC) from the daily NOAA OI SST V2 High Resolution dataset  
178 (<https://psl.noaa.gov/data/gridded/data.noaa.oisst.v2.highres.html>, date accessed: 18 June  
179 2018) at 25 x 25 km spatial resolution. The maximum, minimum, and average summer (May-  
180 August) and winter (January-April) SST were calculated. For SIC data, we also computed for  
181 winter average and pixel-wise persistence of sea ice cover, defined as the number of days where  
182 a grid has a SIC value greater than 15% between February and September. Each environmental  
183 parameter was averaged over similar consecutive years during which, the annual temporal beta-  
184 diversity was computed. The fluctuations in seasonal sea ice dynamics and thermal conditions  
185 in the EBS regulated recent trophic and biogeographic shifts (Mueter and Litzow, 2008; Alabia  
186 et al., 2018). Finally, strongly correlated environmental variables ( $r > 0.5$ ; Fig. S3) were  
187 discarded to prevent problems with model identifiability (Tittensor et al., 2010).

## 188 **2.6 Identifying climatically stable areas**

189 We also identified climatically stable regions (*sensu* Ban et al., 2016) on the EBS shelf based  
190 on sea ice concentration and seasonal (winter and summer) sea surface temperatures from

191 1990-2018. For each environmental variable, we computed pixel-wise anomalies from the  
192 corresponding 29-year average and performed a Mann–Kendall monotonic trend analysis  
193 (Abdi et al., 2019) (Fig. S4a-c). The results were then classified into equal quintiles to  
194 categorize the magnitude of climatic changes (large decrease, small decrease, largely  
195 unchanged, small increase, large increase) and identify areas of stability for each parameter  
196 (Ban et al., 2016) (Fig. S4d-e). Parameter-specific stable areas were selected as pixels in the  
197 middle quintile (largely unchanged/neutral pixels) and climatically stable regions were mapped  
198 as areas of overlapping stable conditions across the three environmental variables.

## 199 **2.7 Environmental correlates with marine biodiversity**

200 To examine the relationships between environmental parameters and alpha and beta-diversity  
201 in the EBS, we developed generalized additive mixed models (GAMMs) using environmental  
202 factors ( $n = 6$ ) according to the following equation:

$$203 \quad n_{i,t} = yr + s(x_i, y_i) + \sum g_k(EV_{i,t}^k) + \varepsilon_{i,t}$$

204 where  $n_{i,t}$  is the observed response variable (either  $\alpha$ - or temporal  $\beta$ -diversity) at station  $i$   
205 sampled in year  $t$ ,  $yr$  is a year-specific intercept,  $x_i$  and  $y_i$  are the longitude and latitude of  
206 station  $i$ ,  $s$  is a two-dimensional thin-plate regression spline,  $g_k$  is a one-dimensional thin-plate  
207 regression spline fit to environmental variable  $EV^k$  measured at station  $i$  in year  $t$ , and  $\varepsilon_{i,t}$  is a  
208 residual error that is assumed to have a Gaussian spatial autocorrelation structure to allow for  
209 year-specific random variations in the spatial patterns (Wood, 2006).

210 For each biodiversity metric, three models were constructed using different correlation  
211 structures (i.e. Gaussian, exponential, and spherical) to account for within-year variability in  
212 spatial patterns of the observed response variable among years. The best model was selected  
213 as the one with the highest proportion of deviance explained based on the adjusted coefficient  
214 of determination (Adj  $R^2$ ) and lowest Akaike Information Criterion (AIC) (Table S4). Using

215 the best model, we then examined the significant partial effects of each environmental factor  
216 as well as spatial and temporal covariates (Fig. S5) to alpha and beta-biodiversity.

## 217 **2.8 Marine biodiversity under contrasting winter sea ice regimes**

218 We examined the spatial and temporal patterns of alpha diversity averaged across periods  
219 characterized by differences in mean winter sea ice concentration (wsic), as determined by the  
220 regime shift detection tool (Rodionov, 2006). The regime shift index was calculated using a  
221 10-year cut-off regime length at a significance level of 0.05 to capture the decadal-scale climate  
222 variability in the EBS. Based on this analysis, our study duration constituted periods of high  
223 (hwsic: 1990-1999; 2008-2013) and low (lwsic: 2000-2007; 2014-2018) winter sea ice  
224 conditions in the EBS (Fig. S6).

225 Finally, we quantified species turnover and nestedness (Baselga, 2013) and identified  
226 indicator species (Cáceres and Legendre, 2009) for low-ice (13 years) and high-ice (16 years)  
227 regimes based on observed species abundances. Using station-specific species abundances by  
228 weight averaged across years within each of the wsic regimes, we computed the abundance-  
229 based temporal beta-diversity between hwsic and lwsic regimes based on the Bray-Curtis index  
230 (Baselga and Orme, 2012). The dissimilarity metric was partitioned into two components that  
231 account for balanced variation in abundance (turnover), whereby the abundance of some taxa  
232 in one site is replaced by an equal abundance of different species in another site; and  
233 unidirectional abundance gradients (nestedness), whereby the abundance of some species  
234 decreases from one site to the other (Baselga, 2013). Further, to quantify the relative species-  
235 specific contributions to the overall dissimilarity we conducted a similarity percentage analysis  
236 using the ‘simper’ function in the vegan package (version 2.5-6) in R (Oksanen et al., 2019).  
237 This function implements a pair-wise comparison of groups and computes the average  
238 contribution of each taxon to the compositional dissimilarity between two regimes. To identify  
239 indicator species associated with each regime we quantified regime affinity using a multi-level

240 pattern analysis based on the point biserial correlation index using the ‘*multipatt*’ function of  
241 the *indicspecies* (version 1.7.7) R package (Cáceres and Legendre, 2009). The index evaluates  
242 the association between species and environmental conditions across the sampling sites based  
243 on the site-group combination with the highest difference between the species observed and  
244 expected abundance (De Cáceres et al., 2010).

### 245 **3. Results**

#### 246 **3.1 Temporal trends in marine biodiversity**

247 Average local alpha and beta-diversity respectively increased (4 species richness/decade,  $p <$   
248 0.001) and decreased (-0.02 dissimilarity/decade) over time across the entire study region (Fig.  
249 1). Overall, the downward trend in the temporal Sorensen dissimilarity was accounted for by a  
250 higher decline in the nestedness (-0.011 dissimilarity/decade,  $p < 0.001$ ) relative to the turnover  
251 (-0.009 dissimilarity/decade,  $p < 0.01$ ) component. Lower than average species richness and  
252 higher than average dissimilarity in community composition relative to the climatological  
253 means (across all years) were recorded until around 2000, then reversed for the rest of the  
254 series (Fig. 1). Nonetheless, there was high variability in the local annual alpha and beta-  
255 diversity. Notably, the temporal Sorensen dissimilarity showed higher variability across survey  
256 sites over the 29-year period.

#### 257 **3.2 Marine refugial zones on the EBS continental shelf**

258 Spatial distributions of the alpha and temporal beta-diversity over the 29-year period showed  
259 salient patterns (Fig. 2) and captured potential refugial zones on the EBS continental shelf (Fig.  
260 2c), exhibiting modest spatial correspondence with climatically stable regions (Fig. 2d, Fig. S4  
261 d-f). The middle shelf (50-100 m) had the highest average species richness (Fig. 2a) and  
262 moderate to high species compositional similarity (Fig. 2b) over the 29-year period. Based on  
263 the combination of both parameters, two geographically-distinct and spatially contiguous  
264 biodiversity refugial zones (refugia index  $> 0.31$ ) were identified: a north and south refugium

265 covering 21 and 16 survey stations, respectively (Fig. 2c). Both refugial areas were primarily  
266 defined by high species richness, but only the northern refugium had elevated compositional  
267 similarity over time. Spatial distributions of climatically stable regions also highlighted two  
268 distinct patches of moderate–high overlap across environmental variables and were spatially-  
269 extensive in the north than in the south portion of the middle shelf (Fig. 2d).

270 Fish taxa dominated taxonomically in both refugial zones by frequency of occurrence,  
271 particularly in the northern refugium where this group reached a total of 36 fish species (Fig.  
272 3). Within the invertebrate group, mollusks and crustacean species represented the highest  
273 number in both refugial zones. Biogeographically, the north refugium accounted for a higher  
274 total number of species (78 taxa) relative to the south refugium (62 taxa). Out of the entire  
275 species pool (159), four taxa were equally present in both refugia while 15 species were absent  
276 in both refugia. Importantly, these refugial zones constitute only 7% of the entire study region  
277 but harbor 91% ( $n = 144$ ) of the species pool, of which 50% ( $n = 79$ ) had higher average  
278 frequencies across stations over the 29-year period inside than outside the refugia. In particular,  
279 16 out of the 19 representative taxa were present at more stations and years inside than outside  
280 the refugia, with the majority (14/16) frequently occurring in the northern refugium (Table 1).

### 281 **3.3 Environmental effects on marine biodiversity**

282 Models of diversity explained a higher proportion of the total variance in alpha diversity ( $R^2 =$   
283  $0.46$ ) than in beta-diversity ( $R^2 = 0.15$ ). Whereas all environmental correlates had a statistically  
284 significant effect on alpha diversity, only four predictors (i.e., winter sea ice concentration,  
285 bottom depth, distance to coast, and bottom temperature gradient) had a significant association  
286 on beta-diversity (Table 2). Nonetheless, both models showed the highest significant effect of  
287 winter sea ice on marine biodiversity patterns in the EBS based on their F-values and statistical  
288 significance.

289           Response curves for significant environmental predictors captured the preferable  
290 ranges that were associated with higher regional marine biodiversity in the EBS (Fig. 4). In  
291 particular, bottom and surface temperature gradients had significant positive effects on alpha  
292 diversity at values closer to zero (Fig. 4a-b). In contrast, a moderate range of maximum summer  
293 SSTs (10-13°C; Fig. 4c), high winter sea ice concentration (wsic > 70%; Fig. 4d), deeper depths  
294 (60-120 m; bdep; Fig. 4e), and farther distances to the nearest coast (50-150 km; Fig 4f) were  
295 associated with higher alpha diversity. Meanwhile, the beta-diversity decreased with increasing  
296 bottom temperature gradient (Fig. 4g). It was also lowest in areas without winter sea ice but  
297 increased rapidly with increasing sea ice concentration and remained high over a broader range  
298 (20-95%; Fig. 4h) compared to alpha diversity. Beta-diversity increased with bottom depth,  
299 similar to yet more gradually than alpha diversity (Fig. 4i). In addition, distances farther away  
300 from the nearest coast had higher temporal beta-diversity (Fig. 4j).

### 301 **3.4 Spatial distributions of marine biodiversity under contrasting sea ice regimes**

302           Contrasting winter sea ice regimes in the EBS exhibited distinct patterns in alpha diversity  
303 distributions (Fig 5). Overall, species richness was substantially lower during the high sea ice  
304 regime ( $22.80 \pm 2.75$  species) compared to levels reached during low ( $25.83 \pm 3.69$  species)  
305 sea ice conditions (Fig. 5a-b). Pronounced changes in species richness between both regimes  
306 were observed across the middle and outer shelves and peaked at the southern part of the middle  
307 shelf, where local assemblages contained up to 10 species more during the low sea ice period  
308 (Fig. 5c).

309           In contrast, patterns in temporal beta-diversity suggest a high similarity in species  
310 composition between regimes over much of the area with the exception of the northeast middle  
311 domain (Fig. 6a). Locally elevated dissimilarity in species composition on the northeast shelf  
312 was largely accounted for by the unidirectional abundance gradient component (nestedness) of  
313 dissimilarity (Fig. 6b). This resulted from the apparent decrease (e.g., Alaska plaice, butterfly

314 sculpin, and great sculpin) and increase (e.g., walleye pollock, northern rock sole, and Pacific  
315 cod) in species abundances within survey sites in the area ( $n = 25$ ) under the low sea ice regime.  
316 In the southern part of the middle shelf, however, the dissimilarity in community composition  
317 is mostly accounted for by the balanced changes in species abundances (turnover) (Fig 6c). The  
318 species pool accounted for 63.27% of the overall between-regime dissimilarity in community  
319 composition. A total of three fish taxa (i.e. walleye pollock, northern rock sole, and arrowtooth  
320 flounder) associated with the lwsic regime, were identified to be most influential in driving  
321 community composition changes, based on their significant average contributions to the overall  
322 dissimilarity (Table S5).

#### 323 **4. Discussion**

324 The increasing and multi-faceted threats to marine biodiversity call for a better understanding  
325 of its long-term spatial patterns and temporal trends, especially within dynamic and climatically  
326 sensitive yet productive regions of the global ocean. Our study examined the contemporary  
327 distributions of taxonomic biodiversity aspects of marine communities on the continental shelf  
328 of the Eastern Bering Sea (EBS) and identified the importance of environmental covariates in  
329 modulating temporal and spatial patterns of local alpha- and beta-diversity. The use of actual  
330 species observations to elucidate spatio-temporal changes in biodiversity over the past 29 years  
331 enabled the identification of geographically distinct biodiversity refugial zones. These areas  
332 provided safe havens for marine species in the EBS under on-going climate changes as evident  
333 from the high species richness and stability in community compositions within these regions.

334 Additionally, the biodiversity refugia showed modest correspondence with climatically  
335 stable regions in the EBS over the past 29 years. Such spatial overlap between refugial features  
336 potentially supports the persistence of elevated marine biodiversity and species compositional  
337 similarity in these areas under recent climatic changes. Nonetheless, it is worth noting that  
338 these biodiversity refugia were also situated in areas of unstable climatic conditions, suggesting

339 that potential processes other than climate buffering are crucial in the formation of these  
340 features. This further underpinned the importance of validation as an essential component of  
341 the climate change refugia conservation cycle (Morelli et al., 2016) and ecosystem-based  
342 management strategies to ensure adaptive and more effective responses in protecting  
343 biodiversity and high-value resources (Barrows et al., 2020).

344         Refugia are indispensable for facilitating the persistence of components of biodiversity  
345 under changing climates over certain ecological time scales (Keppel et al., 2012). In the EBS,  
346 two latitudinally distinct refugia were identified on the middle shelf (50-100 m). Both areas  
347 persisted through spatial and temporal variability in environmental and climatic conditions over  
348 the last three decades. The formation of refugia may be linked to biophysical processes that  
349 enhance productivity at these sites. One of the refugial zones straddles the transition zone  
350 between the outer and middle domains on the southern shelf, a region of elevated summer  
351 productivity due to the presence of structural fronts (Sambrotto et al., 2008). Similarly, the  
352 north refugium is situated on the outer portion of the middle shelf and extends slightly past the  
353 transition zone onto the outer shelf, a region where elevated production rates are fueled by  
354 intense spring ice-edge blooms (Lomas et al., 2012; Stabeno et al., 2012). Hence, the high  
355 summer primary productivity in these areas likely supports the high species richness in these  
356 refugia. Moreover, the higher productivity in the north (58-60°N) relative to the south sector  
357 of the middle shelf (Lomas et al., 2012) could account for higher percent frequencies of species  
358 in the former than in the latter. High productivity may also explain the counterintuitive overlap  
359 between these refugial zones and areas of intensive fishing, particularly the southern refugia,  
360 accumulating the highest area disturbed across gear types (Olson, 2019). High primary  
361 productivity may cushion marine communities against the impacts of fishing, consistent with  
362 the reported minimal long-term effects of fisheries on fish populations in the area (Olson, 2019).  
363 In any case, our results highlight the relevance of biodiversity refugial zones for ecosystem-

364 based management approaches to maintain resilient fisheries and ecosystems under a rapidly  
365 changing climate.

366         While the overall stability in community composition was similar in the two refugia,  
367 the north refugium showed distinct patches of high compositional similarity. It suggests that  
368 the community in this zone is comprised of species that have a particular affinity or close  
369 association to low-temperature waters (e.g., snow crab, wattled eelpout, and polar six-rayed  
370 star) and are therefore generally more abundant on the northern shelf (Rand and Logerwell,  
371 2011). In the south refugium, the highest similarity in community composition occurred close  
372 to the inner front separating the inner and middle shelves, decreasing eastward. The wind-  
373 driven inner front serves as a region of protracted production and an obstacle to faunal  
374 exchanges between the inner and middle shelves (Stabeno and Hunt, 2002), thus likely  
375 promoting the retention of distinct species assemblages at both sides of the inner and middle  
376 shelves proximal to the frontal boundary. Likewise, climatically stable areas in the southern  
377 region of the middle shelf were smaller relative to the north, potentially accounting for a lower  
378 similarity in the species community composition in the south refugium. Despite the differences  
379 in biodiversity components between the two refugia, these zones harbored a persistently large  
380 portion of the species pool providing shelter for marine taxa in this shelf community under  
381 contemporary climatic changes and substantial fishing footprint (Olson, 2019).

382         Nonetheless, we recognize that changing biological interactions at the refugia could  
383 also have fundamental ecological consequences under future environmental and climatic  
384 changes. The dominance of large predatory fish taxa (i.e. walleye pollock, Pacific cod, and  
385 flathead sole) in the refugial zones, particularly in the north refugium, could significantly alter  
386 predatory and competitive interactions within the existing community. For instance, gadoid  
387 predation exerts top-down control of snow crab (*Chionoecetes opilio*) abundance in subarctic  
388 and Arctic seas (Orensanz et al., 2005; Boudreau et al., 2011; Burgos et al., 2013). Similarly,

389 the intensified competition among predators for space and resources in high-density areas can  
390 also modify ecosystem-wide trophic linkages and prey resource dynamics (Hunsicker et al.,  
391 2013; Matassa et al., 2018). Therefore, effective adaptation strategy focusing on the  
392 conservation of climate change refugia can benefit from further incorporation of biological  
393 interactions into the framework (Kavousi, 2019), albeit our current understanding of many of  
394 these biotic interactions remains inadequate.

395 Our analysis of the effects of environmental factors on biodiversity is consistent with  
396 earlier studies on the impacts of sea ice dynamics on contemporary and future spatial  
397 distributions of marine species in the study area (Mueter and Litzow, 2008; Alabia et al., 2018;  
398 Alabia et al., 2020). The overall effect of winter sea ice concentration on species richness and  
399 community composition varied spatially. During periods of low sea ice concentration, the cold  
400 pool structure retracts north (Stabeno et al., 2012), allowing an extensive movement of species  
401 throughout the study area (Mueter and Litzow, 2008). This condition could facilitate foraging  
402 migrations of warm-affinity taxa to the more productive waters in the north sector of the middle  
403 shelf. The enhanced species movement responses, especially for large fish species (e.g.,  
404 walleye pollock, arrowtooth flounder, and northern rock sole), under the lwsic regime increase  
405 the local species richness while promoting the biotic homogenization of local communities.  
406 Thus, resulting in increased similarity in species between periods of high and low winter sea  
407 ice conditions. In contrast, during the hwsic regime, the high species richness was limited to  
408 the southern part of the EBS. In the EBS, a sub-surface summer thermal layer associated with  
409 seasonal sea ice (Hunt et al., 2011), known as the cold pool, largely regulates species movement  
410 (Wyllie-Echeverria and Wooster, 1998). The cold pool feature is characterized by low bottom  
411 temperatures ( $< 2^{\circ}\text{C}$ ) that extend south to the southeastern shelf during periods of extensive  
412 winter sea ice coverage (Stabeno et al., 2012), posing an effective barrier to the movement of  
413 cold-intolerant species across the different domains and sectors of the continental shelf. This

414 results in the observed decrease in average regional alpha diversity over much of the middle  
415 shelf during the high winter sea ice periods.

416 Finally, in light of the rapid ecological transformations of high-latitude environments  
417 due to climate change and extreme events (e.g., marine heatwaves, atmospheric disturbances),  
418 it is all the more imperative to better understand the dynamics of potential refugial zones. In  
419 particular, continually assimilating the most recent and larger pool of biodiversity data into the  
420 analyses can better evaluate the capacity of refugial zones to cushion against emerging and  
421 multifaceted threats. We also recognized that bottom trawl survey data primarily target  
422 demersal fisheries, which may result in the under-representation of pelagic taxa in our analyses.  
423 Future incorporation of a larger species pool from pelagic habitats could offer further, more  
424 holistic insights into the nature of biodiversity refugial zones when that information becomes  
425 available. Additionally, adopting a gradient-based perspective of climate change refugia may  
426 improve the identification and protection of these areas, recognizing the difference in rates at  
427 which various biodiversity components will respond to climate change (Hannah et al., 2014;  
428 Morelli et al., 2020). Recent studies have shown that even marine protected areas in temperate  
429 regions were unable to forestall the heatwave-induced changes in the fish community structure  
430 (Freedman et al., 2020) and future climate change-driven decline in benthic species (Weinert  
431 et al., 2020). More than ever, climate-driven and intensified phenomena exacerbate the already  
432 tremendous challenge of biodiversity conservation, hence emphasizing the importance of  
433 identification and management of potential marine climate change and biodiversity refugia,  
434 ideally within a progressive context (Morelli et al., 2020).

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## 443 **References**

- 444 Abdi, A. M., Boke-Olén, N., Jin, H., Eklundh, L., Tagesson, T., Lehsten, V., and Ardö, J. 2019.  
445 First assessment of the plant phenology index (PPI) for estimating gross primary  
446 productivity in African semi-arid ecosystems. *International Journal of Applied Earth  
447 Observation and Geoinformation*, 78: 249-260.
- 448 Alabía, I. D., García Molinos, J., Saitoh, S.-I., Hirawake, T., Hirata, T., and Mueter, F. J. 2018.  
449 Distribution shifts of marine taxa in the Pacific Arctic under contemporary climate  
450 changes. *Diversity and Distributions*, 24: 1583-1597.
- 451 Alabía, I. D., Molinos, J. G., Saitoh, S.-I., Hirata, T., Hirawake, T., and Mueter, F. J. 2020.  
452 Multiple facets of marine biodiversity in the Pacific Arctic under future climate.  
453 *Science of The Total Environment*, 744: 140913.
- 454 Ashcroft, M. B. 2010. Identifying refugia from climate change. *Journal of Biogeography*, 37:  
455 1407-1413.
- 456 Ashcroft, M. B., Gollan, J. R., Warton, D. I., and Ramp, D. 2012. A novel approach to quantify  
457 and locate potential microrefugia using topoclimate, climate stability, and isolation  
458 from the matrix. *Global Change Biology*, 18: 1866-1879.
- 459 Assis, J., Coelho, N. C., Lamy, T., Valero, M., Alberto, F., and Serrão, E. Á. 2016. Deep reefs  
460 are climatic refugia for genetic diversity of marine forests. *Journal of Biogeography*,  
461 43: 833-844.
- 462 Baker, M. R., and Hollowed, A. B. 2014. Delineating ecological regions in marine systems:  
463 Integrating physical structure and community composition to inform spatial

464 management in the eastern Bering Sea. *Deep Sea Research Part II: Topical Studies in*  
465 *Oceanography*, 109: 215-240.

466 Ban, N. C., Pressey, R. L., and Weeks, S. 2012. Conservation Objectives and Sea-Surface  
467 Temperature Anomalies in the Great Barrier Reef. *Conservation Biology*, 26: 799-809.

468 Ban, S. S., Alidina, H. M., Okey, T. A., Gregg, R. M., and Ban, N. C. 2016. Identifying  
469 potential marine climate change refugia: A case study in Canada's Pacific marine  
470 ecosystems. *Global Ecology and Conservation*, 8: 41-54.

471 Barbier, E. B. 2017. Marine ecosystem services. *Current Biology*, 27: R507-R510.

472 Barceló, C., Ciannelli, L., and Brodeur, R. D. 2018. Pelagic marine refugia and climatically  
473 sensitive areas in an eastern boundary current upwelling system. *Global Change*  
474 *Biology*, 24: 668-680.

475 Barrows, C. W., Ramirez, A. R., Sweet, L. C., Morelli, T. L., Millar, C. I., Frakes, N., Rodgers,  
476 J., et al. 2020. Validating climate-change refugia: empirical bottom-up approaches to  
477 support management actions. *Frontiers in Ecology and the Environment*, 18: 298-306.

478 Baselga, A. 2013. Separating the two components of abundance-based dissimilarity: balanced  
479 changes in abundance vs. abundance gradients. *Methods in Ecology and Evolution*, 4:  
480 552-557.

481 Baselga, A., and Orme, C. D. L. 2012. betapart: an R package for the study of beta diversity.  
482 *Methods in Ecology and Evolution*, 3: 808-812.

483 Baumgartner, J. B., Esperón-Rodríguez, M., and Beaumont, L. J. 2018. Identifying in situ  
484 climate refugia for plant species. *Ecography*, 41: 1850-1863.

485 Boudreau, S. A., Anderson, S., and Worm, B. 2011. Top-down interactions and temperature  
486 control of snow crab abundance in the northwest Atlantic Ocean. *Marine Ecology*  
487 *Progress Series*, 429: 169-183.

488 Burgos, J., Ernst, B., Armstrong, D., and Orensanz, J. 2013. Fluctuations in Range and  
489 Abundance of Snow Crab (*Chionoecetes Opilio*) from the Eastern Bering Sea: What  
490 Role for Pacific Cod (*Gadus Macrocephalus*) Predation? *Bulletin of Marine Science*,  
491 89: 57-81.

492 Burrows, M. T., Schoeman, D. S., Buckley, L. B., Moore, P., Poloczanska, E. S., Brander, K.  
493 M., Brown, C., et al. 2011. The Pace of Shifting Climate in Marine and Terrestrial  
494 Ecosystems. *Science*, 334: 652-655.

495 Cáceres, M. D., and Legendre, P. 2009. Associations between species and groups of sites:  
496 indices and statistical inference. *Ecology*, 90: 3566-3574.

497 Cavanagh, R. D., Broszeit, S., Pilling, G. M., Grant, S. M., Murphy, E. J., and Austen, M. C.  
498 2016. Valuing biodiversity and ecosystem services: a useful way to manage and  
499 conserve marine resources? *Proceedings of the Royal Society B: Biological Sciences*,  
500 283: 20161635.

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

503 Danielson, S., Eisner, L., Weingartner, T., and Aagaard, K. 2011. Thermal and haline  
504 variability over the central Bering Sea shelf: Seasonal and interannual perspectives.  
505 *Continental Shelf Research*, 31: 539-554.

506 De Cáceres, M., Legendre, P., and Moretti, M. 2010. Improving indicator species analysis by  
507 combining groups of sites. *Oikos*, 119: 1674-1684.

508 Duffy-Anderson, J. T., Stabeno, P. J., Siddon, E. C., Andrews, A. G., Cooper, D. W., Eisner,  
509 L. B., Farley, E. V., et al. 2017. Return of warm conditions in the southeastern Bering  
510 Sea: Phytoplankton - Fish. *PLoS ONE*, 12: e0178955.

511 Eisner, L. B., Gann, J. C., Ladd, C., D. Ciciel, K., and Mordy, C. W. 2016. Late summer/early  
512 fall phytoplankton biomass (chlorophyll a) in the eastern Bering Sea: Spatial and

513 temporal variations and factors affecting chlorophyll a concentrations. *Deep Sea*  
514 *Research Part II: Topical Studies in Oceanography*, 134: 100-114.

515 Eisner, L. B., Napp, J. M., Mier, K. L., Pinchuk, A. I., and Andrews, A. G. 2014. Climate-  
516 mediated changes in zooplankton community structure for the eastern Bering Sea. *Deep*  
517 *Sea Research Part II: Topical Studies in Oceanography*, 109: 157-171.

518 Freedman, R. M., Brown, J. A., Caldow, C., and Caselle, J. E. 2020. Marine protected areas do  
519 not prevent marine heatwave-induced fish community structure changes in a temperate  
520 transition zone. *Scientific Reports*, 10: 21081.

521 Genner, M. J., Sims, D. W., Southward, A. J., Budd, G. C., Masterson, P., McHugh, M., Rendle,  
522 P., et al. 2010. Body size-dependent responses of a marine fish assemblage to climate  
523 change and fishing over a century-long scale. *Global Change Biology*, 16: 517-527.

524 Hannah, L., Flint, L., Syphard, A. D., Moritz, M. A., Buckley, L. B., and McCullough, I. M.  
525 2014. Fine-grain modeling of species' response to climate change: holdouts, stepping-  
526 stones, and microrefugia. *Trends in Ecology & Evolution*, 29: 390-397.

527 Hirawake, T., and Hunt, G. L. 2020. Impacts of unusually light sea-ice cover in winter 2017-  
528 2018 on the northern Bering Sea marine ecosystem – An introduction. *Deep Sea*  
529 *Research Part II: Topical Studies in Oceanography*: 104908.

530 Hollowed, A. B., Bax, N., Beamish, R., Collie, J., Fogarty, M., Livingston, P., Pope, J., et al.  
531 2000. Are multispecies models an improvement on single-species models for  
532 measuring fishing impacts on marine ecosystems? *ICES Journal of Marine Science*, 57:  
533 707-719.

534 Hooidonk, R. V., Maynard, J., Maynard, J., and Planes, S. 2013. Temporary refugia for coral  
535 reefs in a warming world. *Nature Climate Change*, 3: 508-511.

536 Hunsicker, M. E., Ciannelli, L., Bailey, K. M., Zador, S., and Stige, L. C. 2013. Climate and  
537 Demography Dictate the Strength of Predator-Prey Overlap in a Subarctic Marine  
538 Ecosystem. *PLoS ONE*, 8: e66025.

539 Hunt, J. G. L., Coyle, K. O., Eisner, L. B., Farley, E. V., Heintz, R. A., Mueter, F., Napp, J. M.,  
540 et al. 2011. Climate impacts on eastern Bering Sea foodwebs: a synthesis of new data  
541 and an assessment of the Oscillating Control Hypothesis. *ICES Journal of Marine*  
542 *Science*, 68: 1230-1243.

543 Isaak, D. J., Young, M. K., Luce, C. H., Hostetler, S. W., Wenger, S. J., Peterson, E. E., Ver  
544 Hoef, J. M., et al. 2016. Slow climate velocities of mountain streams portend their role  
545 as refugia for cold-water biodiversity. *Proceedings of the National Academy of*  
546 *Sciences*, 113: 4374.

547 Jost, L., Chao, A., and Chazdon, R. 2010. Compositional similarity and  $\beta$  (beta ) diversity.

548 Kapsenberg, L., and Cyronak, T. 2019. Ocean acidification refugia in variable environments.  
549 *Global Change Biology*, 25: 3201-3214.

550 Kavousi, J. 2019. Biological interactions: The overlooked aspects of marine climate change  
551 refugia. *Global Change Biology*, 25: 3571-3573.

552 Keppel, G., Mokany, K., Wardell-Johnson, G. W., Phillips, B. L., Welbergen, J. A., and Reside,  
553 A. E. 2015. The capacity of refugia for conservation planning under climate change.  
554 *Frontiers in Ecology and the Environment*, 13: 106-112.

555 Keppel, G., Van Niel, K. P., Wardell-Johnson, G. W., Yates, C. J., Byrne, M., Mucina, L.,  
556 Schut, A. G. T., et al. 2012. Refugia: identifying and understanding safe havens for  
557 biodiversity under climate change. *Global Ecology and Biogeography*, 21: 393-404.

558 Krebs, C. J. 2014. Similarity Coefficients and Cluster Analysis. *In Ecological methodology*,  
559 pp. 486-527. Benjamin/Cummings, Menlo Park, Calif.

560 Lomas, M. W., Moran, S. B., Casey, J. R., Bell, D. W., Tiahlo, M., Whitefield, J., Kelly, R. P.,  
561 et al. 2012. Spatial and seasonal variability of primary production on the Eastern Bering  
562 Sea shelf. *Deep Sea Research Part II: Topical Studies in Oceanography*, 65-70: 126-  
563 140.

564 Lourenço, C. R., Zardi, G. I., McQuaid, C. D., Serrão, E. A., Pearson, G. A., Jacinto, R., and  
565 Nicastro, K. R. 2016. Upwelling areas as climate change refugia for the distribution and  
566 genetic diversity of a marine macroalga. *Journal of Biogeography*, 43: 1595-1607.

567 Malhi, Y., Franklin, J., Seddon, N., Solan, M., Turner, M. G., Field, C. B., and Knowlton, N.  
568 2020. Climate change and ecosystems: threats, opportunities and solutions.  
569 *Philosophical Transactions of the Royal Society B: Biological Sciences*, 375: 20190104.

570 Matassa, C. M., Ewanchuk, P. J., and Trussell, G. C. 2018. Cascading effects of a top predator  
571 on intraspecific competition at intermediate and basal trophic levels. *Functional*  
572 *Ecology*, 32: 2241-2252.

573 Morelli, T. L., Barrows, C. W., Ramirez, A. R., Cartwright, J. M., Ackerly, D. D., Eaves, T.  
574 D., Ebersole, J. L., et al. 2020. Climate-change refugia: biodiversity in the slow lane.  
575 *Frontiers in Ecology and the Environment*, 18: 228-234.

576 Morelli, T. L., Daly, C., Dobrowski, S. Z., Dulen, D. M., Ebersole, J. L., Jackson, S. T.,  
577 Lundquist, J. D., et al. 2016. Managing Climate Change Refugia for Climate Adaptation.  
578 *PLoS ONE*, 11: e0159909-e0159909.

579 Morelli, T. L., Maher, S. P., Lim, M. C. W., Kastely, C., Eastman, L. M., Flint, L. E., Flint, A.  
580 L., et al. 2017. Climate change refugia and habitat connectivity promote species  
581 persistence. *Climate Change Responses*, 4: 8.

582 Mueter, F. J., and Litzow, M. A. 2008. Sea ice retreat alters the biogeography of the Bering  
583 Sea continental shelf. *Ecological Applications*, 18: 309-320.

584 Oksanen, J., Blanchet FG, Friendly M, Kindt R, Legendre P, McGlinn D, Minchin PR, et al.  
585 2019. vegan: Community Ecology Package. R package version 2.5-6. [https://CRAN.R-](https://CRAN.R-project.org/package=vegan)  
586 [project.org/package=vegan](https://CRAN.R-project.org/package=vegan).

587 Olson, J. 2019. Area Disturbed by Trawl Fishing Gear in the Eastern Bering Sea. In: Siddon,  
588 E. and Zador S., Eds. (2019) Ecosystem Status Report 2019: Eastern Bering Sea. North  
589 Pacific Fishery Management Council, 605 W. 4th Avenue, Suite 306, Anchorage, AK  
590 99301, pp. 162-164

591 Orensanz, J. M., Ernest, B., Armstrong, D., Stabeno, P., and Livingston, P. 2005. Contraction  
592 of the geographic range of distribution of snow crab (*Chionoecetes opilio*) in the eastern  
593 Bering Sea: An environmental ratchet?

594 Ortiz, I., Aydin, K., Hermann, A. J., Gibson, G. A., Punt, A. E., Wiese, F. K., Eisner, L. B., et  
595 al. 2016. Climate to fish: Synthesizing field work, data and models in a 39-year  
596 retrospective analysis of seasonal processes on the eastern Bering Sea shelf and slope.  
597 Deep Sea Research Part II: Topical Studies in Oceanography, 134: 390-412.

598 Overland, J. E., and Stabeno, P. J. 2004. Is the climate of the Bering Sea warming and affecting  
599 the ecosystem? Eos, Transactions American Geophysical Union, 85: 309-312.

600 Pinheiro, H. T., Bernardi, G., Simon, T., Joyeux, J.-C., Macieira, R. M., Gasparini, J. L., Rocha,  
601 C., et al. 2017. Island biogeography of marine organisms. Nature, 549: 82-85.

602 Planque, B. 2016. Projecting the future state of marine ecosystems, “la grande illusion”? ICES  
603 Journal of Marine Science, 73: 204-208.

604 Provan, J. 2013. The effects of past, present and future climate change on range-wide genetic  
605 diversity in northern North Atlantic marine species. Frontiers of Biogeography, 5.

606 Rand, K. M., and Logerwell, E. A. 2011. The first demersal trawl survey of benthic fish and  
607 invertebrates in the Beaufort Sea since the late 1970s. Polar Biology, 34: 475-488.

608 Rodionov, S. N. 2006. Use of prewhitening in climate regime shift detection. *Geophysical*  
609 *Research Letters*, 33: L12707.

610 Sala, E., and Knowlton, N. 2006. Global Marine Biodiversity Trends. *Annual Review of*  
611 *Environment and Resources*, 31: 93-122.

612 Sambrotto, R. N., Mordy, C., Zeeman, S. I., Stabeno, P. J., and Macklin, S. A. 2008. Physical  
613 forcing and nutrient conditions associated with patterns of Chl a and phytoplankton  
614 productivity in the southeastern Bering Sea during summer. *Deep Sea Research Part II:*  
615 *Topical Studies in Oceanography*, 55: 1745-1760.

616 Selig, E. R., Turner, W. R., Troëng, S., Wallace, B. P., Halpern, B. S., Kaschner, K., Lascelles,  
617 B. G., et al. 2014. Global Priorities for Marine Biodiversity Conservation. *PLoS ONE*,  
618 9: e82898.

619 Springer, A. M., McRoy, C. P., and Flint, M. V. 1996. The Bering Sea Green Belt: shelf-edge  
620 processes and ecosystem production. *Fisheries Oceanography*, 5: 205-223.

621 Stabeno, P. J., and Bell, S. W. 2019. Extreme Conditions in the Bering Sea (2017–2018):  
622 Record-Breaking Low Sea-Ice Extent. *Geophysical Research Letters*, 46: 8952-8959.

623 Stabeno, P. J., Duffy-Anderson, J. T., Eisner, L. B., Farley, E. V., Heintz, R. A., and Mordy,  
624 C. W. 2017. Return of warm conditions in the southeastern Bering Sea: Physics to  
625 fluorescence. *PLoS ONE*, 12: e0185464.

626 Stabeno, P. J., and Hunt, G. L. 2002. Overview of the Inner Front and Southeast Bering Sea  
627 Carrying Capacity Programs. *Deep Sea Research Part II: Topical Studies in*  
628 *Oceanography*, 49: 6157-6168.

629 Stabeno, P. J., Kachel, N. B., Moore, S. E., Napp, J. M., Sigler, M., Yamaguchi, A., and Zerbini,  
630 A. N. 2012. Comparison of warm and cold years on the southeastern Bering Sea shelf  
631 and some implications for the ecosystem. *Deep Sea Research Part II: Topical Studies*  
632 *in Oceanography*, 65–70: 31-45.

633 Stauffer, G. 2004. NOAA protocols for groundfish bottom trawl surveys of the nation's fishery  
634 resources. Technical Memorandum NMFS-F/SPO-65, U.S. Department of Commerce,  
635 NOAA, Washington, D.C., USA.

636 Stevenson, D. E., and Hoff, G. R. 2009. Species identification confidence in the eastern Bering  
637 Sea (1982–2008). 46 pp. pp.

638 Stevenson, D. E., and Lauth, R. R. 2019. Bottom trawl surveys in the northern Bering Sea  
639 indicate recent shifts in the distribution of marine species. *Polar Biology*, 42: 407-421.

640 Stewart, J. R., Lister, A. M., Barnes, I., and Dalén, L. 2010. Refugia revisited: individualistic  
641 responses of species in space and time. *Proceedings of the Royal Society B: Biological*  
642 *Sciences*, 277: 661-671.

643 Storlazzi, C. D., Cheriton, O. M., van Hooijdonk, R., Zhao, Z., and Brainard, R. 2020. Internal  
644 tides can provide thermal refugia that will buffer some coral reefs from future global  
645 warming. *Scientific Reports*, 10: 13435.

646 Sydeman, W. J., Poloczanska, E., Reed, T. E., and Thompson, S. A. 2015. Climate change and  
647 marine vertebrates. *Science*, 350: 772.

648 Tittensor, D. P., Mora, C., Jetz, W., Lotze, H. K., Ricard, D., Berghe, E. V., and Worm, B.  
649 2010. Global patterns and predictors of marine biodiversity across taxa. *Nature*, 466:  
650 1098-1101.

651 Weinert, M., Mathis, M., Kröncke, I., Pohlmann, T., and Reiss, H. 2020. Climate change effects  
652 on Marine Protected Areas: projected decline of benthic species in the North Sea.  
653 *Marine Environmental Research*: 105230.

654 Wessel, P., Smith, W. H. F., Scharroo, R., Luis, J., and Wobbe, F. 2013. Generic Mapping  
655 Tools: Improved Version Released. *Eos, Transactions American Geophysical Union*,  
656 94: 409-410.

- 657 Wood, S. 2006. Generalized Additive Models: An Introduction with R, Chapman and  
658 Hall/CRC, Boca Raton, Florida.
- 659 Wyllie-Echeverria, T., and Wooster, W. S. 1998. Year-to-year variations in Bering Sea ice  
660 cover and some consequences for fish distributions. *Fisheries Oceanography*, 7: 159-  
661 170.

662 **Table 1.** Average percent frequency of annual occurrence of representative taxa inside (37 stations) and outside (339 stations) of the designated  
 663 refugia zone over the 29 years of the study period. Species with higher frequencies within the refugia are highlighted in bold.

Common name	Scientific name	Percent frequency			
		Inside refugia			Outside refugia
		South	North	Overall	
<b>Walleye pollock</b>	<i>Gadus chalcogrammus</i>	42.96	56.66	99.63	96.23
<b>Pacific cod</b>	<i>Gadus macrocephalus</i>	42.78	56.10	98.88	95.04
<b>Basketstar</b>	<i>Gorgonocephalus eucnemis</i>	41.66	54.89	96.55	55.11
<b>Snow crab</b>	<i>Chionoecetes opilio</i>	36.63	56.48	93.10	68.80
<b>Flathead sole</b>	<i>Hippoglossoides elassodon</i>	41.94	50.51	92.45	73.41
<b>Alaska plaice</b>	<i>Pleuronectes quadrituberculatus</i>	41.47	45.67	87.14	64.33
<b>Tanner crab</b>	<i>Chionoecetes bairdi</i>	41.01	42.40	83.41	61.40
<b>Polar six-rayed star</b>	<i>Leptasterias polaris</i>	30.20	52.10	82.29	30.38
<b>Northern rock sole</b>	<i>Lepidopsetta polyxystra</i>	34.11	43.62	77.73	67.10
<b>Alaska skate</b>	<i>Bathyraja parmifera</i>	32.62	44.45	77.07	69.81
<b>Wattled eelpout</b>	<i>Lycodes palearis</i>	28.15	47.72	75.86	32.27
Pacific halibut	<i>Hippoglossus stenolepis</i>	32.53	35.79	68.31	71.59
<b>Yellowfin sole</b>	<i>Limanda aspera</i>	42.87	23.95	66.82	66.30
<b>Great sculpin</b>	<i>Myoxocephalus polyacanthocephalus</i>	26.75	34.86	61.60	42.56
<b>Circumboreal toad crab</b>	<i>Hyas coarctatus</i>	33.92	26.75	60.67	41.82
Purple-orange sea star	<i>Asterias amurensis</i>	38.30	20.32	58.62	64.42
<b>Arrowtooth flounder</b>	<i>Atheresthes stomias</i>	19.66	33.74	53.40	48.91
Sturgeon poacher	<i>Podothecus accipenserinus</i>	37.09	16.31	53.40	57.13
<b>Pribilof whelk</b>	<i>Neptunea pribiloffensis</i>	10.07	42.03	52.10	33.26

665 **Table 2.** Generalized additive mixed model outputs for alpha and beta-diversity. Estimated degrees of freedom, F-values (t-values for factor terms)  
666 obtained for each environmental correlate and asterisks represent significance levels at  $p$  less than 0.05 (\*), 0.01 (\*\*) or 0.001(\*\*\*). Model  
667 performance were assessed based on adjusted  $R^2$  and Akaike Information Criterion (AIC) values.

Models	Predictors	Abbreviation	Estimated degrees of freedom (edf)	t/F-value	Adj $R^2$	AIC
$\alpha$ -diversity					0.458	49941
	year	yr		46.76***		
	longitude,latitude	x,y	27.79	36.59**		
	bottom temperature gradient	btg	1.95	14.22**		
	surface temperature gradient	stg	1.90	9.92***		
	bottom depth	bdep	1.91	5.70*		
	maximum summer sea surface temperature (SST)	ssst <sub>max</sub>	1.90	4.05*		
	winter sea ice concentration	wsic	1.97	15.57***		
	distance to the nearest coast	dist <sub>coast</sub>	1.88	3.27*		
$\beta$ -diversity					0.150	-21493
	year	yr		-15.86***		
	longitude,latitude	x,y	24.85	10.69***		
	bottom temperature gradient	btg	1.00	5.12*		
	surface temperature gradient	stg				
	bottom depth	bdep	1.91	9.09**		
	maximum summer SST	ssst <sub>max</sub>				
	winter sea ice concentration	wsic	1.92	31.44***		
	distance to the nearest coast	dist <sub>coast</sub>	1.92	5.83**		

668 **Figure legends**

669 **Figure 1.** Temporal trends in (a) regionally (polygon in inset map) averaged species richness  
670 and (b) change in species composition (Sorensen dissimilarity) with vertical bars  
671 representing one positive and negative standard deviation. Gray broken lines  
672 correspond to the climatological average of alpha (24.48, 1990-2018) and temporal  
673 beta-diversity (0.26, 1991-2018). Blue lines show the least-squares linear regressions  
674 of each biodiversity metric on year.

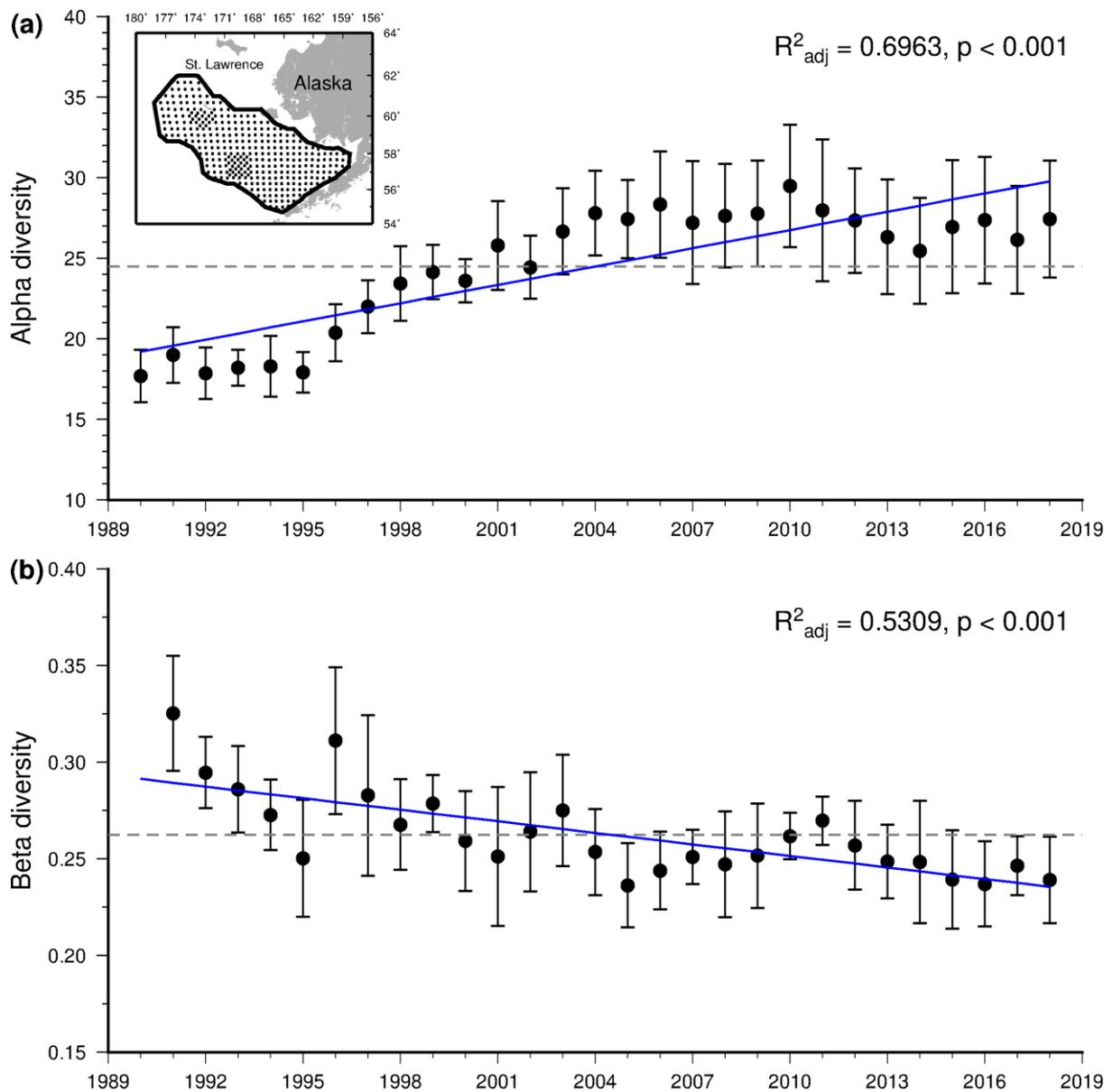
675 **Figure 2.** Spatially-interpolated distributions of (a) mean  $\alpha$ -diversity (rescaled to 0–1), (b)  
676 mean within-site temporal community similarity (presented as the inverse of Sorensen  
677 dissimilarity), (c) the resultant refugia index computed as the product of mean  $\alpha$ - and  
678 mean within-site temporal  $\beta$ -diversity, and (d) climatic stability based on the sum of  
679 neutral (largely unchanged trend) pixels for winter sea ice concentration and seasonal  
680 sea surface temperatures. Regions in blue did not have any neutral pixels; areas in red  
681 contained neutral pixels in all three variables. The polygons denote the identified  
682 refugia zones (refugia index value of 0.31, 90% quantile of refugia index) and the  
683 broken lines correspond to the 50 and 100 m isobaths.

684 **Figure 3.** Number of species inside the refugia and their biogeographic affinity between the  
685 north (21 stations) and south (16 stations) refugia (inset map).

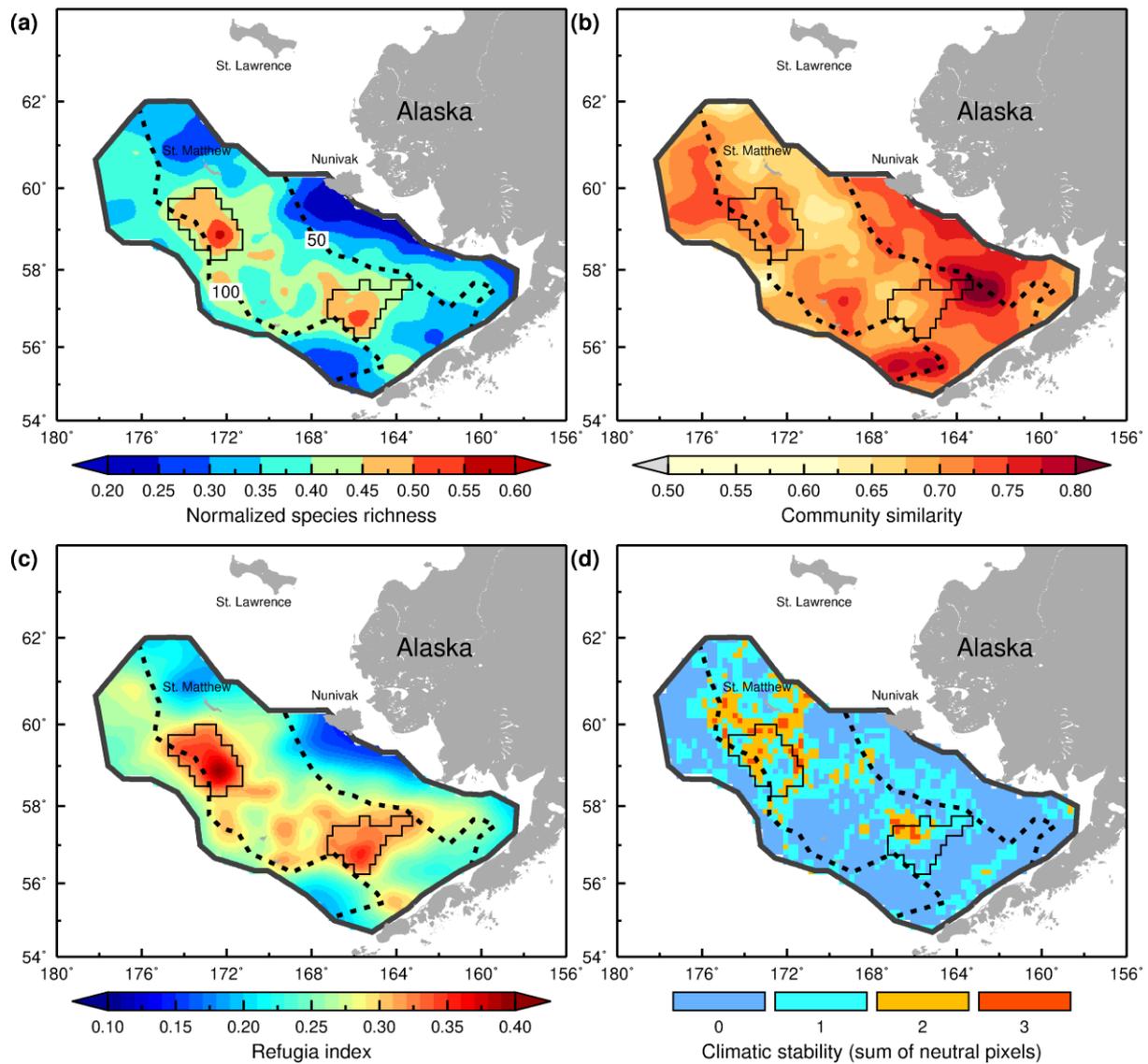
686 **Figure 4.** Significant partial effects of environmental variables (a-f) on alpha diversity (species  
687 richness) and (g-j) beta diversity (Sorensen dissimilarity) predicted from a generalized  
688 additive mixed model. The solid lines are estimated mean effects, the gray shaded areas  
689 are the 95% point-wise confidence intervals, and 0 represents the reference for a null  
690 effect (broken lines). Ticks along the x-axis are points at which observations were  
691 obtained between 1990 and 2018.

692 **Figure 5.** Spatial structures of averaged annual alpha diversity during (a) the high (1990-1999;  
693 2008-2013), (b) low (2000-2007; 2014-2018) winter sea ice (wsic) regimes in the  
694 Eastern Bering Sea, and (c) the species richness difference between the contrasting  
695 regimes. Broken lines correspond to the 50 and 100 m isobaths.

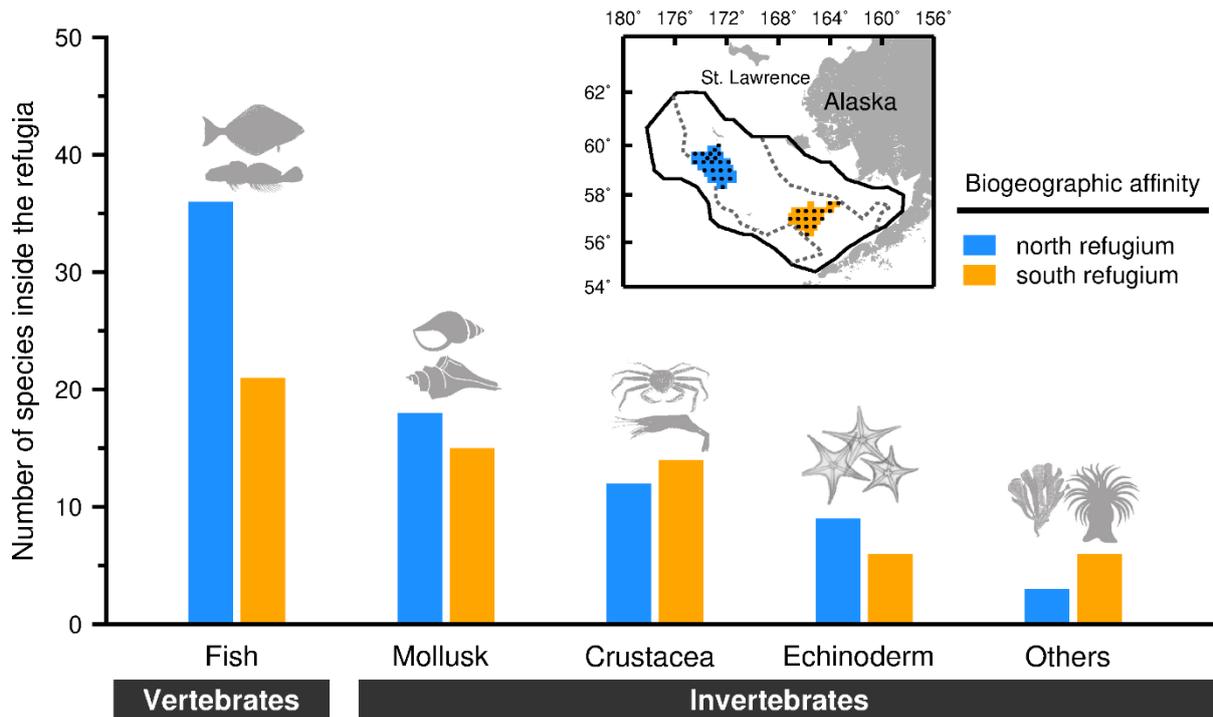
696 **Figure 6.** Spatial patterns of (a) abundance-based Bray-Curtis dissimilarity and (b-c) respective  
697 components between high and low wsic regimes. Broken lines correspond to the 50 and  
698 100 m isobaths.



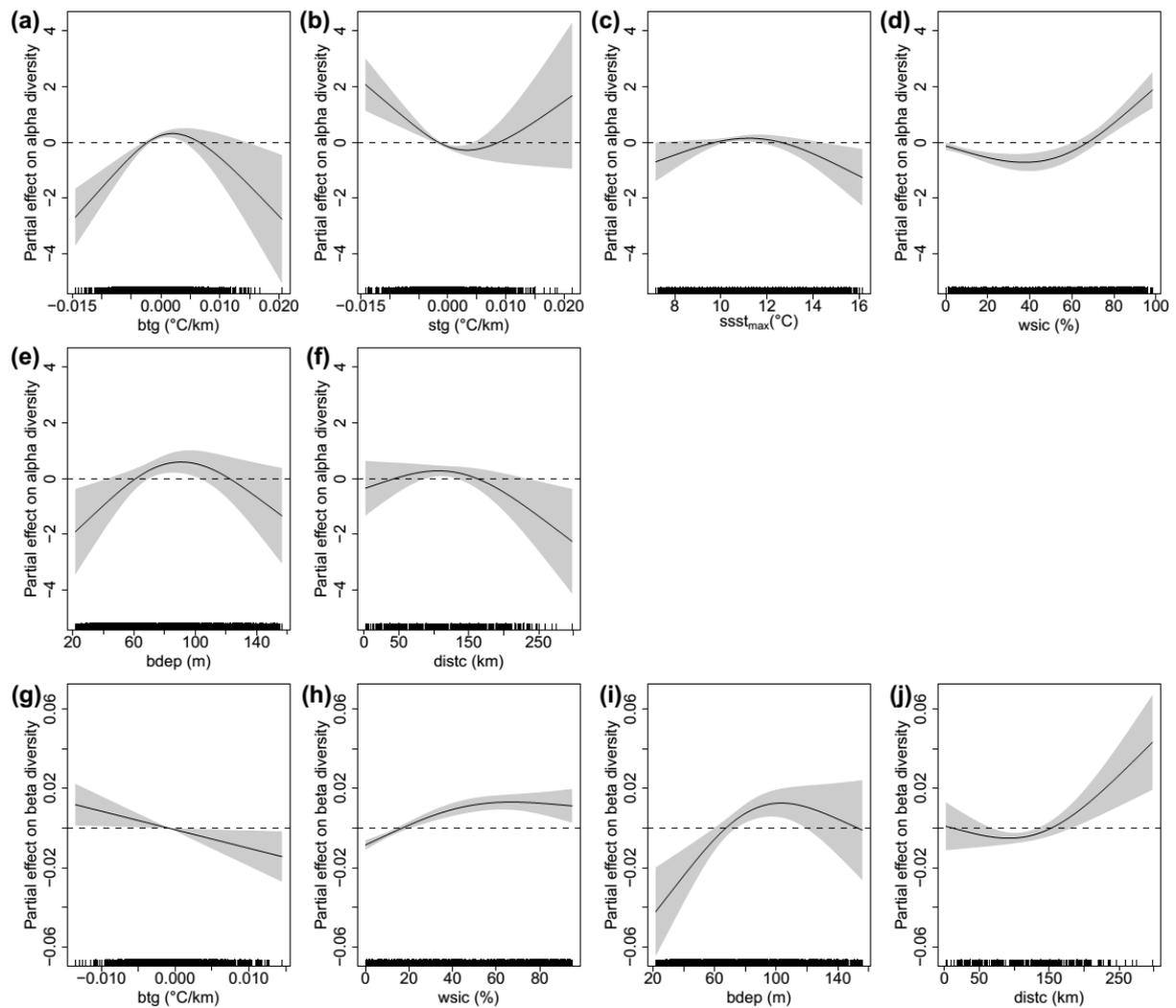
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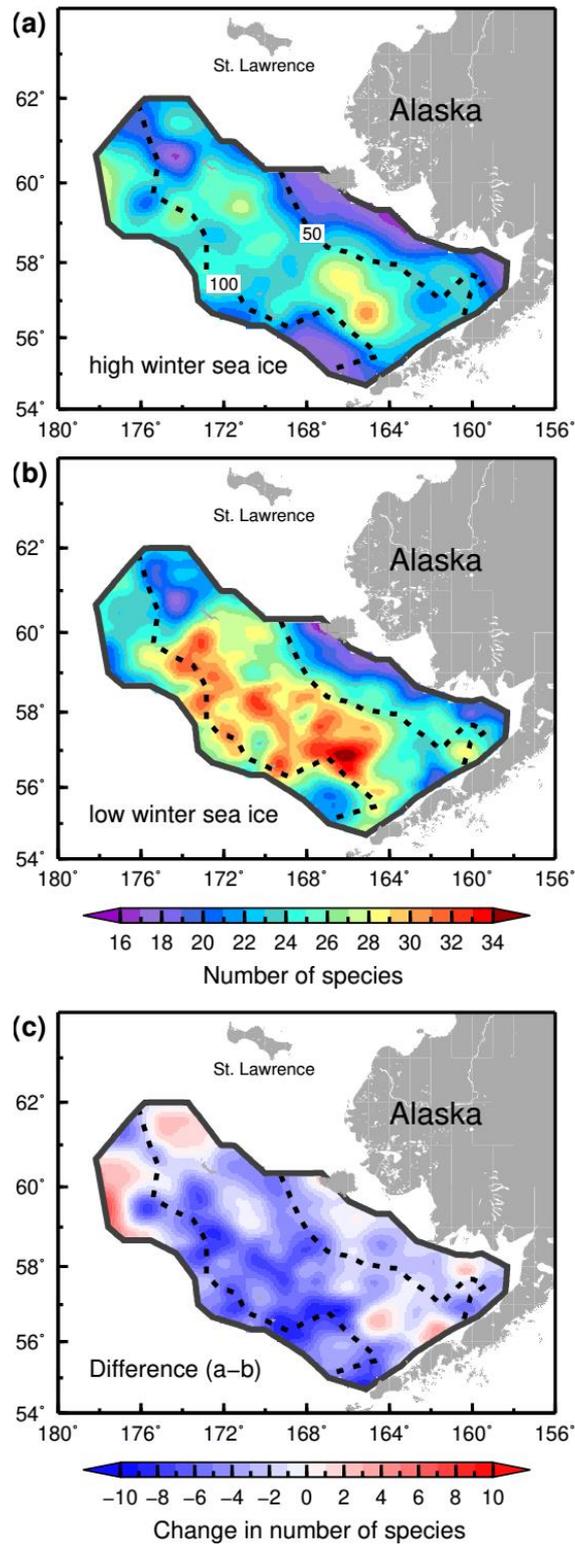
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 709 Regions in blue did not have any neutral pixels; areas in red contained neutral pixels in all three  
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 711 quantile of refugia index) and the broken lines correspond to the 50 and 100 m isobaths.



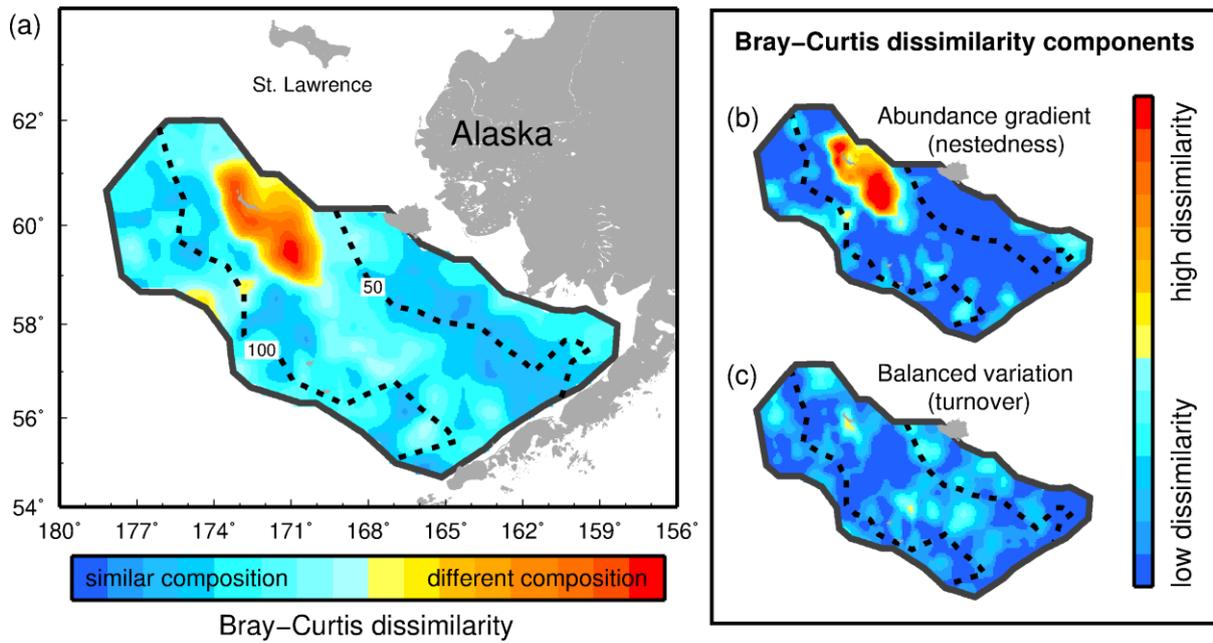
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