

Environmental filtering influences functional community assembly of epibenthic communities

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Conflict of interest statement

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest

Author contribution statement

LS conceived the ideas, carried out all analyses, and wrote the first draft of the manuscript. BAB and KI contributed data. FJM contributed to the analyses and statistics. All authors contributed to development of this study and ideas and commented on and edited the manuscript.

Keywords

community assembly, Environmental filtering, functional traits, Trait convergence, Arctic

Abstract

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Community assembly theory states that species assemble non-randomly as a result of dispersal limitation, biotic interactions, and environmental filtering. Strong environmental filtering likely leads to local assemblages that are similar in their functional trait composition (high trait convergence) while functional trait composition will be less similar (high trait divergence) under more benign environmental filters. We used two Arctic shelves as case studies to examine the relationship between functional community assembly and environmental filtering using the geographically close but functionally and environmentally dissimilar shelf epibenthic communities on the Chukchi and Beaufort Sea shelves. Environmental drivers were compared to functional trait composition and to trait convergence within each shelf. Functional composition in the Chukchi Sea was more strongly correlated with environmental gradients compared to the Beaufort Sea, with 45% and 21% of the total functional variance explained in the two seas, respectively. In the Chukchi Sea, epibenthic functional composition, particularly fragility, larval development, and several behavioral traits (i.e., feeding habit, living habit, movement), was most strongly related to sediment grain size, temperature, salinity, and depth. In the Beaufort Sea, epibenthic functional composition, particularly of behavioral traits, was related to depth and sediment grain size. The stronger environmental filter in the Chukchi Sea confirmed the hypothesized relationship with higher trait convergence. Strong environmental filtering generally provides a challenge for biota and can be a barrier for invading species, a growing concern for the Chukchi Sea shelf communities under warming conditions. Weaker environmental filtering, such as on the Beaufort Sea shelf, generally leads to communities that are more structured by biotic interactions, and possibly representing niche complementarity from intermediate disturbance levels. We provide evidence that environmental filtering can structure functional community composition, providing a baseline of how community function could be affected by stresses such as changes in environmental conditions or increased anthropogenic disturbance.

Contribution to the field

This research article examines the concept of community assembly based on functional traits through an environmental filtering lens. Here, we examine if and how environmental filters drive functional community assembly processes using two Arctic shelf epibenthic communities as case studies. We use Chukchi and Beaufort Sea epibenthic shelf communities because they are geographically close to one another, but are functionally and environmentally distinct. These systems exemplify regions of rapid change, a common and increasing global environmental problem, and may be bellwethers of functional community change for other marine systems. We discuss how this approach can inform about the invasive species potential based on functional traits. The strength of our work is that it does not focus on specific species that are unique to the case study regions but on functional traits, making this approach highly transferrable. We believe there is great promise and management potential in applying the idea of environmental filtering as part of the larger community assembly theory to evaluate how functional traits interact with current and changing environments.

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Ethics statements

Studies involving animal subjects

Generated Statement: No animal studies are presented in this manuscript.

Studies involving human subjects

Generated Statement: No human studies are presented in this manuscript.

Inclusion of identifiable human data

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Data availability statement

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1 **Running head:** Environmental filtering of communities
2
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In review

14 **Abstract**
15
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17 limitation, biotic interactions, and environmental filtering. Strong environmental filtering likely
18 leads to local assemblages that are similar in their functional trait composition (high trait
19 convergence) while functional trait composition will be less similar (high trait divergence) under
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24 functional trait composition and to trait convergence within each shelf. Functional composition
25 in the Chukchi Sea was more strongly correlated with environmental gradients compared to the
26 Beaufort Sea, with 45% and 21% of the total functional variance explained in the two seas,
27 respectively. In the Chukchi Sea, epibenthic functional composition, particularly fragility, larval
28 development, and several behavioral traits (i.e., feeding habit, living habit, movement), was most
29 strongly related to sediment grain size, temperature, salinity, and depth. In the Beaufort Sea,
30 epibenthic functional composition, particularly of behavioral traits, was related to depth and
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32 hypothesized relationship with higher trait convergence. Strong environmental filtering generally
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34 the Chukchi Sea shelf communities under warming conditions. Weaker environmental filtering,
35 such as on the Beaufort Sea shelf, generally leads to communities that are more structured by
36 biotic interactions, and possibly representing niche complementarity from intermediate
37 disturbance levels. We provide evidence that environmental filtering can structure functional
38 community composition, providing a baseline of how community function could be affected by
39 stresses such as changes in environmental conditions or increased anthropogenic disturbance.
40

41 **Keywords:** community assembly, environmental filtering, functional traits, trait convergence
42

43 **Introduction** 44

45 A central question of community ecology is why species from a regional pool form similar or
46 distinct local species compositions (Weiher et al., 1998). In other words, what are the driving
47 forces in the assembly of local biological communities? Three main filters have been proposed
48 for species to pass through in order to be part of a local community based on their functional
49 traits. These include dispersal limitation, biotic interactions, and environmental filters (Keddy,
50 1992; Pearson et al., 2018). This idea of filtering based on functional traits was first tested with
51 terrestrial vegetation (Weiher et al., 1998; Götzenberger et al., 2012), terrestrial invertebrates (de
52 Bello et al., 2009), and freshwater invertebrates (Conti et al., 2014), but has been used throughout
53 all ecological systems in the framework of community assembly theory (Keddy, 1992; Weiher et
54 al., 2011). This theory assumes species have a suite of measurable functional traits that allow
55 them to persist in a given environment over time (Kraft et al., 2015). Conversely, community
56 assembly theory assumes that a series of hierarchical filters can prevent a prospective species to
57 enter a community if a species' functional traits would not perform well in the specific local
58 ecosystem conditions (Keddy 1992; Menegotto et al., 2019). The combined traits of community
59 members should reflect the ability of communities to maintain ecosystem functions within a

60 given environment (McGill et al., 2006; Sutton et al., 2020). If the functional traits represented
61 by a local community do not optimally fill ecological niches and ecosystem functions, missing
62 traits could predict the success of new species invasions (Webb et al., 2010; Pearson et al.,
63 2018).

64
65 One of the primary filters of species into a local community is the environment. The relationship
66 between abiotic conditions and functional traits can differ depending on the strength of
67 environmental filtering occurring within a system (Blonder et al., 2015). While the effects of
68 environmental filtering on community assembly can be seen worldwide in many different
69 systems, the Arctic provides an excellent region to closely examine environmental filtering
70 where narrow environmental ranges and highly seasonal conditions affect the species and their
71 traits' ability to persist (Peck et al., 2004). Most Arctic shelves, including the Alaskan Arctic
72 shelves, are considered benthic-driven systems where tight pelagic-benthic coupling, a result of
73 the timing of sea-ice retreat, supports a high benthic biomass (Grebmeier et al., 2006). These
74 benthic systems, in turn, support many higher trophic level fish (Whitehouse et al., 2017) and
75 marine mammal consumers (Bluhm & Gradinger, 2008). Many Arctic epibenthic invertebrates
76 are long-lived (e.g., Bluhm et al., 1998; Ravelo et al., 2017) and relatively slow moving as
77 adults; they are, thus, mostly confined to local environmental conditions. Consequently, Arctic
78 epibenthic invertebrates must express a range of functional traits that allow them to thrive in
79 those local conditions (Sutton et al., 2020). Environmental variables acting as filters on Arctic
80 benthic community assembly have been well studied from a taxonomic perspective (Bluhm et
81 al., 2009; Blanchard et al., 2013; Ravelo et al., 2014; Grebmeier et al., 2015a) but few studies
82 explicitly looked at these filters from a functional trait perspective (but see Rand et al., 2018;
83 Jørgensen et al., 2019; Liu et al., 2019). Conversely, Arctic benthic taxa can be quite plastic in
84 their environmental tolerance ranges and may be more robust to environmental changes than
85 previously assumed (Renaud et al., 2015, 2019); this could lessen the influence of environmental
86 filters. In light of the strong environmental changes due to climate impacts, specifically in the
87 Arctic, as well as likely increased anthropogenic influence, there is urgency to better understand
88 the relationship between benthic invertebrate functional traits and environmental conditions
89 (Renaud et al., 2019).

90
91 We used two Alaskan Arctic shelves as case studies in which to test and compare the effect of
92 environmental filtering on functional community assembly. The Alaskan marine Arctic
93 comprises the Chukchi Sea to the west and the Beaufort Sea to the north (Figure 1), two regions
94 that are geographically close but vary considerably in their environmental influences. The
95 Chukchi Sea is a seasonally ice-covered, broad and shallow inflow shelf (Carmack and
96 Wassmann 2006). It is influenced by a diverse set of water masses entering through Bering
97 Strait: the fresh and warm Alaska Coastal Current, and the Chukchi Shelf Currents that are cold
98 and nutrient-rich (Danielson et al., 2020). These water masses and the food supply they provide
99 have previously been linked to Chukchi Sea benthic community composition and biomass
100 (Bluhm et al., 2009; Ravelo et al., 2014; Grebmeier et al., 2015b), benthic larval meroplankton
101 distribution (Ershova et al., 2019), and benthic food web structure (Iken et al., 2010). In addition,
102 Chukchi Sea epibenthic assemblages are also correlated with sediment grain size (Bluhm et al.,
103 2009), which in turn is related to current speed of these water masses (Pisareva et al., 2015).
104 Similar to the Chukchi Sea, the Beaufort Sea is also seasonally ice-covered, with much of the
105 narrow shelf covered by landfast ice and pack ice (Mahoney et al., 2014). As an interior Arctic

106 shelf, the Beaufort Sea is exposed to temperature and salinity ranges from downstream
107 influences from the colder and fresher Alaska Coastal Current from the west (Danielson et al.,
108 2020) and from warmer and saline upwelled water from the Beaufort Sea slope (Pickart et al.,
109 2013; Bluhm et al., 2020). In addition, the Beaufort Sea shelf benthos is impacted by riverine
110 input from the Colville and Mackenzie rivers (Weingartner et al., 2017), plus receives additional
111 terrestrial organic material from coastal erosion (Divine et al., 2015; Doxaran et al., 2015). The
112 Beaufort Sea shelf has a distinct depth gradient from on- to offshore, which reflects a gradient
113 for landfast ice, and depth drops rapidly into a steep slope after the shelf break (Bluhm et al.,
114 2020). These Beaufort Sea shelf characteristics have been previously correlated with patterns in
115 taxonomic diversity of epibenthic (Ravelo et al., 2020) and zooplankton communities (Smoot &
116 Hopcroft, 2017), and benthic food web structure (Divine et al., 2015, Bell et al., 2016). Here, we
117 build on previous knowledge of these two shelf systems to investigate if and how environmental
118 variables related to sediment properties (i.e., sediment grain size), food supply (i.e., sediment
119 chlorophyll) and elements of hydrography (i.e., depth, salinity, temperature) affect the filtering
120 of functional traits of epibenthic invertebrates both within each of the two shelves as well as how
121 processes compare between the two shelves.

122
123 If filtering on these two shelves is indeed driven by strong gradients of distinct environmental
124 conditions, we would expect the functional traits of local assemblages to be more similar at the
125 more extreme values of these gradients. This means we expect local assemblages to express high
126 local functional trait convergence at the more extreme values of the existing gradients. Across an
127 environmental gradient, assemblages should exhibit a bell-shaped relationship between
128 functional dissimilarity and environmental gradients (Muscarella & Uriarte, 2016; Denelle et al.,
129 2019; Figure 2). For example, within the realized niche of the physiological range of many
130 benthic invertebrates living in the Arctic, one might expect fewer functional traits to be
131 competitive at either very low or very high temperatures, meaning that the traits of community
132 members would exhibit high trait convergence at these more extreme values of the local
133 environmental spectrum. Measuring trait convergence is a way to aggregate the complexities of
134 different trait responses to environmental filtering into a single value; however, trait convergence
135 can also inform further about the role of biological interactions and niche complementarity in a
136 system after species and their traits have passed through the environmental filter (Pillar et al.,
137 2009). In short, trait convergence not only represents the assembly of traits that were able to
138 overcome the environmental filter, it also informs about the subsequent ecological sorting on the
139 community level (Webb et al., 2010). Strong environmental filtering should provide less
140 hospitable conditions for invading species unless the invaders possess the functional traits that
141 are necessary to survive at the more extreme values of the local environmental gradients
142 (Andersen et al., 2015). Alternatively, in locations where environmental filtering is relaxed,
143 functional divergence within that local assemblage should increase, meaning the species are
144 more dissimilar (more diverse) in their functional trait composition (Spasojevic & Suding, 2012).
145 This weaker environmental filtering leads to increased niche complementarity, where species
146 differ in their realized niches and resource partitioning allows species to coexist (MacArthur &
147 Levins, 1967; Mason et al., 2005; Baltar et al., 2019).

148
149 The goal of this study was to investigate how environmental filtering influences functional
150 composition and trait convergence within the community assembly framework. We use two
151 geographically close but environmentally dissimilar Arctic epibenthic shelf systems as case

152 studies to address four primary questions: (1) Is there a relationship between epibenthic
153 functional trait composition and environmental gradients? (2) Is the strength of this
154 environmental filtering similar on both the Chukchi and Beaufort Sea shelves? (3) If
155 relationships between functional composition and environmental gradients exist, are they driven
156 by the same trait modalities on the two shelves? (4) Do epibenthic communities follow the
157 expected relationship of higher trait convergence with stronger environmental filtering?

158

159 **Methods**

160

161 **Study sites and sample collection**

162

163 Epibenthic taxa used in this study were collected from the Chukchi and Beaufort Sea shelves
164 from research cruises in 2014 and 2015 (Figure 1). Stations in the Chukchi Sea were sampled as
165 part of the Arctic Marine Biodiversity Observing Network survey in 2015 (AMBON 2015).
166 Stations in the Beaufort Sea were sampled as part of the US-Canada Transboundary Project 2014
167 and the Arctic Nearshore Impact Monitoring in Development Area project III (ANIMIDA 2014,
168 2015). Bottom depth ranged from 11 – 54 m for the 67 stations in the Chukchi Sea and 10 – 64 m
169 for the 46 stations in the Beaufort Sea. Epibenthic invertebrates were collected with a plumb-
170 staff beam trawl with a mouth opening of 2.6 m wide and 1.2 m high as well as a 7 mm mesh and
171 4 mm codend liner (modified after Gunderson & Ellis, 1986). Environmental variables
172 previously shown to influence epibenthic taxonomic composition (Bluhm et al., 2009; Blanchard
173 et al., 2013; Ravelo et al., 2014, 2015) were collected at each station to reflect hydrography
174 (depth, bottom water salinity, bottom water temperature; all from CTD profiles taken with a
175 Seabird Model SBE911), sediment properties (percent gravel, sand, and mud), and food supply
176 (sediment chlorophyll-a). Sediment properties and food supply were both sampled from top 1 cm
177 sediments from van Veen grab samples, following analyses described in Grebmeier et al. (1989)
178 and Cooper et al. (2012), respectively (also see Iken et al., 2019). Variability of environmental
179 variables between the Chukchi and the Beaufort Sea was compared using a Levene's test. All
180 environmental data are available through the MBON Data Portal
181 (https://mbon.ioos.us/#search?type_group=all&tag=ambon-projects&page=1), the Alaska
182 Ocean Observing System (AOOS) Data Portal (<https://portal.aoos.org/#module-metadata/af3a4323-b854-4bce-890e-793c02b24394/cd3ada75-3897-444f-9d9c-42f8840f1018>),
183 and the National Centers for Environmental Information
184 (<https://www.ncei.noaa.gov/access/metadata/landing-page/bin/iso?id=gov.noaa.nodc:0162530>,
185 Kasper et al. 2017).

186

187 **Epibenthic functional composition**

188

189 Epibenthic invertebrate functional composition was expressed through a combination of
190 biological traits that describe the taxa's life history, morphology, and behavior, following
191 commonly accepted definitions and categories (Degen & Faulwetter, 2019). Nine biological
192 traits for a total of 327 taxa were assessed, with almost identical taxon richness in the Chukchi
193 and Beaufort seas (n=227, n=226, respectively) at the same levels of taxonomic identification
194 (Sutton et al., 2020). Each trait was categorized by modalities, which are specific categories
195 within each trait (see Table 1). Modalities within each trait were assigned to each taxon using a
196 fuzzy coding approach, where a minimum value of 0 indicated no affiliation with that modality
197

198 and a maximum value of 3 indicated a strong affiliation of a taxon with a modality (Chevenet et
199 al., 1994; Sutton et al., 2020). This process created unique biological trait profiles for all taxa,
200 which were normalized between 0 and 1 to create a trait by taxon matrix (Q matrix). The Q
201 matrix was then multiplied with a square root transformed, biomass-weighted taxon by station
202 matrix (L matrix) to create a trait by station matrix (LQ matrix). The LQ matrix represented the
203 functional composition at a station as community-weighted-means (CWM) (Lavorel et al., 2008;
204 Sutton et al., 2020). Trait information for all epibenthic taxa in this study can be accessed in the
205 supplementary material for this manuscript or via The Arctic Traits Database
206 (<https://www.univie.ac.at/arctictraits/>) for more detailed descriptions.
207

208 Relationships between functional composition and environmental variables

209

210 The relationship between functional composition and environmental variables, expressed as
211 covariance at each station, was tested using a forward selection CWM redundancy analysis
212 (CWM-RDA, (Nygaard & Ejrnaes, 2004; Kleyer et al., 2012). Environmental variables for each
213 shelf were standardized to a mean of zero and a variance of one, and a matrix of pairwise
214 Euclidean distances between stations was created. First, a forward model selection using the
215 lowest Akaike Information Criterion (AIC) was performed for each shelf to select the
216 environmental variables most strongly related to functional composition of all nine functional
217 traits across all stations. Because we used a forward selection procedure to select environmental
218 variables, we included all variables in our model, although we recognize that including
219 correlated environmental variables should be considered in the interpretation of the results (see
220 Figure S1 for correlations of environmental variables). Next, we performed additional and
221 separate forward-selection CWM-RDAs for individual functional traits to determine which
222 functional traits accounted for the highest amount of variance in functional composition and how
223 modalities were related to environmental variables. Modalities with the highest relative loadings
224 for each shelf on these CWM-RDA axes were selected to further focus on strongest relationships
225 between individual modalities and environmental variables. Cut-off loading values were chosen
226 for modalities greater than 0.5 in the Chukchi and 0.4 in the Beaufort Sea, based on the overall
227 range of loadings for each shelf.
228

229 Trait convergence

230

231 Trait convergence was evaluated using the measure of functional dispersion (FDis) where a
232 lower dispersion value indicates more similar functional composition and, therefore, higher trait
233 convergence of taxa at a station. First, trait space for each station was calculated using a principal
234 coordinate analysis (PCoA), where PCoA axes were used as the derived “traits” quantified from
235 the previously described CWM matrix (Laliberté & Legendre, 2010). FDis was then calculated
236 as the mean distance of all taxa at a station to the biomass-weighted centroid of the stations in
237 trait space (Anderson et al., 2006; Laliberté & Legendre, 2010). Average FDis was compared
238 between the Chukchi and Beaufort epibenthic shelf communities using a generalized least
239 squares (GLS) linear model while accounting for spatial autocorrelation:

$$240 \quad y = \alpha_k + \varepsilon \quad (\text{equation 1})$$

241 where y is FDis, the intercept α_k denotes the mean value of y for the Beaufort Sea ($k = 1$) and
242 Chukchi Sea ($k = 2$). The error, ε , was modeled as a spatial random process with a correlation
243 structure that declined exponentially with distance between stations to account for spatial

244 autocorrelation. Models were fit using a generalized least squares approach (Pinheiro et al.,
245 2020) when autocorrelation significantly improved the model; otherwise, ordinary least squares
246 were used.

247

248 Trait convergence and environmental gradients

249

250 Axes of the CWM-RDA are the linear projections of the environmental explanatory variables on
251 functional composition (Nygaard & Ejrnaes, 2004; Kleyer et al., 2012). We used the axes that
252 accounted for the majority of variance from the CWM-RDAs from the Chukchi Sea and Beaufort
253 Sea as proxies for overall environmental gradients. The relationships of FDis to these overall
254 environmental gradients (i.e., axes) were tested using a GLS model of FDis as a linear or
255 quadratic function of the first two axes from the CWM-RDA, with autocorrelated residuals as in
256 equation 1. We chose quadratic relationships for the full model due to the expected bell-shaped
257 relationship for environmental filtering (see Figure 2). Model selection using the corrected AIC
258 (AICc) that accounts for small sample size, was used to assess whether FDis had a significant
259 linear or quadratic relationship with one or both of the RDA axes for each shelf. All analyses
260 were performed in R version 4.0.2 (R Core Team 2020) using the ade4 (Dray & Dufour, 2007),
261 vegan (Oksanen et al., 2020), FD (Laliberté & Legendre, 2010), and nlme (Pinheiro et al., 2020)
262 packages.

263

264 Results

265

266 Functional composition and relationship to environmental conditions

267

268 Functional composition of epibenthic communities was correlated to environmental variables on
269 both shelves; however, this relationship was stronger on the Chukchi Sea shelf compared to the
270 Beaufort Sea shelf (adj. $R^2=0.41$ and 0.17, respectively, CWM-RDA: total variance explained =
271 45% and 21%, respectively; Table 2). The first two axes of the Chukchi Sea CWM-RDA
272 accounted for 60% and 21%, respectively, of the total explained variation in functional
273 composition (Figure 3a). Based on the loadings, RDA1 represented a gradient of warmer water
274 and sandier conditions with negative RDA1 values to cooler, more saline, deeper, and muddier
275 conditions with positive RDA1 values. The second axis represented a gradient of warmer, larger
276 sediment grain-sized, generally deeper and more saline conditions associated with more positive
277 values to cooler, sandier conditions associated with more negative values (Table 2, Figure 3a). In
278 the Beaufort Sea, depth and percent gravel accounted for 72% and 28%, respectively, of the total
279 variation in functional composition (Table 2, Figure 3b). Based on the loadings, RDA1
280 represented a gradient of deeper stations with more negative values and shallow stations with
281 more positive values (Figure 3b). Additionally, RDA2 represented a gradient of larger-sized
282 substrates associated with more negative values and smaller sediment grain-sized substrates
283 associated with more positive values (Figure 3b). The larger amount of variation explained in the
284 Chukchi Sea pointed to stronger environmental filtering compared to the Beaufort Sea. See
285 Figure 6 for the spatial patterns of environmental variables.

286

287 Trait and modality distribution in relation to environmental conditions

288

289 The stronger environmental filtering of overall functional composition in the Chukchi Sea
290 compared to the Beaufort Sea was also seen for individual functional traits. In the Chukchi Sea,
291 the functional traits with the strongest correlation with environmental variables were living habit,
292 feeding habit, movement, fragility, and larval development (total variance explained = 53%,
293 50%, 47%, 47%, and 42%, respectively), followed by weaker correlations of body size, body
294 form, sociability, and reproductive strategy (each < 40% of variance, Figure 4a, Table S1). The
295 behavioral traits (living habit, feeding habit, and movement) and larval development were most
296 strongly related to percent mud while fragility was most correlated to temperature (Figure 4a).
297 None of the functional traits in the Beaufort Sea had any correlation with environmental
298 variables of more than 31%. The functional traits with the strongest correlation with
299 environmental variables included movement, feeding habit, living habit, larval development, and
300 sociability (total variance explained = 31%, 26%, 23%, 20%, and 20%, respectively), followed
301 by reproductive strategy, body form, body size, and fragility (each <20% of variance, Figure 4b,
302 Table S1). Beaufort Sea functional traits were mostly correlated with depth, except for body
303 form, body size and living habit, which were mostly correlated with percent gravel (Figure 4b).
304 Complete forward-selection model outputs can be found in Table S1.
305

306 Modalities with the highest loadings along the first axis of the CWM-RDA in the Chukchi Sea
307 tended to follow the spatial patterns of sediment grain size and water mass characteristics
308 (temperature) gradients while aligning along a gradient of depth and sediment grain size (percent
309 gravel) in the Beaufort Sea (Figure 5b, 6a). In the Chukchi Sea, this pattern was most obvious for
310 the modalities with absolute loadings > 0.5 along the first axis of the CWM-RDA (Table 3,
311 Figure 5a). These included the proportions of the modalities predator, planktotrophic, free-living,
312 and crawler, all of which increased in prevalence with greater percent mud while the proportion
313 of the modality filter-feeding decreased with percent mud (Figure 5a, 6a). Additionally, the
314 proportion of robust and filter-feeding modalities increased with temperature (Figure 5a, 6a). In
315 the Beaufort Sea, the pattern between modalities and the depth gradient were most obvious for
316 modalities with absolute loadings > 0.4 along the first axis of the CWM-RDA (Table 3, Figure
317 5b, 6a). The proportion of the modality crawler increased with depth while the proportions of the
318 modalities scavenger and swimmer decreased with depth (Figure 5b, 6a).
319

320 **Relationship between environmental gradients and trait convergence**

321

322 Influential environmental variables and functional dispersion (FDis), our measure of trait
323 convergence, tended to exhibit cross-shelf spatial patterns in both the Chukchi and Beaufort seas.
324 Environmental gradients in the Chukchi Sea generally exhibited on- to offshore patterns for
325 percent mud, percent sand, and salinity (Figure 6a). FDis decreased largely along a south to north
326 gradient, representing higher trait convergence in the northern study region (Figure 6a) but also
327 aligning with local gradients of environmental variables in the Chukchi Sea. For example,
328 greater trait convergence was found at the southern end of the most coastal along-shore transect,
329 an area characterized by high temperatures, high percent sand, and low salinity. In contrast, areas
330 of greater trait divergence were found, for example, with more mixed sediment conditions in the
331 northern-most coastal region (Figure 6a). The Beaufort Sea exhibited a gradient of low to high
332 salinity from west to east and a strong depth gradient increasing from on- to offshore (Figure 6a).
333 Greater trait convergence on the Beaufort Sea shelf was found in the shallow western, nearshore
334 stations while trait divergence was greater at the deeper offshore eastern sites (Figure 6a).

335
336 Environmental variability differed between the Chukchi and Beaufort seas. The Chukchi Sea had
337 larger variability in percent sand, percent mud, and temperature while the variability in percent
338 gravel and depth were larger in the Beaufort Sea (Figure 6b, Table S3). Salinity and chlorophyll-a
339 variability was similar in both seas; however, the Chukchi Sea had higher mean values for both
340 these variables. FDis was significantly lower in the Chukchi Sea compared to the Beaufort Sea ($p < 0.001$, adj. $R^2 = 0.137$, $F = 18.71$; Figure 6b). This indicated greater trait convergence, or more
341 similar functional composition, in the Chukchi Sea. Additionally, the variability of FDis was
342 much larger in the Chukchi Sea compared to the Beaufort Sea (Figure 6b). This suggested that
343 Chukchi Sea stations covered a greater range of trait convergence, reflecting stations with very
344 similar functional composition and stations with very dissimilar functional composition. In
345 contrast, Beaufort Sea stations exhibited more consistent levels of trait divergence (higher FDis).
346
347

348 FDis followed the expected bell-shaped relationship with environmental gradients more closely
349 in the Chukchi Sea than in the Beaufort Sea, although FDis was significantly related to the main
350 environmental gradients (as measured by the CWM-RDA axes) in both seas (adj. $R^2 = 0.118$, $p < 0.001$, $F=16.03$). The best AIC selection model in the Chukchi Sea for FDis included both
351 CWM-RDA axes (Figure 7, Table S2). This model implied a bell-shaped (quadratic)
352 relationships of FDis with the first axis (representative of a sediment grain size gradient from
353 sand to mud) and second axis (representative of a gradient of percent sand and temperature)
354 (Figure 7a, b). In other words, functional trait convergence was greater at very high and very low
355 temperatures, sand, mud, and salinity values. The best AIC selection model in the Beaufort Sea
356 for the relationship of FDis with environmental gradients included a decreasing (quadratic)
357 relationship with the first axis (representative of a depth gradient) and an increasing (linear)
358 relationship with the second axis (representative of a percent gravel gradient) (Figure 7c, d,
359 Table S2). Here, functional convergence was higher at greater depths and higher percent gravel.
360
361

362 Discussion

363 This study explored whether and how the concepts of environmental filtering in community
364 assembly theory applied to the functional composition of epibenthic communities using the
365 Arctic Chukchi and Beaufort Sea epibenthic shelf communities as case studies. Both shelf
366 systems exhibited a relationship between functional composition and environmental filtering;
367 however, while many of the most influential traits on community assembly were similar, the
368 driving environmental variables differed between shelves. The Chukchi Sea, for the most part,
369 had larger environmental gradients, and exhibited higher trait convergence as evidenced by the
370 expected bell-shaped relationship with environmental gradients compared to the Beaufort Sea.
371 This provided evidence for the community assembly concept that aligns more extreme ends of an
372 environmental gradient with fewer functional traits (higher trait convergence) (Figure 2).
373
374

375 Drivers of functional composition and environmental variables

376 Environmental filtering, exhibited through the relationship of functional composition and
377 environmental conditions, was especially evident on the Chukchi Sea shelf. Functional
378 composition on the Chukchi Sea shelf, namely several behavioral traits (i.e., feeding habit, living
379 habit, movement), fragility, and larval development, were correlated to some water mass
380

characteristics (temperature and salinity) and sediment grain size, specifically a gradient from sand to mud. Sediment grain size is globally an important driver of soft-bottom benthic community composition and diversity (Snelgrove et al., 2001; Thrush et al., 2004) as well as on the Chukchi Sea shelf (Bluhm et al., 2009; Feder et al., 1994; Iken et al., 2019). Our results expand our understanding of this relationship beyond taxonomic composition to epibenthic functional traits in the study regions. Similarly, variation in sediment grain size has been linked to behavioral traits such as mobility and feeding habit in the Canadian Arctic (Krumhansl et al., 2016), as well as larval settlement selection along the eastern seaboard of the United States (Snelgrove et al., 1999). Sediment grain size can be a proxy for water flow intensity and deposition (Snelgrove & Butman, 1994). Patterns of distribution of finer sediments on the Chukchi Sea shelf are the result of variation in current velocities that carry finer sediment particles downstream of the Bering Strait, then deposit them in regions of reduced water flow such as in Hope Basin in the south-central Chukchi Sea and the northern and offshore regions of the shelf (Darby et al., 2009; Grebmeier et al., 2015b; Pisareva et al., 2015). Temperature and salinity are generally representative of dominant water masses; in the Chukchi Sea, these are most notably the mid-shelf cold, saline, and high-nutrient Chukchi Shelf Currents, while the Alaska Coastal Current (ACC) is warm, fresh, and low in nutrients (Danielson et al., 2020, Figure 1).

Areas with a high mud content on the Chukchi shelf were positively associated with predatory feeding habits, crawling movements, free-living habits, and planktotrophic larval development. These results are similar to the relationships of benthic traits and sediment grain size in the Canadian Arctic (Krumhansl et al., 2016) and seminal work on the US East Coast on the interaction between feeding habits and movement types with sediment grain size (Rhoads & Young, 1970). In the south-central Chukchi Sea, Hope Basin (Fig. 1) is known for the especially high deposition rates of small particle sizes when water slows after transitioning the narrow Bering Strait. This deposition supplies ample food for deposit feeding clams, which in turn act as prey for many epibenthic invertebrates or marine mammals (Grebmeier et al., 2015a, b). The middle shelf in the northern Chukchi Sea was also particularly characterized by high percent mud in our study. This may be the result of converging water masses around Hanna Shoal, which leads to high deposition rates and reduced current flow (Blanchard et al., 2013; Weingartner et al., 2013), resulting in a shallow biological hotspot known to support many higher trophic levels (Young et al., 2017). The invertebrate movement type crawler and free-living habit that were most common in these areas are indicative of taxa that can easily move on fine-grained sediments and generally have predatory feeding habits (Grebmeier et al., 2006). These behavioral traits provide important ecosystem functions in muddy areas because crawling movement types and free-living habits increase bioturbation of the sediment, increasing oxygenation of the sediments and the resuspension of organic material (Snelgrove et al., 2000; Queiros et al., 2013). This especially benefits the lower trophic level food web. This effect can be seen in the fact that some of these areas coincide with “hotspots” in macrobenthic biomass that benefit from the deposition of fine-particle organic matter (Grebmeier et al., 2015b) but also high biomass of highly mobile epibenthic invertebrates (Bluhm et al., 2009; Iken et al., 2019).
Planktotrophic larval development is typically advantageous for limiting local competition with adults and siblings of conspecifics, and/or spreading far across a region (Pechenik, 1999; Shanks, 2009). The slower water motion in areas of higher percent mud explained above may also benefit

427 the settlement of larvae of species with planktotrophic larval development. Planktotrophic larvae
428 in these environments likely exploit favorable food conditions of high organic matter loading (Li
429 et al., 2017) or a seasonally ice-algal rich water column environment (Ershova et al., 2019).

430
431 In our study, filter feeding had a strong negative relationship with mud. Filter-feeding taxa are
432 generally limited by such finer sediments as they tend to clog filter-feeding appendages (Rhoads
433 & Young, 1970). This process forces filter feeders to allocate energy to clearing feeding
434 apparatuses instead of growth and reproduction (Ellis et al., 2002). Many epifaunal filter-feeding
435 taxa are sessile and, thus, require hard substrate for attachment (e.g., Almond et al., 2021), which
436 would create better habitat suitability for this feeding type in the more coastal Chukchi Sea
437 waters, where faster water flow creates coarser sediments (Pisareva et al., 2015). This may also
438 explain the positive relationship of robust, filter-feeding taxa with increasing temperature, as the
439 coastal Chukchi ACC is also characterized by higher temperatures (Weingartner et al., 2005;
440 Danielson et al., 2020), rather than a causal relationship between filter feeding with temperature
441 *per se*. More robust taxa in coastal Chukchi Sea regions may be more likely to withstand an
442 increased risk of disturbance along the dynamic coastal environment.

443
444 While not as strong as in the Chukchi Sea, environmental filtering of epibenthic functional
445 composition was also evident on the Beaufort Sea shelf. Feeding habit, movement, living habit,
446 larval development, and sociability were correlated to depth and sediment grain size (gravel).
447 Depth has also been identified as a driving force of functional traits in inflow Arctic shelves such
448 as the Bering Sea (Liu et al., 2019) and the Barents Sea (Cochrane et al., 2012) and has long
449 been suggested as a general key environmental variable to track functional traits (Costello et al.,
450 2015). Similar to our findings in the Chukchi Sea, our results reflected those of previous studies
451 of taxonomic epibenthic composition where community composition changed with depth along
452 the Beaufort Sea shelf (Ravelo et al., 2015, 2020). Depth increases unidirectionally with distance
453 from shore across the narrow Beaufort Sea shelf and often is a proxy for many environmental
454 drivers (Jakobsson et al., 2012) such as salinity, temperature, and, in polar seas, influences of ice
455 cover and scour. For example, in the shallower coastal Beaufort Sea, environmental conditions
456 are especially related to the degree and extent of nearshore ice scouring (Mahoney et al., 2014),
457 input of sediments and terrestrial matter from coastal erosion (Doxaran et al., 2015), and riverine
458 influence from major rivers such as the Mackenzie and Colville rivers (Rachold et al., 2005).
459 Therefore, our interpretation of the association of modalities with depth will also consider
460 environmental drivers that are related to depth in the study area but that were not specifically
461 measured in this study due to sampling limitations.

462
463 Depth was negatively associated with the modalities swimmer and scavenger and positively
464 associated with the modality crawler. Swimming allows species to quickly move away from
465 predators (Degen & Faulwetter, 2019) and disturbances, such as burial from high levels of
466 sedimentation (Hinchey et al., 2006) or ice-scouring (Conlan et al., 1998). The modality
467 scavenger allows taxa to take advantage of animals that become vulnerable after disturbance
468 (e.g., infaunal tube-dwellers or burrow-dwellers, or even higher trophic level taxa that have
469 sustained injuries or loss of habitat) (Conlan et al., 1998). Similar to our results, previous studies
470 in Antarctic shallow waters and shallow Canadian Arctic waters found that the intensity of ice-
471 scour disturbance was a good predictor for increased densities of highly mobile and higher
472 trophic level taxa such as scavengers and predators (Conlan et al., 1998; Smale et al., 2007). In

473 deeper Beaufort shelf regions close to the shelf edge, disturbance is less common but there is
474 increased influx of nutrients and warmer water from upwelling from the deep slope that add
475 environmental variability (Pickart et al., 2013). This allows for taxa to exploit more diverse
476 resources and likely leads to the presence of taxa that have predominantly a crawling movement
477 type such as ophiuroids and gastropods that thrive in more established soft-bottom Arctic
478 communities.

479

480 **The influence of environmental filters on trait convergence**

481

482 We assumed that optimal suites of functional modalities of species should be more similar
483 (higher trait convergence) at the more extreme local values of an environmental gradient and
484 should be dissimilar (higher trait divergence) at more moderate levels of a local environmental
485 gradient (Figure 2). Overall, we saw that environmental drivers with greater variability, i.e.,
486 covering a greater range of the environmental gradient, had an increased correlation with
487 functional composition and trait convergence. Our results in the Chukchi Sea exemplified this
488 expected relationship of higher trait convergence towards the more extreme values of a gradient
489 of sediment grain size and water mass characteristics while we saw higher trait divergence at
490 more intermediate levels. This bell-shaped pattern, however, was less clear in the Beaufort Sea,
491 where community assembly was mostly driven by a depth gradient. Seemingly, only one side of
492 the relationship between depth and trait convergence was represented, where shallow depths had
493 high trait convergence and traits at deeper depths were more divergent. The model indicated,
494 however, that trait convergence may increase again at yet greater depth. This may be due to our
495 analysis only investigating functional composition on the Beaufort shelf within a narrow section
496 (10 – 60 m) of the entire shelf depth gradient. While we investigated the same absolute depth
497 range in both seas, this range covered the entire depth gradient of the broad and relatively flat
498 Chukchi shelf, whereas the total depth gradient of the Beaufort Sea shelf increases steadily
499 beyond our depth selection to 100 m at the shelfbreak (Jakobsson et al., 2012). It is possible that
500 trait convergence along the Beaufort Sea depth gradient would increase if we were to include
501 trait composition from deeper depths of the shelf. We see such a depth-related pattern across the
502 entire shelf depth range in taxonomic diversity (Ravelo et al., 2020), and given that functional
503 composition patterns generally match those of taxonomic composition (Sutton et al., 2020), it
504 may be reasonable to assume that trait composition would trend towards greater convergence at
505 deeper Beaufort Sea shelf regions.

506

507 The weaker environmental filtering on the Beaufort Sea shelf could represent a system where a
508 second filter of biotic interactions may shape community function more prominently rather than
509 the environment. This interpretation matches well with our previous findings that epibenthic
510 functional composition on the Beaufort shelf had higher functional dissimilarity and evenness
511 than that in the Chukchi Sea (Sutton et al., 2020). This more balanced interplay of environmental
512 and biological filters (Weiher et al., 2011) that we propose for the Beaufort Sea may promote
513 higher trait divergence and the coexistence of many functional roles (Cornwell et al. 2006). The
514 environmental conditions in the Beaufort Sea may be more representative of disturbance, such as
515 seasonal ice-scouring and spring freshet, rather than continuous environmental gradients.
516 Intermediate disturbance regimes promote functional richness (Grime, 2006; Cadotte et al.,
517 2011), where more diverse functional traits are used to exploit more diverse resources, a process
518 known as disturbance-induced niche complementarity (Roxburgh et al., 2004). This niche

519 complementarity resulting from intermediate disturbance is different from strong environmental
520 filtering, the latter limiting the functions that are able to thrive at the more extreme values of a
521 local gradient and limiting niche complementarity (Valdivia et al., 2017). In contrast, we
522 observed stronger environmental filtering with higher trait convergence in areas located along
523 the more extreme values of the environmental gradients on the Chukchi Sea shelf.

524

525 Conclusion

526

527 The influence of environmental filtering on the functional community assembly was evident for
528 both case studies, although the strength of this filtering differed between the two Arctic shelves.
529 Our case studies provided two scenarios with differing driving environmental gradients but
530 resulted in similar functional traits responding to the filters. This suggests a certain commonality
531 of functional responses in epibenthic communities to environmental gradients that are similar to
532 those in our study. For example, the relationships were particularly strong in both our study
533 systems for larval development and behavioral traits (i.e., feeding habit, living habit, movement).
534 These traits are likely good indicators of environmental filtering in regions that are experiencing
535 strong changes of environmental conditions due to climate change such as the Arctic. In the
536 study regions, these changes include an increasing influx of warmer water from the North Pacific
537 (Woodgate, 2018), conditions that may negatively affect taxa with characteristics of crawling
538 movement types, free-living habits, predatory feeding habits, and planktrophic larval
539 development. In addition to changes in hydrographic conditions, increased current speed through
540 Bering Strait (Woodgate, 2018) could lead to coarser sediments on the southern Chukchi Sea
541 shelf (Abe et al., 2019). While these environmental changes may challenge the fitness of some
542 traits currently abundant in the Arctic shelf systems, they likely contribute to a northward shift of
543 benthic taxa into the Arctic (Mueter & Litzow, 2008; Grebmeier et al., 2015b; Renaud et al.,
544 2015). This study suggests that these northward-moving benthic taxa will have a competitive
545 advantage over current Chukchi Sea shelf inhabitants if they possess favorable behavioral and
546 life history functional traits that can pass through local environmental filters. In the interior shelf
547 systems such as the Beaufort Sea, warmer temperatures will lead to less seasonal sea ice and,
548 therefore, less ice-scour on the shallow shelf (Wadhams, 2012), along with increased wave
549 action along the coast (Pickart et al. 2009). Simultaneously, this may also lead to more
550 disturbances from increased terrestrial input from coastal erosion (Rachold et al., 2000; Doxaran
551 et al., 2015) and increased sedimentation from river outflow (Weingartner et al., 2017; Bonsell &
552 Dunton, 2018). While the disturbance regime may shift, our study suggests that benthic taxa with
553 the behavioral traits of swimming and scavenging will likely maintain a competitive advantage.

554

555 One caveat to consider in our study, which is typical for many field studies, is the fact that the
556 environmental measurements used were all taken during a relatively short sampling period. In
557 our case that was during summer when these Arctic shelf systems are accessible. The expected
558 local range for some dynamic variables, such as temperature and salinity, will be much larger
559 than used here if year-round ranges would be considered. Hence, the mostly long-lived Arctic
560 invertebrates are exposed to larger local environmental gradients of some variables than applied
561 in this study. Applying full seasonal ranges of environmental gradients would likely even
562 strengthen the relationship with certain functional traits or with trait convergence. Since those
563 environmental data are often not available at the spatial resolution of a specific station
564 distribution, modeling approaches will be needed to more fully predict future scenarios of

565 functional changes in such benthic systems. Here, we provided a benchmark to predict which
566 functional traits of taxa will have competitive advantages by evaluating community assembly
567 through an environmental filtering lens. While we focused on two Arctic shelf regions, we
568 postulate that our framework of examining functional trait-environment relationships is
569 applicable to many other systems. We suggest that this environmental filter lens will be
570 particularly critical in regions of rapid environmental change such as the Arctic.
571

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590

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932

933 Table 1. Biological traits, modalities, descriptions, and ecological relevance are shown for
 934 epibenthic invertebrates collected in the Chukchi and Beaufort seas, following Degen and
 935 Faulwetter (2019). Abb: Modality abbreviations used in figures.
 936

Biological trait	Modality	Abb.	Description	Ecological relevance
Body Form	Globulose	BF1	Round	Ecological role of species (e.g., habitat forming) and/or vulnerability to mechanical disturbances
	Vermiform	BF2	Wormlike	
	Dorso-ventrally compressed	BF3	Flattened/encrusting	
	Laterally compressed	BF4	Thin	
	Upright	BF5	Body forms upward from seafloor	
Size (wet weight in grams)	Small	BS1	0.01-0.1	Effect on productivity, energy flow, trophic and food web structure
	Small-medium	BS2	0.1-1.0	
	Medium	BS3	1.0-10	
	Medium-large	BS4	10-100	
	Large	BS5	>100.0	
Feeding Habit	Deposit feeder	FH1	Removal of detrital material from sediment	Indicative of hydrodynamic conditions and carbon transport
	Filter/suspension feeder	FH2	Filter food from the water column	
	Opportunist/scavenger	FH3	Scavenges food	
	Predator	FH4	Actively hunts live prey	
	Parasite	FH5	Feeds off other organisms	
Fragility	Fragile	F1	Easily damaged due to physical impacts	Sensitivity to physical and/or predatory disturbances
	Intermediate	F2	Moderately damaged due to physical impacts	
	Robust	F3	Unlikely damaged due to physical impacts	
Larval Development	Planktotrophic	LD1	Larvae feed and grow in water column	Ability to disperse, become invasive, or recover from disturbance
	Lecithotrophic	LD2	Larvae with yolk sac, pelagic for short periods	
	Direct development	LD3	No larval stage (eggs develop into juveniles)	
Living Habit	Free living	LH1	Not limited to any restrictive structure	Vulnerability to predation and perturbations, habitat facilitation, storage and movement of energy
	Crevice dwelling	LH2	Inhabiting coarse/rock or algal holdfasts	
	Tube dwelling	LH3	Tube lined with sand, mucus or CaCO ₃	
	Burrow dwelling	LH4	Species inhabiting burrows in the sediment	
	Epi/endo zoic/phytic	LH5	Biogenic species or algal holdfasts	

	Attached	LH6	Adherent to a substratum	
Movement	Sessile/none	MV 1	No movement as adult	Movement of energy through nutrient cycling, carbon deposition, and maintain habitat stability
	Burrower	MV 2	Movement in the sediment	
	Crawler	MV 3	On surface via movement of appendages	
	Swimmer	MV 4	Movement above the sediment	
Reproductive strategy	Asexual	R1	Budding	
	Sexual -external	R2	Eggs/sperm released into water	Ability to withstand disturbances
	Sexual - internal	R3	Eggs deposited on substrate / internal fertilization	and carbon transportation
	Sexual - brooder	R4	Eggs are brooded, larvae/minи-adult hatches	
Sociability	Solitary	SO1	Single individual	Sensitivity to disturbance and/or habitat forming
	Gregarious	SO2	Single individuals found in groups	
	Colonial	SO3	Living in permanent colonies	

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939 Table 2. CWM-RDA outputs are shown as the loadings of environmental variables for the first
940 two axes. The order of environmental variables represents the order in which environmental
941 variables were selected by the forward-selection model.

942

Environmental variable	Chukchi Sea		Environmental variable	Beaufort Sea	
	RDA1	RDA2		RDA1	RDA2
% Mud	0.92	-0.05	Depth	-0.99	0.02
Depth	0.23	0.22	% Gravel	-0.32	-0.95
Temperature	-0.63	0.39			
Salinity	0.67	0.23			
% Sand	-0.78	-0.16			
% Gravel	-0.31	-0.31			
Adjusted R ² :	0.41		Adjusted R ² :	0.17	
Total variance:	45%		Total variance:	21%	

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944

945 Table 3. CWM-RDA modality loadings whose absolute values are > 0.5 for the Chukchi Sea and
946 > 0.4 for the Beaufort Sea.

947

Trait	Modality	Chukchi Sea $ RDA1 > 0.5$	Beaufort Sea $ RDA1 > 0.4$
Feeding habit	Filter-feeder	-0.74	---
Feeding habit	Scavenger	---	0.41
Feeding habit	Predator	0.55	---
Fragility	Robust	-0.72	---
Larval development	Planktotrophic	0.66	---
Living habit	Free-living	0.75	---
Movement	Crawler	0.75	-0.44
Movement	Swimmer	---	0.47

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949

- 950 Figure 1. Stations sampled for epibenthic communities during four cruises in the Chukchi and
951 Beaufort seas in 2014 and 2015. Depth contours in the study regions are shown in gray at 10 m
952 intervals. Stations are designated by symbols for different cruises.
- 953
- 954 Figure 2. Environmental filtering can be expressed as the relationship between community
955 dissimilarity and environmental gradients. Community dissimilarity decreases towards the more
956 extreme values of an environmental gradient (i.e., strong environmental filtering). Adapted from
957 Muscarella & Uriarte (2016).
- 958
- 959 Figure 3. Community-weighted-mean redundancy analysis (CWM-RDA) showing the
960 relationship of station functional composition (denoted by points) and forward-selected
961 environmental variables for the Chukchi Sea in dark gray circles (**A**) and Beaufort Sea in light
962 gray circles (**B**). Total variance in functional composition explained by the CWM-RDA is listed
963 above the plot for each sea. Partial variance of this total variance explained by each axis is
964 denoted for each axis.
- 965
- 966 Figure 4. Community-weighted-mean redundancy analysis (CWM-RDA) of functional traits and
967 environmental variables in the Chukchi Sea (**A**) and the Beaufort Sea (**B**). Environmental
968 variables were forward-selected for each functional trait and are shown in white boxes in each
969 plot. Modalities within each functional trait are indicated by points. Length of vectors represent
970 the loadings of environmental variables and modalities. When only one environmental variable
971 was selected in the model, modalities and environmental variables only centered around the first
972 axis. Total variance for each functional trait is shown above each RDA and is also given in the
973 supplemental material (**S2**).
- 974
- 975 Figure 5. Spatial representation of the most influential modalities with absolute loadings > 0.5 on
976 the first axis of the CWM-RDA in the Chukchi Sea (**A**) and modalities with absolute loadings $>$
977 0.4 on the first axis of the CWM-RDA in the Beaufort Sea (**B**) (see Fig. 4). Modality cutoff
978 levels were chosen based on the highest relative loadings on the first axis for the CWM-RDA
979 among all traits for each shelf. Points represent stations on each shelf and are shaded based on
the average density of the community-weighted-mean value for the selected modality. The full
suite of spatial representations for all modalities in both seas is shown in Figure S2.
- 980
- 981 Figure 6. Spatial representation of the Chukchi and Beaufort Sea environmental variables and of
982 functional dispersion (FDis) (**A**). Variance of environmental variables and mean FDis were
983 compared between the Chukchi Sea (dark gray) and the Beaufort Sea (light gray) (**B**). Horizontal
984 lines: median, boxes: inter-quartile range (IQR); whiskers: highest/lowest values $\leq 1.5 \times$ IQR
985 above/below box; black points: outliers; large black circle: mean; *: significance ($p < 0.05$) of
986 variance of environmental variables using Levene's Tests; °: significance $p < 0.05$ of mean FDis
using a generalized linear model.
- 987
- 988 Figure 7. The relationship of functional dispersion (FDis) with environmental gradients via a
989 generalized-least-squares polynomial linear model is shown for the Chukchi Sea (**A, B**) for (from
990 left to right along the RDA axis) high percent sand to high percent mud (**A**), high percent sand to
991 high temperature (**B**), and the Beaufort Sea (**C, D**) for deep to shallow depths (**C**), and high to
low percent gravel (**D**). Model outputs are shown in Table S2.

Figure 1.JPEG

Figure 1

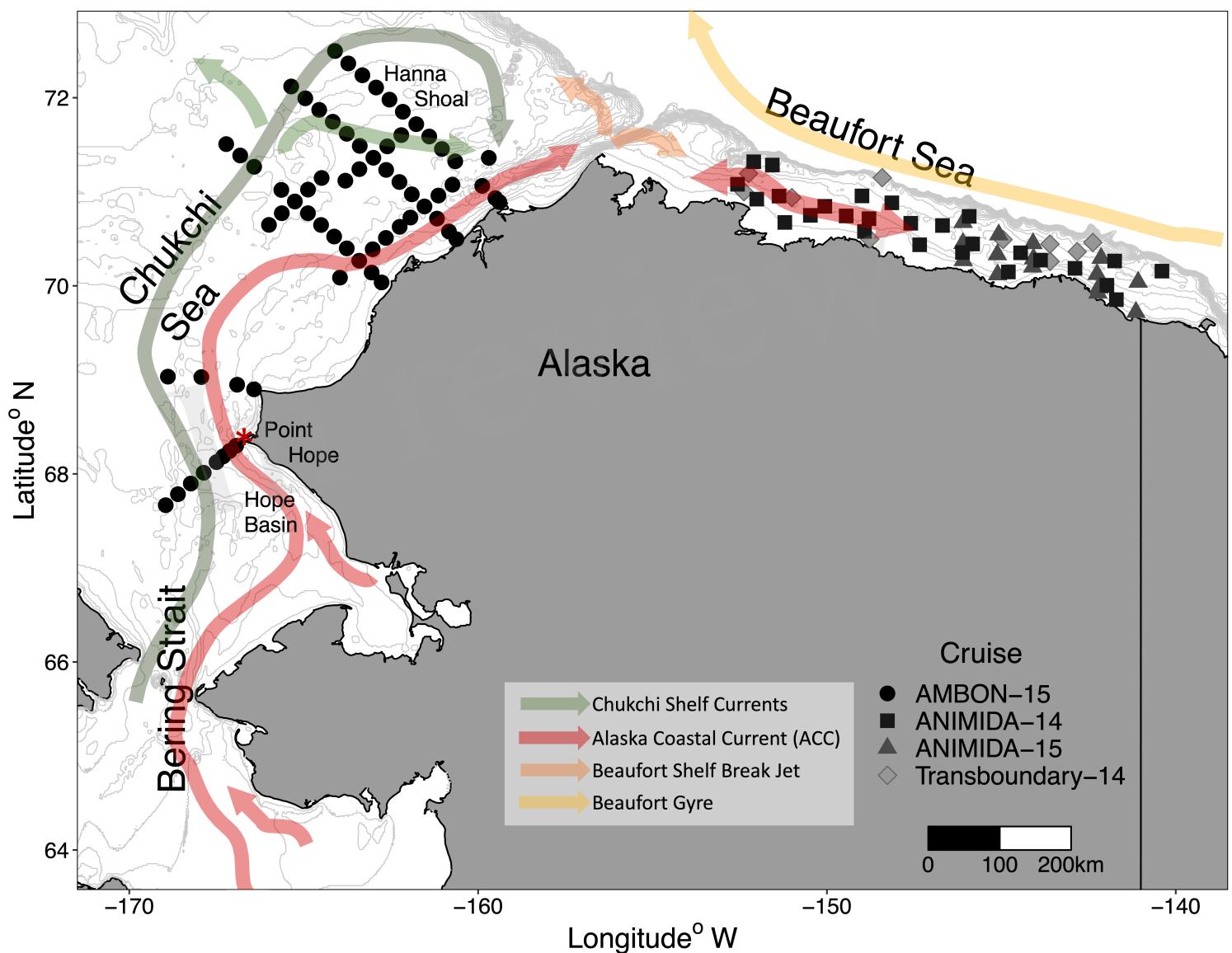


Figure 2.JPEG

Figure 2

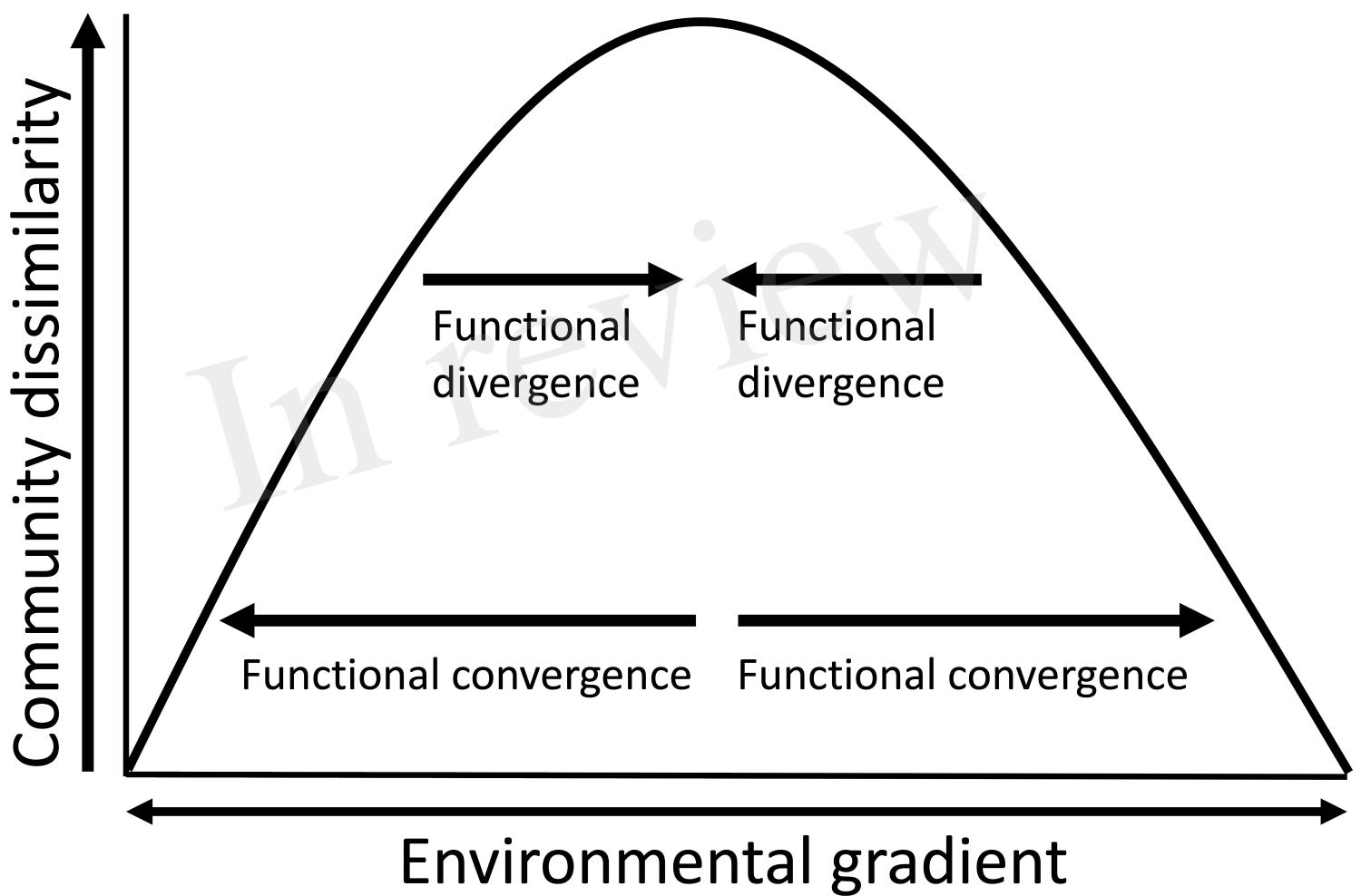


Figure 3.JPG

Figure 3

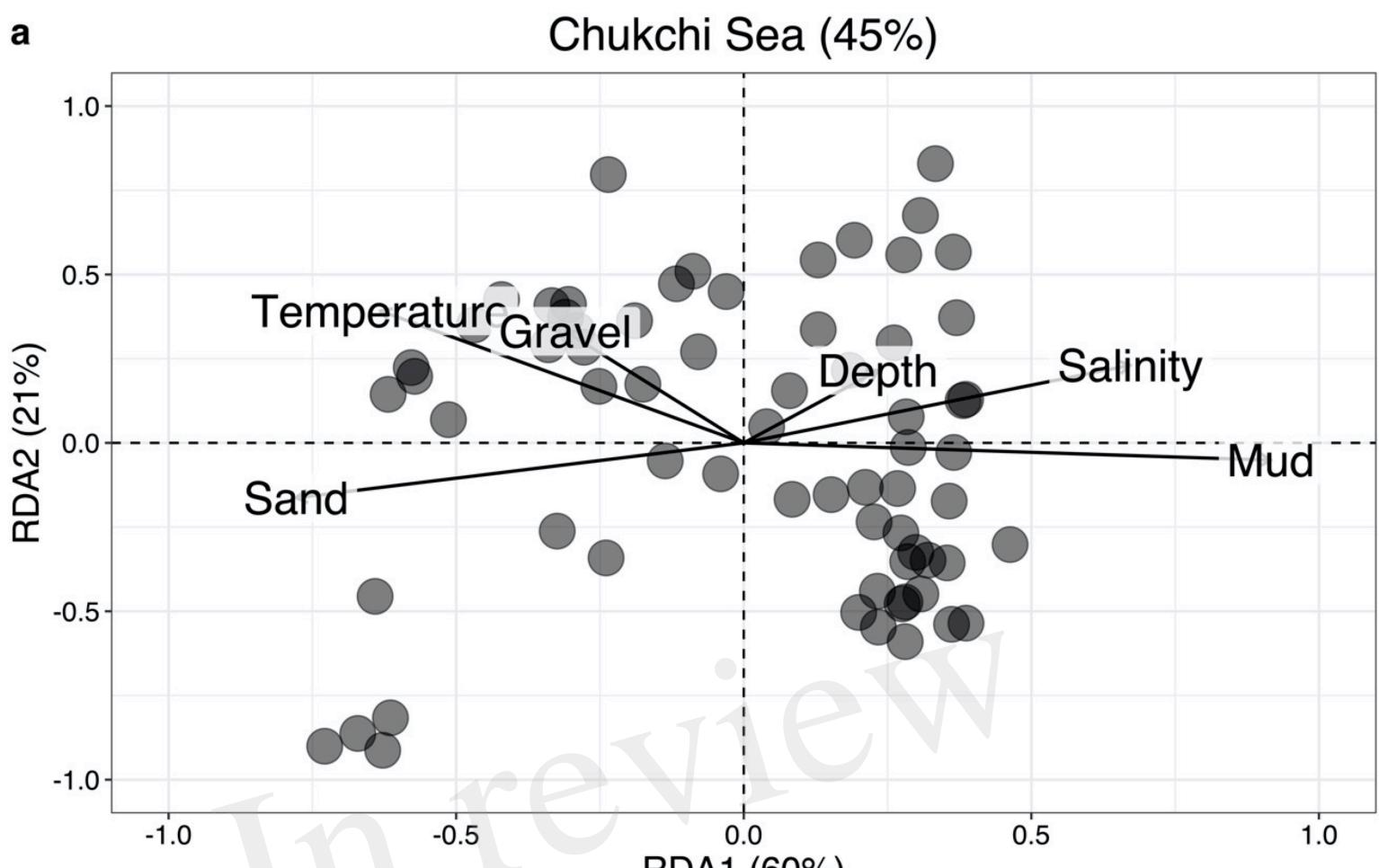
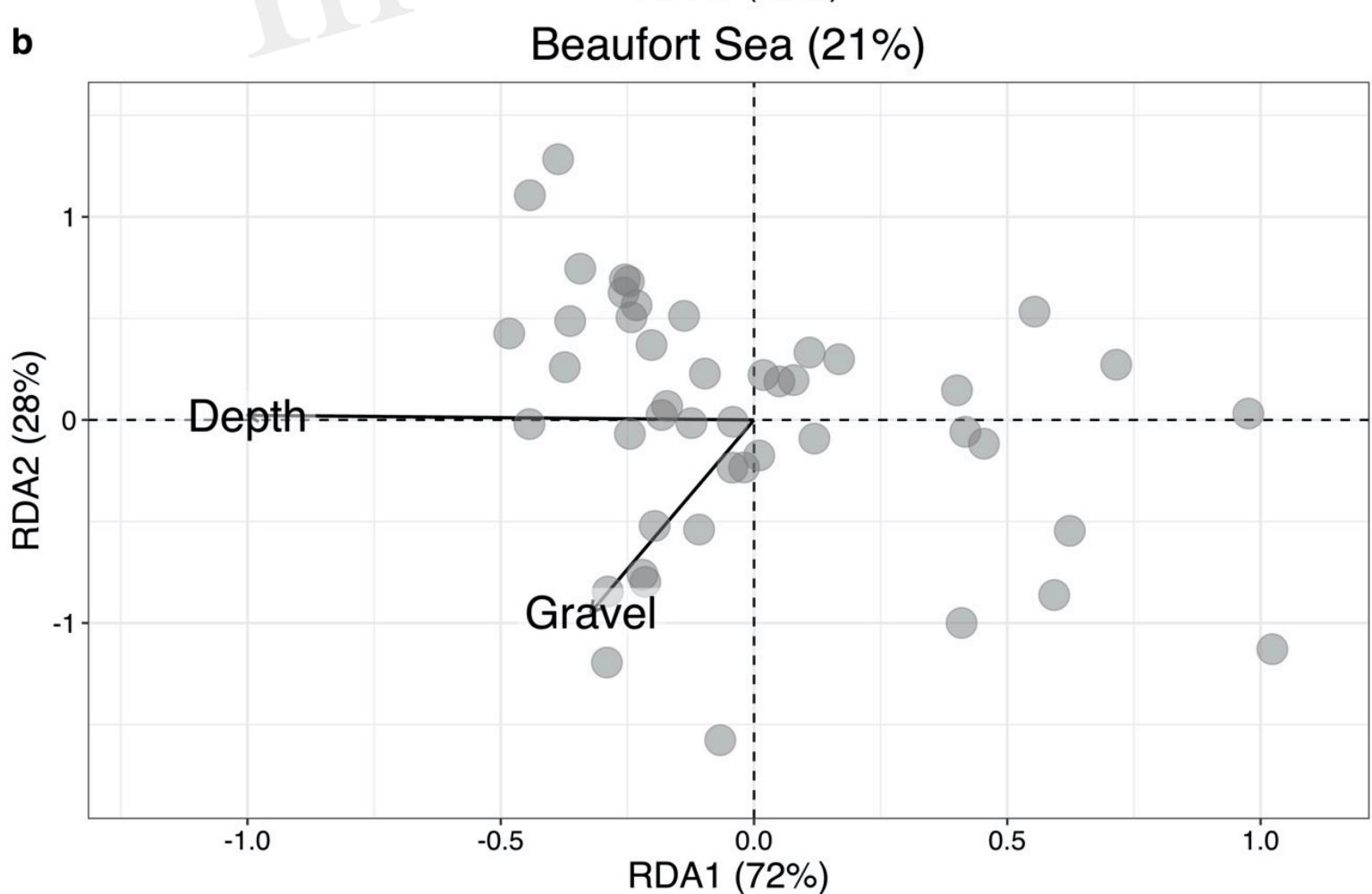
a**b**

Figure 4.JPG

Figure 4

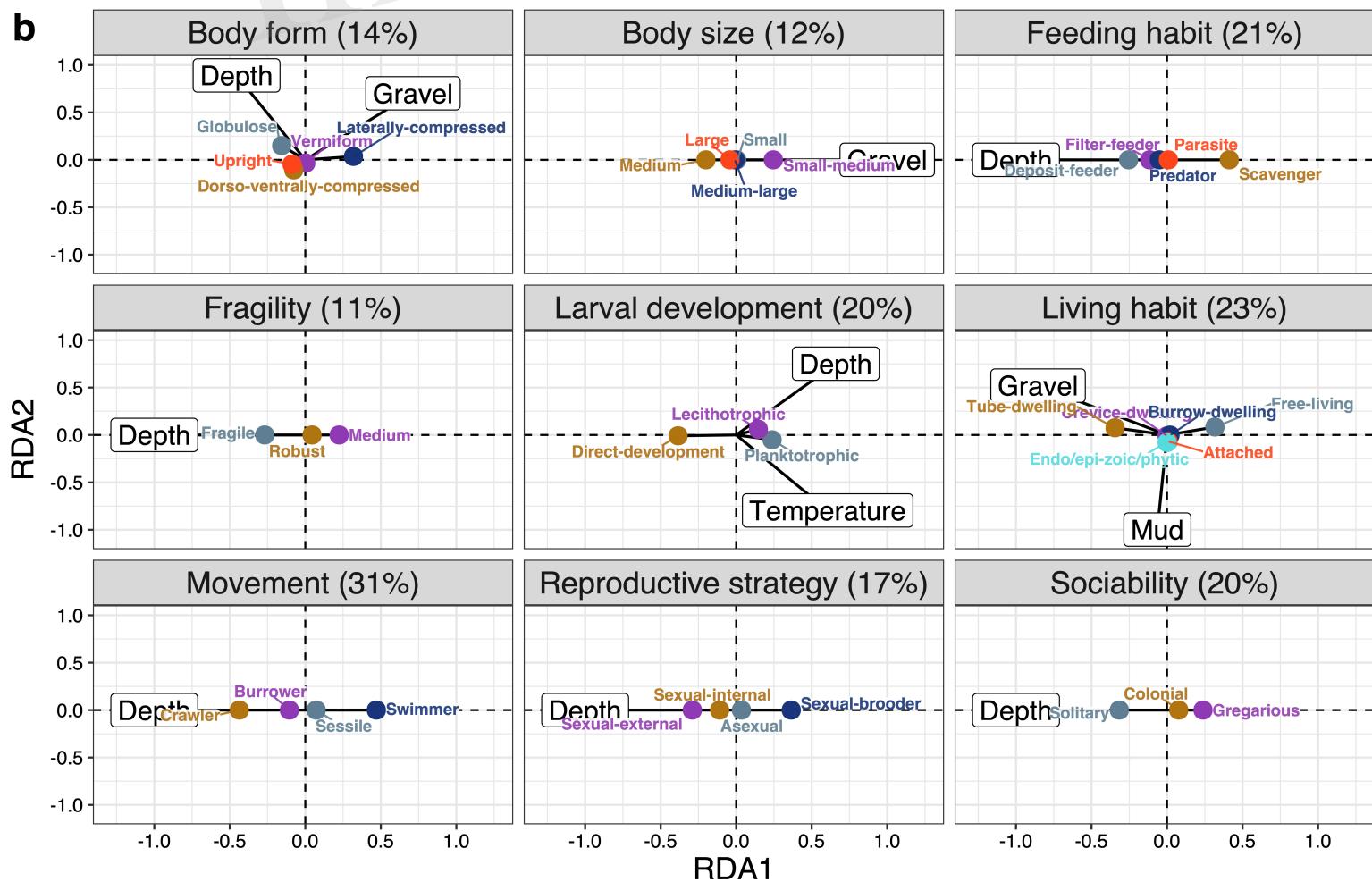
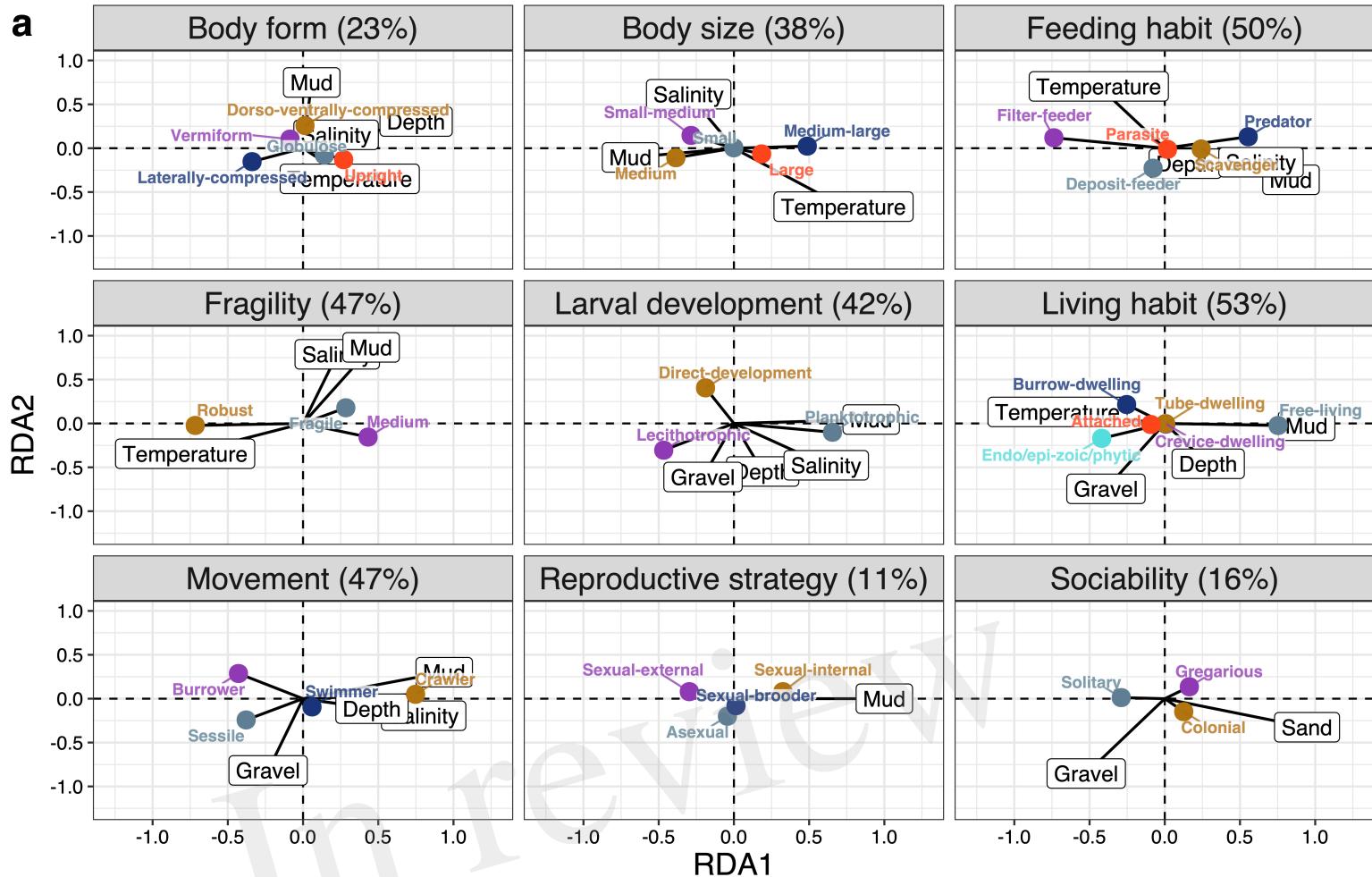
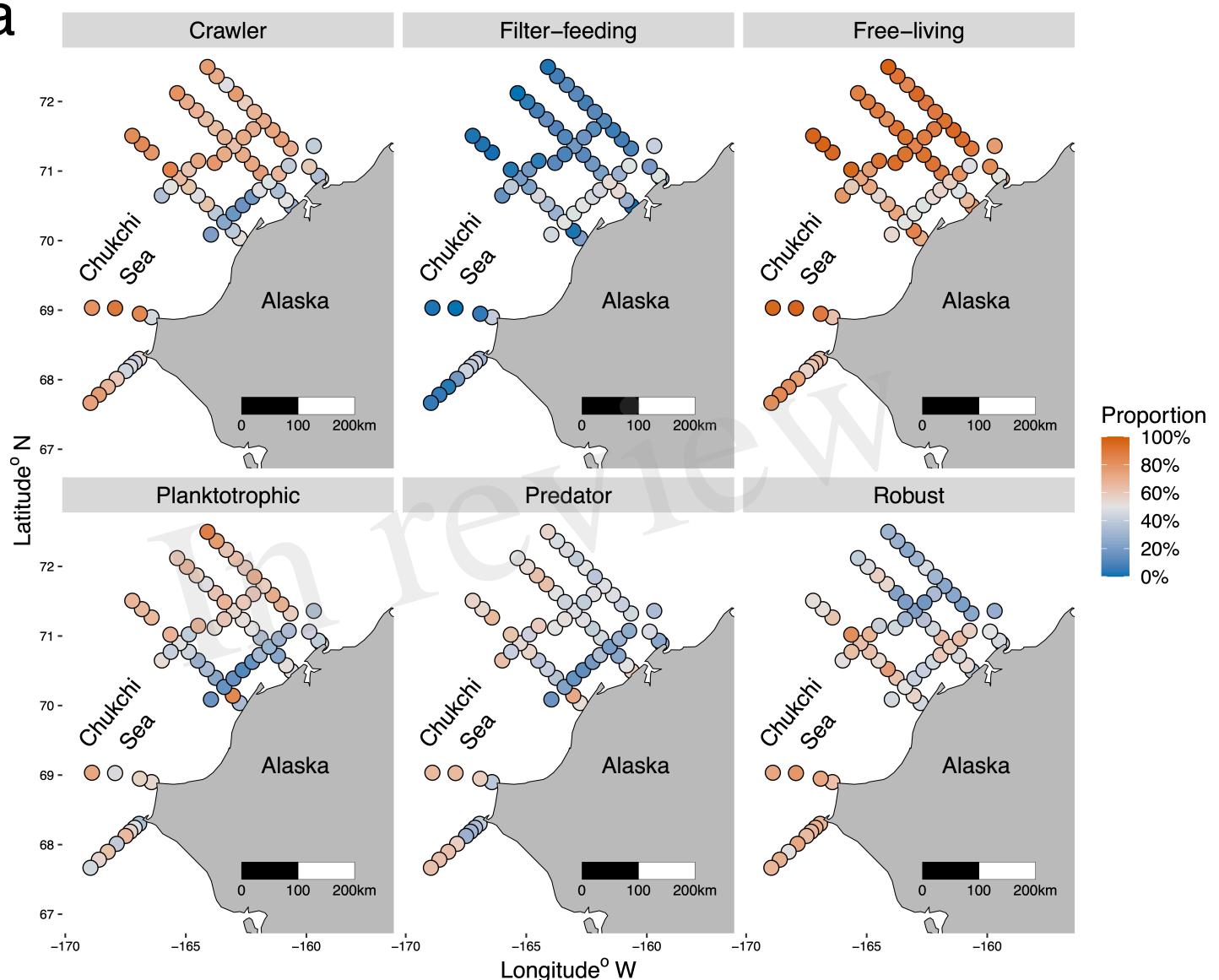


Figure 5.JPEG

Figure 5

a



b

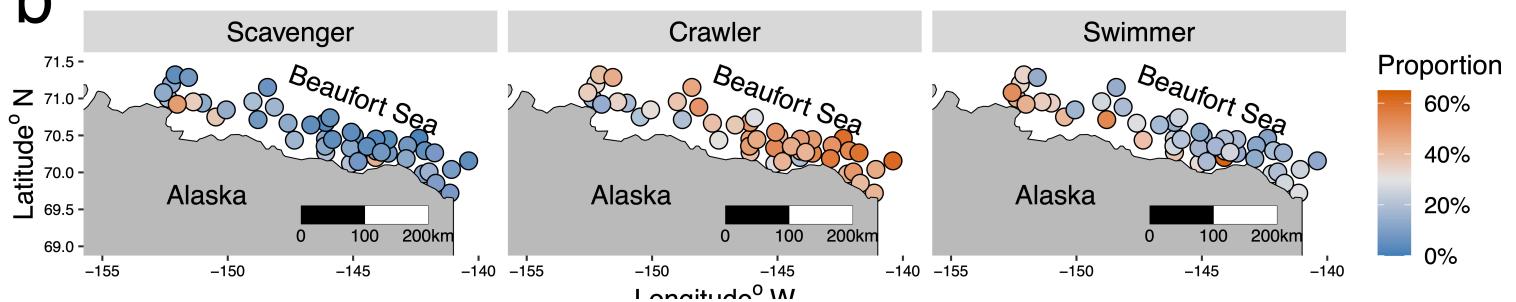


Figure 6

Figure 6.JPG

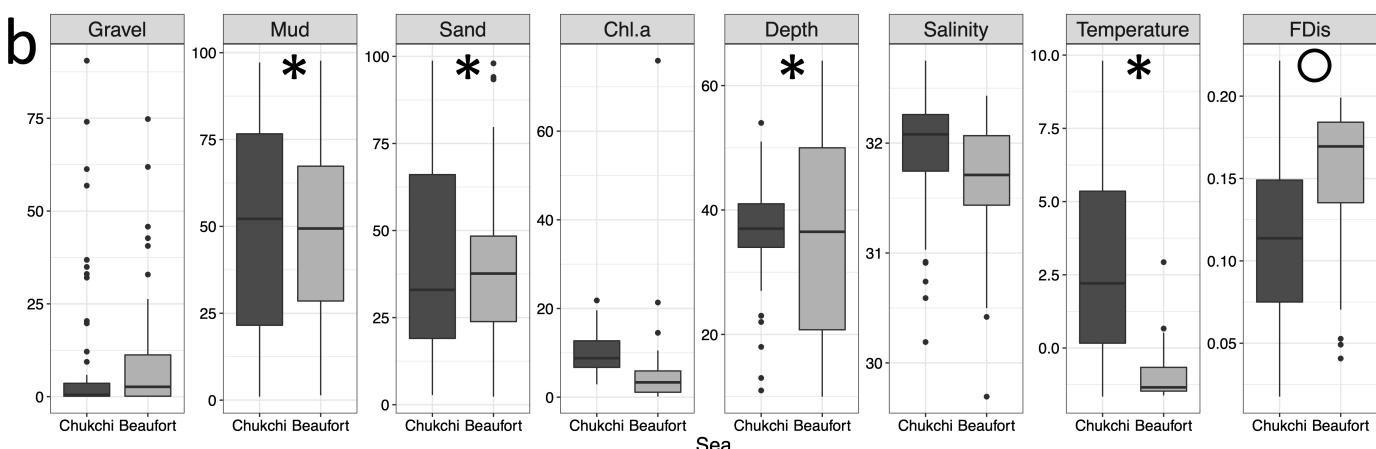
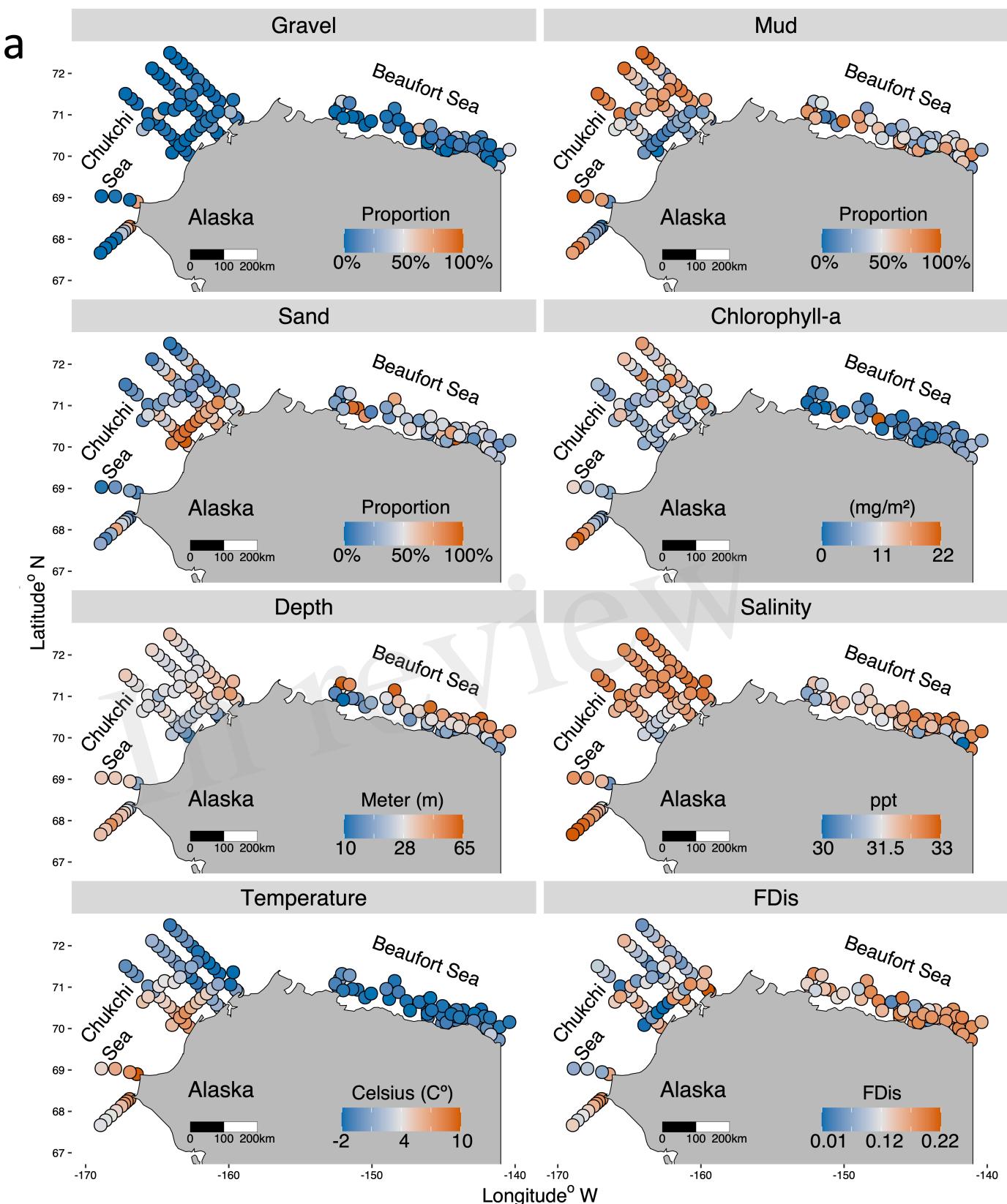


Figure 7.JPEG

Figure 7

