

1 Using biological traits and environmental variables to characterize two Arctic  
2 epibenthic invertebrate communities in and adjacent to Barrow Canyon

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10

11 ABSTRACT

12 The Arctic’s Barrow Canyon, located in the northeastern Chukchi and western Beaufort seas, supports a  
13 rich and diverse benthic ecosystem and is often termed an ecological “hotspot” of productivity. Within  
14 and adjacent to Barrow Canyon, the epibenthic invertebrate communities vary, with biomass and  
15 taxonomic distributions related to habitat variation. Here we asked if the patterns observed are due to  
16 Barrow Canyon’s variation in near-seafloor physical hydrography, and whether differences in taxonomic  
17 distribution also reflect differences in functional properties of the epibenthic invertebrate community.  
18 Data were collected using a standardized 83-112 bottom trawl during two surveys in and adjacent to  
19 Barrow Canyon: the northeast Chukchi Sea survey in 2013 and the western Beaufort Sea survey in 2008.  
20 A portion of the Beaufort Sea survey also used a liner to retain smaller organisms. A suite of nine  
21 environmental variables were examined, that included depth, bottom water temperature, bottom  
22 hardness as measured by acoustics, and circulation model hindcast current speed. They explained 18-  
23 47% of observed variance for each of the three data sets (Chukchi Sea, Beaufort Sea lined net (LN),  
24 Beaufort Sea unlined net (UN)). In the Chukchi Sea, bottom hardness and depth were significant  
25 variables. In the Beaufort Sea LN hauls, depth, bottom temperature, and the mean current speed on the  
26 day of sampling were significant variables and in the Beaufort Sea UN hauls, depth was the only

27 significant variable. Of the 150+ collected taxa from each survey, ~20 made up 90% of the total biomass  
28 in the Beaufort and Chukchi Seas, and six of the 20 taxa were common to both study areas. We used  
29 biological traits analysis (BTA) of body morphology, trophic, and reproductive traits to further  
30 characterize the epibenthos at the head of Barrow Canyon in the Chukchi Sea and into Barrow Canyon in  
31 the Beaufort Sea. Although the Chukchi and Beaufort seas differed taxonomically in abundance and  
32 distribution, they were functionally similar based on the biological traits we examined. A traits analysis  
33 can advance knowledge of a community of organisms; however, it is most informative if used as a  
34 complement to a taxonomic composition analysis of abundance and distribution.

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39 Keywords: Chukchi Sea; Beaufort Sea; Barrow Canyon; epibenthic invertebrates; biological traits

## 40 **1. Introduction**

41

42 Barrow Canyon (Fig. 1) is an important marine geologic feature situated in the northeast  
43 Chukchi Sea and is frequently referred to as the gateway to the Pacific Arctic Basin. The head of Barrow  
44 Canyon starts approximately 150 km southwest of Point Barrow and extends into the Beaufort Sea with  
45 depths up to 300 m. Several water masses transiting from the Bering and Chukchi continental shelves  
46 flow northward into the Arctic Basin through Barrow Canyon (Weingartner et al., 2005a; Gong and  
47 Pickart, 2015). Upwelling in Barrow Canyon causes locally elevated primary production (Hill and Cota,  
48 2005) which supports large numbers of both pelagic- and benthic- feeding seabirds (Kuletz et al., 2015;  
49 Lovvorn et al., 2015) and marine mammals (Moore et al., 2010) during the summer months. Arctic cod  
50 (*Boreogadus saida*) are also common, both within the vicinity of Barrow Canyon and in the canyon itself,  
51 where abundance is highest in colder and more saline near-bottom waters (Logerwell et al., this issue).  
52 In the areas adjacent to Barrow Canyon, the Chukchi and Beaufort Sea shelves, epibenthic communities  
53 have been well described (Feder et al., 1994; Bluhm et al., 2009; Blanchard et al., 2013a, b; Ravelo et al.,  
54 2014; Grebmeier et al., 2015a, b; Ravelo et al., 2015), including a macrofaunal benthic “hotspot” that  
55 has persisted for decades, just northwest of the canyon on the Chukchi shelf (Grebmeier et al., 2015).  
56 However, despite the oceanographic and biological importance of Barrow Canyon, few studies have  
57 explicitly examined the benthic invertebrate fauna within the canyon. In this study, we examined two  
58 communities that together encompass most of Barrow Canyon; the Chukchi study area is located at the  
59 head of Barrow Canyon, extends onto the Chukchi shelf, and is relatively shallow. The Beaufort study  
60 area is located north of the Chukchi study area, in the deeper portion of Barrow Canyon and extends  
61 onto the Beaufort Shelf.

62 In both the northeast Chukchi and western Beaufort seas, benthic invertebrate communities are  
63 characterized by moderate species diversity, compared to other Arctic shelf seas (Piepenburg et al.,

2011), and high biomass (~5000 kg/km<sup>2</sup>) when compared to the corresponding benthic fish communities (Rand and Logerwell, 2011). Within each community, patchiness of both species distribution and biomass are common (Ravelo et al., 2014, 2015). Several features of the local habitat influence the structure of Arctic benthic communities, such as currents (Grebmeier et al., 2006), nutrient fluxes and food availability (Grebmeier et al., 1989; Cusson and Bourget, 2005; Dunton et al., 2005), and geological characteristics (e.g., sediment, geological structure; Feder et al., 1994; Cusson and Bourget, 2005). The study region's currents within and adjacent to Barrow Canyon consists of swift flows associated with the Alaskan Coastal Current (ACC), the Beaufort Gyre, the Beaufort shelfbreak jet, and wind-driven events (including upwelling), that cause meanders and eddies to disrupt the background circulation field (Pickart et al., 2013). The ACC typically flows from the Chukchi Shelf along the axis of Barrow Canyon toward the continental slope where the Chukchi and Beaufort seas meet (Fig. 2). The Barrow Canyon mean flow opposes the prevailing winds that blow from the northeast but the winds are often strong enough to reverse the circulation here and that of the shelfbreak jet, as well as cause upwelling of subsurface waters within Barrow Canyon and along the Beaufort Slope (Mountain et al., 1976; Weingartner et al., 1998; Pickart et al., 2013; Danielson et al., 2016). Elevated levels of turbulent mixing within the canyon is likely biologically important (Shroyer, 2012). The waters leaving Barrow Canyon, in general, tend to follow topographic isobaths eastward and transition into the Beaufort shelfbreak jet (Nikolopoulos et al., 2009; von Appen and Pickart, 2012; Gong and Pickart, 2015). The complex bathymetry of the canyon and slope intersection routinely causes eddies to form near the canyon mouth (Pickart et al., 2005; Watanabi and Hasumi, 2009) which propagate into the deep adjoining basin or get caught in the westward-flowing Beaufort Gyre (Watanabe et al., 2011). The currents here evolve over time as a function of the wind and the various water densities, together determining the structure of the flows in and adjacent to Barrow Canyon. This energetic flow environment – and associated fronts, advection, convergence, turbulent mixing, and particulate export – sets the stage for areas of

88 locally elevated biological activity and benthic production in and near Barrow Canyon. How the currents  
89 and thermohaline properties influence the structuring of the local benthic invertebrate community is  
90 complex (Day et al., 2013) and not well understood in detail.

91           While the Chukchi and Beaufort Sea shelves benthic and pelagic communities are reasonably  
92 well characterized with respect to species diversity (e.g. richness and evenness), biomass, relative  
93 abundance, and trophic structure (Feder et al., 1994; Bluhm et al., 2009; Blanchard et al., 2013a, b;  
94 McTigue et al., 2014; Ravelo et al., 2014; Divine et al., 2015; Grebmeier et al., 2015a, b; Ravelo et al.,  
95 2015), other functions performed by dominant benthic organisms in this region are less well  
96 characterized. At the most basic level, functional ecology is defined as the study of ecological processes,  
97 patterns, and underlying mechanisms within an ecological community. Further, a functional or  
98 biological trait (herein the same) infers the underlying processes of that trait, such as feeding or growth.  
99 The degree of overlap between species diversity and functional diversity is different among systems. A  
100 system that may be rich in species diversity could have little functional diversity (i.e. most species feed  
101 similarly) or very high functional diversity (e.g. several different feeding strategies; Hewitt et al., 2008).  
102 Thus, functional community structure can inform us about the energy flow and resource partitioning in a  
103 system and provide insight into a system's resilience to change. Incorporating ecological function into a  
104 diversity analysis is especially important in the benthic marine system because of the strong relationship  
105 between habitat variability and taxonomic diversity and distribution (Hewitt et al., 2008).

106           In addition to characterizing the epibenthic community structure in these communities, we  
107 applied a biological traits analysis (BTA) to better understand the influence of bottom hardness and  
108 hydrography on the ecological functions of epibenthos in and adjacent to Barrow Canyon. This approach  
109 has been used most recently in other Arctic communities (Oug et al., 2012; Krumhansl et al., 2016),  
110 including the Barents Sea (Cochrane, et al., 2012; Wlodarska-Kowalczyk et al., 2012), and the Canadian

111 Arctic (Krumhansl et al., 2016). A BTA approach (Bremner et al., 2003, 2006) is a tool used to examine a  
112 suite of biological traits simultaneously across the dominant taxa in a study system to aid in identifying  
113 those habitat characteristics that may influence the selection of traits (Bremner et al., 2003). Our  
114 approach in this study followed the general framework of several earlier studies that used biological  
115 traits to characterize invertebrates in freshwater (Jackson, 1993; Usseglio-Polatera et al., 2000; Haybach  
116 et al., 2004; Bonada et al., 2007; Conti et al., 2014), lagoons (Sigala et al., 2012), estuaries (Alves et al.,  
117 2014), and marine ecosystems (Bremner et al., 2006; Hewitt et al., 2008; Pacheco et al., 2010; Paganelli  
118 et al., 2012; Krumhansl et al., 2016). To our knowledge, a BTA approach has not been used to examine  
119 the epibenthic community structure in both the Chukchi Sea or US Beaufort Sea.

120           In this study, we assessed both the taxonomy and biological traits of two adjacent epibenthic  
121 communities in a hydrographically complex region of the Pacific Arctic shelf; the Chukchi community  
122 that sits at the head of Barrow Canyon and the Beaufort community that sits in Barrow Canyon and onto  
123 the Beaufort shelf. Because the Chukchi and Beaufort portions of Barrow Canyon share similar water  
124 masses, we expected that the epibenthic invertebrate communities shared both taxonomic and  
125 biological trait similarities. Specifically, we 1) used environmental variables to explain the spatial  
126 variability in benthic invertebrate taxa that comprise the top 90% of the biomass, and further we 2)  
127 described each community using a suite of biological traits to identify patterns in their distribution and  
128 how these relate to the regional oceanographic characteristics. Finally, we discuss how a biological  
129 traits analysis could be potentially useful in monitoring the effects of change within the Arctic epibenthic  
130 invertebrate communities.

131

## 132 **2. Methods**

133

134 *2.1. Data collection in the Chukchi Sea*

135

136 Chukchi Sea samples were taken during the 2013 SHELFFZ (Shelf Habitat and Ecology of Fish and  
137 Zooplankton) survey in the northeast Chukchi from Wainwright (160° W) to Point Barrow (155° W) and  
138 encompassed the southern portion of Barrow Canyon from 17 August to 5 September 2013 (Fig. 1).  
139 Epibenthic invertebrates were collected from 29 bottom hauls. The standardized 83-112 eastern otter  
140 trawl net (Stauffer, 2004) was used for all sampling and has a 25.3-m headrope and a 34.1-m footrope  
141 with a 10.16 cm mesh in the wings and body, and an 8.89 cm mesh in the intermediate and codend. The  
142 net towed at constant speed (3 knots) on a relatively straight tow path for 15 min, maintaining constant  
143 bottom contact as measured by the HOBO Pendant G Acceleration Data Logger. The measured net  
144 opening was approximately 2 m from the head rope to the foot rope and 18-20 m in width, from wing to  
145 wing. The width and spread of the net were measured using wing and head rope sensors by Marport  
146 Deep Sea Technologies (Milford, NH) to insure the net maintained consistent specifications, and bottom  
147 contact measured distance fished. All hauls were conducted during daylight hours. The catch was  
148 brought onboard the vessel, sorted to the lowest taxonomic level, counted and weighed in its entirety  
149 on a motion compensated Marel scale. The invertebrate portion of the catch was quantitatively  
150 subsampled for species composition. The invertebrate subsample was identified to the lowest possible  
151 taxonomic level and within the lowest taxonomic level, counted and weighed to obtain a total for each  
152 taxonomic group in the subsample. Total invertebrate catch compositions, counts and weights were  
153 extrapolated by weight from the subsample.

154 In addition to processing the bottom haul catch, water column hydrographic profiles were  
155 collected. Conductivity, temperature, and depth (CTD) data were collected using a Seabird SBE-19  
156 equipped with a fluorometer and photosynthetically available radiation sensor. Data were processed

157 using a combination of the manufacturer's software (Seabird Electronics, 2012) and custom Matlab  
158 software (version 14a, 2014, Mathworks) designed for visual inspection and despiking of the profile  
159 data. Raw data were binned to 1 decibar pressure levels (approximately 1 m depth intervals). The  
160 measured environmental variables used in the analysis of taxonomic distribution in the Chukchi Sea  
161 survey were bottom temperature (°C), bottom depth (m), bottom salinity, and bottom hardness, as  
162 measured by acoustics. Acoustic measurements for bottom hardness were collected using a Simrad  
163 ES60 echosounder operating at 38 kHz (12° beam angle between half power points). The echosounder  
164 was calibrated prior to the survey. Water column and seabed backscatter (i.e. reflected echoes) were  
165 recorded continuously along survey transects, sampling at a rate of 1 Hz. All transects were divided into  
166 100 m horizontal bins. Bottom types were quantified using substrate hardness metrics (unitless) on a  
167 scale of 1 (least) to 10 (most) by integrating the first and second bottom reflections in Echoview  
168 software (v6.1). The entire second bottom echo was integrated for the bottom hardness metric based  
169 on the acoustic impedance mismatch between the seabed and the water column (Chivers et al., 1990).  
170 To estimate bottom hardness at the Chukchi Sea bottom trawl stations, approximately 20 bottom  
171 hardness data points, as measured with acoustics, were selected using ESRI ArcGIS version 10.3 at or  
172 within the vicinity of the bottom trawl location. These selected points were then averaged within  
173 ArcGIS to give a single estimate of bottom hardness for that station. The number of data points selected  
174 (~20) was based on the average distanced fished by the bottom trawl.

175

## 176 *2.2. Data collection in the Beaufort Sea*

177

178 Epibenthic invertebrates were surveyed in the western Beaufort Sea in 2008. The survey  
179 extended from Point Barrow (155°W) east to 152°W (Fig. 1). The survey also used an 83-112 Eastern  
180 otter trawl; however, in a portion of the hauls a small mesh liner was added to the codend (mesh liner



181 was 3.8 cm). The portion of the survey using a lined net is termed Beaufort LN and the portion of the  
182 survey using an unlined net is termed Beaufort UN. Because the net and possibly the catchability of the  
183 net were altered with the mesh liner, the data were analyzed separately and the two gear types were  
184 considered two surveys; Beaufort Sea LN and Beaufort Sea UN hereafter. Full details of the survey and  
185 the effects of the different gear types can be referenced in Rand and Logerwell (2011). The invertebrate  
186 catch was quantitatively subsampled, counted and weighed using the same procedure outlined in the  
187 Chukchi Sea survey. All invertebrates were identified to the lowest possible taxonomic level and  
188 counted and weighed at that level to obtain a total for each taxon in the subsample. For both regions,  
189 field identifications were confirmed in the lab from voucher material with the assistance of the  
190 taxonomic experts listed in the acknowledgments and taxonomic names were standardized to the World  
191 Register of Marine Species.

192           The water column profile characteristics were measured using the Seabird 19-*Plus* at or near the  
193 bottom haul stations, and processed following the procedures described for the Chukchi Sea survey.

194           The measured environmental variables used in both the Beaufort Sea LN and Beaufort Sea UN  
195 hauls were the same as those used in the Chukchi Sea survey with the exception of bottom hardness.  
196 Although an acoustic-trawl survey took place in the Beaufort Sea in 2008, the second bottom echo data  
197 were not collected, precluding bottom hardness as an environmental variable in the Beaufort Sea  
198 analysis.

199

### 200 *2.3. Epibenthic invertebrate density*

201

202           The catch-per-unit effort (CPUE) in kg wet weight km<sup>-2</sup> was estimated for both the Chukchi and  
203 Beaufort Sea surveys for all taxa. To calculate CPUE, the net width and distance fished was used to  
204 estimate the area swept by the net for each haul and estimated catch weight (kg) was divided by area

205 swept ( $\text{km}^2$ ). This gives an estimate of biomass density for each species or taxa in each haul. To  
206 estimate the average CPUE for each taxa in each survey, zero catches were also included at each station  
207 for taxa that were not present in the haul. All analyses were done on individual taxa, by survey, (Table  
208 1) and all three surveys were treated independently. To reduce skewness that is common with CPUE  
209 data, CPUE estimates were cube-root transformed preceding analyses.

210

#### 211 *2.4. Biological Traits*

212

213 To focus on those invertebrates and the biological traits that dominated each of the three data  
214 sets, only the taxa in the top 90% by total biomass estimated from CPUE were used in all analyses. This  
215 reduced the number of taxa whose biological traits we examined for each system from >100 to less than  
216 20 (Table 1). The taxa from the top 90% by total biomass were selected for each survey, independent of  
217 the other surveys. Any invertebrates in the trawls that were generally considered infaunal (e.g.  
218 polychaetes) were further removed from the top 90%. We chose the taxa that made up the top 90%  
219 total biomass for each survey to address the basic ecological function of the epibenthic invertebrates  
220 that dominate areas in and adjacent to Barrow Canyon. Detailed life history information for even the  
221 dominant invertebrate taxa in the sub-arctic and Arctic is sparse at best. The 10% of invertebrate taxa  
222 not used in the analysis were even more difficult to collect life history information on and often times  
223 would reflect the life histories of those taxa found in the top 90%, since the family level was often used  
224 in assigning trait modalities.

225 Ten biological traits that summarize basic biological characteristics (size, shape) as well as  
226 fundamental trophic (feeding type and mechanisms), reproductive and life history ecology (dispersal  
227 and larval types) were selected and divided into 31 trait modalities (Table 2). The selected traits are  
228 common to several recent studies using biological traits analysis (Bremner et al., 2003; Haybach et al.,

229 2004; Hewitt et al., 2008; Paganelli et al., 2012), and maximize some of the fundamental differences in  
230 the biology and ecology of species. The only biological trait that was quantitatively measured was Size,  
231 determined as the average weight per individual animal for each taxon calculated from the catch. An  
232 extensive literature search was used to assign each taxon to a category in each of the ten trait groups.  
233 When little or no information on a species' life history could be found, information from the genus level  
234 or species within the same family was used.

235 Three matrices were produced for the analyses: 1) a haul by taxon biomass (CPUE) matrix, 2)  
236 taxon by trait matrix, and 3) haul by trait matrix. The third matrix was a product of the haul by taxon  
237 biomass matrix and taxon by trait matrix (Bremner et al., 2003). This was constructed by multiplying  
238 trait modalities for each taxon present in a haul by its CPUE in that haul, and then summing the biomass  
239 across each trait modality over all taxa present in that haul to obtain a single value for each trait  
240 modality in each haul. Essentially, this weights the occurrence of a biological trait or trait modality  
241 across taxa at the haul level (Charvet et al., 1998).

242

### 243 *2.5. Numerical model integration*

244

245 In order to depict the mean regional circulation field for the purpose of providing additional  
246 environmental context to the biological analyses and interpretations, we compiled results from a 3-  
247 dimensional ocean and ice circulation numerical hindcast model (Curchitser et al., 2013; Danielson et al.,  
248 2016b), which was integrated over 2005 to 2011 within the Regional Ocean Modeling System (ROMS)  
249 framework (Fig. 2). Quantitative comparisons of model output to year-long in situ mooring-based  
250 current velocity data show that the model reproduces (at the 95% confidence level) the observed mean  
251 velocity vector components at nearly all of the 19 Beaufort and Chukchi evaluation sites (Curchitser et  
252 al., 2013). Results from the new integration (Danielson et al., 2016b) and this study are driven with the

253 same initial conditions, boundary conditions and atmospheric forcing described in Curchitser et al.  
254 (2013). A number of improvements were implemented in the present version including extending the  
255 Pacific side southern boundary from Bering Strait to south of the Bering Sea, an improved sea-ice  
256 formulation, and more realistic coastal river discharges (Danielson et al., 2016b). Model horizontal  
257 resolution is about 6 km in the Barrow Canyon region and there are 50 terrain-following layers in the  
258 vertical dimension. Several model-derived variables were included in the initial analyses for all three  
259 surveys: speed of the near-bottom current averaged over the day of sampling (Speed Day of Sample),  
260 eastward velocity component averaged over the day of sampling (East Velocity), northward velocity  
261 component averaged over the day of sampling (North Velocity), year-long mean near-bottom speed at  
262 this sampling site (Mean Year Speed), and year-long mean near-bottom speed variance at this sampling  
263 site (Mean Year Speed Var).

264

## 265 *2.6. Statistical Analysis*

266

267 The taxa in the top 90% by biomass were analyzed in two ways: 1) a canonical correspondence  
268 analysis (CCA) using taxon biomass estimates and environmental variables (Cajo and Braak, 1986;  
269 McGarigal et al., 2000), and 2) a fuzzy correspondence analysis (FCA) to quantify the variation in  
270 biological trait distribution for each survey (Chevenet et al., 1994).

271 For the taxonomic distribution and environmental variables analysis, the taxon biomass matrix  
272 was ordinated using a constrained ordination (i.e. a CCA), and displays only the variation that can be  
273 explained by the constraining variables (e.g. temperature, depth) using Chi-square distances. Further,  
274 the haul scores are constrained to be linear combinations of the constraining variables. Because of the  
275 small sample size in the Beaufort Sea LN and Beaufort Sea UN surveys, the environmental variables  
276 examined were limited to those that were not tightly correlated. For example, density and salinity are

277 tightly correlated, therefore we chose a single variable, salinity, for the analysis. Even though  
278 intercorrelated variables do not affect the CCA, a reduced number of variables can aid in interpretability,  
279 especially when the number of variables approaches the number of samples, as in the case of the  
280 Beaufort LN and UN hauls (McGarigal et al. 2000). Also, if the ordination contains as many variables as  
281 samples, the ordination is no longer “constrained” by the environmental variables, also termed  
282 overfitting. The initial CCA analysis was completed for each survey and included all variables (9 for the  
283 Chukchi and 8 for the Beaufort LN and UN surveys). Initially, we performed a variance inflation factor  
284 (VIF) test, which measures the extent of multicollinearity between variables. This aided in informing  
285 which variables would be used in the final CCA analysis and which variables could be eliminated (i.e.  
286 high VIF). Additionally, variables whose arrows were in close proximity (same length and direction), a  
287 single variable was selected for further analysis. In all three surveys, salinity and bottom depth were  
288 tightly correlated along with year-long mean near-bottom speed at the sampling site (Mean Year Speed)  
289 and year-long mean near-bottom speed variance at the sampling site (Mean Year Speed Var); the  
290 variables used in the model were bottom depth and Mean Year Speed. In the Chukchi survey, bottom  
291 hardness and Mean Year Speed were tightly correlated, bottom hardness was the variable used in the  
292 model for further analysis. After the variables were selected, the final CCA was performed on the taxon  
293 biomass and the selected variables (termed the “full model”). The first two axes from the final CCA were  
294 permuted ( $x=999$ ) and an ANOVA-like test (“pseudo-F statistic”) was used to determine those  
295 variables that were most significant at  $p<0.05$  (Dray and Dufour, 2007a, b). This analysis tested the  
296 reduced model’s results after removing a variable against the full model’s results.

297 For the biological traits analysis, the haul by traits matrix was ordinated using fuzzy coding  
298 correspondence analysis (FCA) (Chevenet et al., 1994). It is used to assign multiple modalities to a single  
299 taxon using percentages. This process accounts for differences in trait modalities within and among life  
300 history stages. For example, a gastropod species may be both predator (70% of the time) and scavenger

301 (30% of the time) during the adult phase. In the absence of this detailed information for many of the  
302 Arctic species in this analysis, we instead chose a binary coding procedure where each taxon is assigned  
303 to one category within each biological trait based on what the taxon exhibits a majority of the time. For  
304 example, the species *Neptunea heros* was classified as a predator under the trait modality “feeding  
305 mechanism”; however, this species may also be an “opportunist/scavenger” at times. FCA is an  
306 extension of correspondence analysis (CA) that incorporates discrete variables such as biological traits  
307 that are either coded as binary (i.e., 0,1) or fuzzy (i.e., 0.3, 0.7). FCA is able to correct for the fact that  
308 each biological trait (e.g. Body Design) has multiple trait modalities (e.g. “soft”, “hard shell”) and the  
309 sum of all trait modalities within a biological trait can be no more than one. Even though biological  
310 traits data in this analysis were binary and not coded as fuzzy, this sets up the framework for  
311 incorporating additional trait information should it become available. The results of an FCA explain the  
312 amount of variation in trait distribution on each axis. To interpret the results, the relationship of hauls  
313 (rows) can only be compared to other hauls (rows) and columns (traits) to other columns (traits). Hauls  
314 that have similar FCA coordinates and are close to one another on the ordination plot are similar relative  
315 to the frequency of traits. Since the haul by traits matrix table contained the same trait modalities for all  
316 three surveys, a Kruskal-Wallis test was used to determine if the first axis scores from the FCA ordination  
317 for all three surveys differed from one another. The first axis scores account for the greatest amount of  
318 variation. No statistical difference would suggest that the variation in biological trait distributions within  
319 in each of three surveys were the same. To quantify how much of the variance was accounted for by  
320 each biological trait and trait modalities (Table 2) on each axis, correlation ratios and eigenvalues were  
321 calculated for each biological trait. Correlation ratios represent percentage of variance accounted for by  
322 a given axis. The eigenvalues can be considered the amount of variance as part of the total variance (i.e.  
323 total inertia) accounted for by each axis.

324 Statistical analysis and graphical results were carried out in the statistical program R (R  
325 Development Core Team 2014), version 3.1.2, with R packages ade4 (Chessel and Dufour, 2004; Dray  
326 and Dufour, 2007a, b) and Vegan (Oksanen et al., 2015). All maps were created in ESRI ArcGIS version  
327 10.3.

328

### 329 **3. Results**

330

#### 331 *3.1. Diversity and dominant taxa*

332

333 The number of taxa in the Chukchi Sea survey ranged from 26-57 per haul with a total of 215  
334 taxa identified, of those 151 were identified to species. The number of taxa ranged from 27-58 per haul  
335 in the Beaufort Sea LN survey with a total of 132 taxa. The number of taxa ranged from 35-50 per haul  
336 in the Beaufort Sea UN survey with a total of 109 taxa. In total, 17 taxa made up 90% of the total  
337 biomass in the Chukchi Sea survey, 10 taxa in the Beaufort Sea LN survey, and 11 taxa in the Beaufort  
338 Sea UN survey (Table 1). Within the species contributing the top 90% wet weight biomass, the  
339 northeastern Chukchi Sea survey and the western Beaufort Sea surveys (LN and UN combined) shared at  
340 least six benthic invertebrate species.

341 The CPUE estimates in the Chukchi Sea hauls were highest at the western-most portion of the  
342 study area (Fig. 1). The dominant invertebrates in the Chukchi Sea hauls from nearshore to the canyon  
343 were *Gorgonocephalus* spp. (basket star), and other ophiuroids, and four species of large gastropods  
344 (Fig. 3) (Table 1). Of the other biomass-dominant taxa, the sea star, *Solaster dawsoni arcticus*, occurred  
345 in all the Chukchi Sea hauls (Fig. 3) while the mud star *Ctenodiscus crispatus*, only occurred on the outer  
346 shelf in the north part of the Chukchi study area (Fig. 3). The sea cucumber, *Psolus peronii*, was only  
347 present in the western portion of the Chukchi study area (Fig. 3).

348 In order to spatially note the taxonomic composition for all three surveys, several taxa were  
349 lumped into a single group and were mapped using pie charts (Fig. 3). The Beaufort Sea LN hauls  
350 occurred predominantly on the Beaufort slope and in Barrow Canyon (>200 m) and were dominated by  
351 brittle stars (mostly *Ophiura sarsii*), snow crab (*Chionoecetes opilio*) and gastropods (Fig. 3). Total CPUE  
352 estimates were consistently high in the mouth of Barrow Canyon and along the western Beaufort Sea  
353 shelf break in water deeper than 300 m (Figs. 2 and 3). Overall, the CPUE estimates for the Beaufort Sea  
354 LN hauls were two to three times greater than the estimates for both the Beaufort Sea UN and Chukchi  
355 Sea hauls. This discrepancy is in part related to the smaller mesh size (Fig. 1) used for the Beaufort Sea  
356 LN hauls; of 12 hauls, only two (12 and 13) had CPUE estimates considerably lower than all other hauls.

357 The Beaufort Sea UN hauls occurred mostly on the shelf and were dominated by a sea cucumber  
358 (*Psolus peronii*) and hermit crab (*Pagurus trigonocheirus*) in the two western hauls, next to Barrow  
359 Canyon (Fig. 3) (Table 1). The catch composition transitioned to hauls dominated by the mud star  
360 (*Ctenodiscus crispatus*) and the same hermit crab (*Pagurus trigonocheirus*) in the central part of the  
361 study area to hauls dominated by the sea peach (*Halocynthia aurantium*) and two genera of  
362 demosponges, *Polymastia* and *Vulcanella*, in the east part of the study area (Fig. 3) (Table 1). The CPUE  
363 estimates varied across all hauls, but was, with the exception of haul 17, lower than the western- and  
364 southernmost Chukchi Sea hauls, and there was no quantitative pattern relating to depth or location  
365 (Fig. 1).

366

### 367 3.2. Environmental variables and epifaunal biomass

368

369 The bottom temperature ranges observed in the Chukchi Sea survey during the sampling period  
370 ranged from -1.72 to 2.68°C, the bottom salinity ranged from 30.93 to 33.28, and bottom depths ranged  
371 from 26 to 155 m. Bottom hardness measurements at or near the bottom trawl stations ranged from



372 3.5 (least hard) to 5.9 (most hard) within the Chukchi Sea study area. During the Beaufort Sea LN  
373 survey, the bottom temperatures ranged from -1.70 to 1.94°C, the bottom salinity ranged from 30.94 to  
374 34.85, and bottom depths ranged from 47 to 445 m. During the Beaufort Sea UN survey, the bottom  
375 temperatures ranged from -1.26 to 2.19°C, the bottom salinity ranged from 30.69 to 34.11, and bottom  
376 depths ranged from 40 to 187 m.

377 The three environmental variables in the CCA accounted for 17% of the variability in taxon  
378 biomass (Fig. 4a) (Table 3) on the first two axes, and the only significant term from the ANOVA was  
379 bottom hardness on the CCA1 axis ( $p < 0.05$ ) (Table 3). All the hauls with a positive CCA1 axis score (Fig.  
380 4a) corresponded to those hauls located either in or in close proximity to Barrow Canyon; this aligned  
381 with both an increase in bottom hardness and current flow (Fig.1). The hauls with both a negative CCA1  
382 and CCA2 score were those hauls located on the upper Chukchi shelf in the northern most stations (Figs.  
383 1 and 4a, hauls 11, 12, 13, and 16). These hauls were also located close to 180° degrees from the  
384 direction of bottom hardness, which indicates a decrease in bottom hardness in the location of these  
385 hauls (Fig. 4a).

386 In the Beaufort Sea LN hauls four environmental variables were used in the CCA and accounted  
387 for 46% of the variability in taxon biomass (Fig. 4b) (Table 3) on the first two axes. The ANOVA  
388 permutations resulted in three significant terms ( $p < 0.05$ ); bottom temperature, bottom depth, and  
389 Mean Year Speed (Table 3). The arrows for bottom depth and Mean Year Speed are at a 180° angle  
390 indicating these two variables are inversely related; at deeper hauls, current flow is slower (Fig. 4b).  
391 Hauls 3, 11 and 12 (Fig. 4b) were at the shallowest stations but had the highest current flows whereas all  
392 the hauls clustered in the upper right quadrant were the deepest stations and had the lowest current  
393 flows.

394 In the Beaufort Sea UN hauls, 48% of the variability on taxon biomass in the CCA was accounted  
395 for by bottom depth, North Velocity, and Mean Year Speed Var (Fig. 4c). The significant variables from  
396 the ANOVA were bottom depth and North Velocity (Table 3).

397

### 398 *3.3. Biological Traits Analysis*

399

400 The FCA accounted for 58% of the variance in the distribution of traits for the Chukchi Sea hauls  
401 (Figs. 5a-b) (Table 4). Hauls with a positive axis 1 score were dominated by large, predatory carnivores  
402 that sexually reproduce and shed eggs (Fig. 5b). Flat bodied, predatory organisms with an endoskeleton  
403 also dominated these hauls and similar to the results of the taxon biomass and environmental variables,  
404 these traits occurred where there was an increase in hard bottom (Fig. 5a, black circle). Hauls 11-13 and  
405 16 had a positive axis 2 score and grouped together; these hauls were dominated by small opportunistic  
406 scavengers with a hard exoskeleton (Figs. 5a-b). These four hauls were located on the Chukchi shelf,  
407 north of Barrow Canyon (Fig. 1).

408 The FCA accounted for 73% of the variance in the distribution of traits for the Beaufort Sea LN  
409 hauls (Figs. 5c-d) (Table 4). Similar to the results based on taxon abundance and environmental  
410 variables, the tight cluster of hauls with a negative axis 1 score were hauls that corresponded to the  
411 stations >200 m in the Beaufort Sea survey (Fig. 5c, black circle). These hauls were dominated by small,  
412 flat bodied deposit feeders, and predators with a hard exoskeleton, reflecting the dominance of brittle  
413 stars and snow crab in these hauls (Figs. 5c-d). Those hauls with a positive axis 1 score were dominated  
414 by soft, medium/large bodied, filter/suspension feeders (Fig. 5d). These stations were positioned from  
415 the slope onto the Beaufort shelf and, in general, were in water <200 m (Figs. 5c-d).

416 The FCA accounted for 79% of the variance in the distribution of traits for the Beaufort Sea UN  
417 hauls (Fig. 5e-f) (Table 4). Unlike the clustering of hauls in the Chukchi and Beaufort LN surveys, the

418 Beaufort Sea UN survey showed little clustering among the hauls based on traits. This likely reflects the  
419 higher degree of taxonomic diversity where many of the species do not overlap in trait similarities  
420 compared to the Chukchi and Beaufort LN surveys (Fig. 5e). Traits with a positive axis 1 and axis 2 score  
421 were dominated by soft body/protected, erect, and medium size traits and were associated with hauls  
422 23 and 24 (axis 2) on the southern slope/shelf of Barrow Canyon, which also coincided with a  
423 predominance of sea cucumbers in these two hauls (Fig 3c). Hauls that had a negative axis 2 score (17,  
424 20, 21) occurred on the Beaufort Sea shelf in the east part of the Beaufort study area, and were  
425 dominated by large, filter/suspension feeders that sexually reproduce and shed larvae (Figs. 5e-f). Flat  
426 bodied deposit feeders dominated hauls 18 and 26 and were located on the Beaufort Sea shelf (Figs. 5e-  
427 f).

428           The axis score coordinates for each trait from the FCA analysis were plotted by survey to  
429 visualize which trait scores accounted for the most variance in the distribution of hauls (i.e. points  
430 located far from the zero coordinate for both axes). For example, the trait modality “small” for both the  
431 Chukchi and Beaufort Sea UN surveys showed coordinate scores distant from zero on both axes, which  
432 means this trait contributed to the observed variance in the pattern of haul distribution (Fig. 6). In  
433 contrast, the variation in the distribution of the trait modality “large” showed little to no variation in  
434 trait distribution for all three surveys (i.e. all three points are located at or near the zero coordinate)  
435 (Fig. 6). Biological traits and their subsequent modalities, that showed little to no variation in their  
436 distribution across hauls, included Degree of Attachment, Mobility, Propagule Dispersal, and Larval  
437 Dispersal (Fig. 6). The trait modality “deposit feed” showed large variation in the distribution of the trait  
438 both within a survey (e.g. the Chukchi Sea, asterisk) and between surveys (e.g. the three points are  
439 widely distributed); however, there was little variation in the distribution both within and between  
440 surveys for the other trait modalities within Feeding Mechanism (e.g. “filter/sus”, “opp/scavenger”) (Fig.  
441 6).

442           There was no significant difference in the variation of biological trait distribution among the  
443 three surveys (Chukchi Sea, Beaufort Sea LN, Beaufort Sea UN) based on the results of the Kruskal-Wallis  
444 test for significance on the first axis of the FCA ordination ( $p=0.90$ ).

445           To further characterize the variation in the distribution of biological traits, we mapped biological  
446 traits and the corresponding trait modalities with correlation ratios greater than 0.20 on axis 1 (Body  
447 Design, Body Form, General Prey Type, and Feeding Mechanism) (Fig. 7a-d). (Table 4). Correlation ratio  
448 scores greater than 0.20 can be considered those traits with the most variable distribution within a  
449 survey. The Chukchi and Beaufort Sea LN surveys each had three traits that met this criteria, followed  
450 by one trait in the Beaufort Sea UN survey that met this criteria (Fig. 7a-d). The biological traits with  
451 ratios  $>0.2$  showed the highest variation in their distribution within each survey (Fig. 7a-d) (Table 4).  
452 There were three biological traits that explained the greatest amount of variation in their distribution on  
453 axis 1 and that was Feeding Mechanism (Fig. 7c) in the Beaufort Sea LN and UN surveys and both Body  
454 Design and General Prey Type (Figs. 7a and 7d) in the Chukchi and Beaufort Sea LN surveys (Table 4).  
455 In the Chukchi Sea survey, the biological trait Body Design had the highest correlation ratio for axis 1  
456 explaining 23% of the variability among the traits on axis 1, followed by Body Form and General Prey  
457 Type (Table 4). In that, the “soft/protected” (Fig. 7a), “erect” (Fig. 7b), and “herbivore” (Fig. 7d) trait  
458 modalities occurred in their highest proportion in the western part of the survey area and, in general,  
459 these trait modalities did not occur on the southern slope of Barrow Canyon. Opposite this result, the  
460 southern slope of Barrow Canyon in the Chukchi Sea survey was dominated by “endoskeleton/hard  
461 shell” (Fig. 7a), “flat/round” (Fig. 7b), “carnivore/omnivore” (Fig. 7d) trait modalities. In the Beaufort  
462 Sea LN survey, Body Design and subsequent modalities also had the highest correlation ratio on axis 1,  
463 likely due to the trait modality “soft/protected” only occurring at depths  $<200$  m, on the Beaufort Sea  
464 Shelf (Fig. 7a). Alternatively, the deep slope stations in the Beaufort Sea LN survey showed an absence  
465 of the “soft/protected” (Fig. 7a), “erect” (Fig. 7b), “filter/suspension” (Fig. 7c), and “herbivore” (Fig. 7d)

466 trait modalities. The trait modality “deposit feeder” (Fig. 7c) that only occurred in the northeast portion  
467 of the Chukchi Sea survey area, was the largest proportion of the Beaufort Sea LN hauls in the deep  
468 slope stations. The trait modality “deposit feeders” was also not common on the Beaufort Sea shelf  
469 (mostly UN) hauls, which were mostly dominated by “filter/suspension” feeders (Fig. 7c). In the  
470 Beaufort Sea UN survey, the biological trait Feeding Mechanism was the only trait  $>0.2$  with a  
471 correlation ratio explaining 23% of the variability on axis 1 (Table 4), likely due to the increased  
472 occurrence of the trait modality “deposit feeders” around the 50 m depth contour (Fig. 7c, 3 hauls).

473 We selected the two biological traits with ratios less than 0.05 on axis 1 (Propagule Dispersal  
474 and Larval Development) for all three surveys to further illustrate patterns in trait distribution between  
475 regions (Figs. 7e-f) (Table 4). These two biological traits and subsequent trait modalities showed the  
476 least variation in their distribution within each survey. Even though the distribution of trait modalities  
477 within a survey was homogenous for these low correlation ratios, the proportion of trait modalities  
478 between surveys was quite variable (Figs 7e-f). Specifically, the biological trait Larval Development had  
479 a higher proportion of “planktotrophic” larvae (long pelagic larval durations) in the Beaufort Sea LN  
480 survey than the Chukchi Survey based on the pie charts (Fig. 7e). In contrast, the Chukchi survey had a  
481 higher proportion of “direct” development (low dispersal potential) and “lecithotrophic” larvae (yolk  
482 sack attached as source of nutrition; shorter dispersal range than “planktotrophic”) throughout the  
483 survey area compared to lower proportions in waters  $> 200$  m in the Beaufort Sea LN survey (Fig. 7e). In  
484 general, the trait modality “direct” was homogeneously distributed and in every haul except one in the  
485 Chukchi Sea survey, compared to the other two surveys where the trait is more patchily distributed (e.g.  
486 a few hauls in the Beaufort Sea LN and UN surveys have high proportions). The trait modality  
487 “substrate” occurs in greater proportions in the Chukchi Sea survey compared to the proportions this  
488 trait occurs in both the Beaufort Sea LN and UN surveys (Fig. 7f). In general, the trait modality “pelagic”

489 was dominate in most of the Chukchi survey hauls and dominated all hauls in the Beaufort Sea surveys  
490 (Fig. 7f).

491

## 492 **4. Discussion**

493

### 494 *4.1. Environmental variables and epibenthic invertebrate biomass*

495

496 The epibenthos in the Arctic's Barrow Canyon are both taxonomically and functionally diverse  
497 reflecting the high levels of production and the confluence of three water masses into the canyon. The  
498 environmental variables used in this study accounted for a moderate portion of the variance (<47%) in  
499 benthic community structure and these results generally aligned with recent studies in the northeast  
500 Chukchi and Beaufort seas. In this study, depth was an important factor in the deeper Beaufort Sea  
501 stations (Beaufort UN) in that some of the largest biomass estimates from the Beaufort survey occurred  
502 at the deepest depths and this result was not entirely due to gear differences (Rand and Logerwell,  
503 2011). Ravelo et al. (2015) also showed depth was an important factor in structuring the benthic  
504 invertebrate community of the Beaufort Sea shelf and the northeastern Chukchi Sea. In addition,  
505 previous studies also showed correlative relationships between water depth and temperature and the  
506 structuring of benthic communities (Blanchard et al., 2013; Ravelo et al., 2014).

507 Although bottom hardness measurements were not available for the Beaufort Sea in our study,  
508 sediment characteristics are also important factors in structuring the epibenthic communities on the  
509 Beaufort Sea shelf (Ravelo et al., 2015) and were influential in the northeast Chukchi Sea, both in our  
510 study and Ravelo et al. (2014). In this region, it is well documented that variation in current velocities  
511 can act to deposit or carry finer sediments downstream (Darby et al., 2009); in this study, we noted that  
512 there was a decrease in bottom hardness on the north part of the Chukchi shelf, suggesting this part of

513 the study area was comprised of finer sediments. This was corroborated by Grebmeier and Cooper  
514 (2014) who reported that sediment becomes finer from the west side of Barrow Canyon, onto the  
515 offshore Chukchi (Fig. 8). One of the variables we examined that represented current velocity in our  
516 study was “speed (velocity) on the day of sampling” and the results were narrowly insignificant in the  
517 Chukchi Study area ( $p=0.059$ ). In this study area of the Chukchi Sea, current velocity does coincide with  
518 the Pacific-origin WW (PWW) that flows from the northeastern shelf of the Chukchi Sea but then shifts  
519 from the west side of Barrow Canyon to the eastern side as it heads northward into the Pacific Arctic  
520 Basin (Gong and Pickart, 2015). This water mass flow erodes the fine sediment especially in the central  
521 Canyon and leaves coarser sediments (Pisareva et al., 2015).

522 Our analysis for the Chukchi Sea shows that the faunal distribution patterns are in part related  
523 to these sediment and associated current velocity patterns, but the moderate to low correlation factors  
524 suggest that other factors, such as competitive interactions, may also influence faunal distribution  
525 patterns as examples illustrate here. The coarser sediment and higher flow is associated with taxa that  
526 are larger bodied such as the basket star, *Gorgonocephalus* spp., gastropods, and sea stars (Asteroidea).  
527 The basket star, *Gorgonocephalus* spp., is known to inhabit areas of high current since they filter  
528 organisms from the water column (Patent, 1970). In the Chukchi Sea, *Gorgonocephalus* spp., was  
529 almost exclusively located in this higher current flow (i.e. bottom hardness and Mean Year Speed were  
530 correlated). The dominance of predatory sea stars within this PWW and coarser sediment coincides with  
531 both the absence of snow crabs, possibly due to competitive interactions, and a marked increase in  
532 nutrient rich waters transported from the Pacific into Barrow Canyon (Grebmeier et al., 2006). Another  
533 example of faunal changes with sediment and current velocity patterns is the presence of the filter-  
534 feeding sea cucumber, *Psolus peronii*. This species of sea cucumber occurred in high abundances (Figs. 1  
535 and 3) in areas of higher current velocity and increased bottom hardness (Fig. 2). The predatory lyre  
536 crab, *Hyas coarctatus*, also occurs primarily west and on the Chukchi Sea Shelf and does not co-occur

537 with the basket star *Gorgonocephalus* spp.; possibly, this may indicate avoidance of sea stars and  
538 gastropods due to competition and/or a preference for finer sediment and lower current velocities.  
539 Only four hauls captured the deposit feeding mud star, *Ctenodiscus crispatus*, in the northeast corner of  
540 the Chukchi Sea study area. This result may indicate that this portion of the Chukchi Sea study area may  
541 have the finest sediment and lowest current velocities as supported in Figs. 2 and 8. The brittle star  
542 *Ophiura sarsii* occurred in very low numbers in the northeastern Chukchi Sea survey even though it was  
543 dominant in several other studies in the Chukchi Sea (Frost and Lowry, 1983; Ambrose et al., 2001;  
544 Feder et al., 2005; Bluhm et al., 2009; Ravelo et al., 2014). This does not appear to be an artifact of the  
545 sampling method because this species was captured with the same gear in the Beaufort Sea UN hauls.  
546 Possibly, this may be due to competitive interactions between these large, predatory taxa in the central  
547 part of Barrow Canyon.

548         We observed another taxonomic transition between the Barrow Canyon slope in the Beaufort  
549 Sea and the Beaufort Sea Shelf. There is higher benthic biomass on the Beaufort Sea slope and a shift in  
550 dominant taxa between the Beaufort slope (brittle stars and snow crab) and the Beaufort Shelf (sea  
551 cucumbers, mussels, mud stars, etc.). This taxonomic transition coincides with a transition from the  
552 PWW and Chukchi summer water (CSW) entering Barrow Canyon in the Chukchi Sea to both the  
553 Beaufort shelfbreak jet <200 m, and the warmer more saline Atlantic water that dominates depths >200  
554 m along the Beaufort Sea slope (Pickart, 2004; Weingartner et al., 2005b; Gong and Pickart, 2015).  
555 Unlike the Chukchi Sea portion of Barrow Canyon, the brittle star *Ophiura sarsii*, and the snow crab,  
556 *Chionoecetes opilio*, dominate these deeper depths (>200 m) that exit Barrow Canyon and lead into the  
557 deep Arctic basin. Our results also illustrated an inverse relationship between depth and current velocity  
558 in that these deeper basin stations also experience, on average, lower currents than those stations on  
559 the Beaufort slope and shelf. Although we do not know the exact mechanism influencing these  
560 distributions, they are consistent with previous findings by Frost and Lowry (1983) and Ravelo et al.



561 (2015), and we hypothesize that *O. sarsii* and snow crabs prefer the warmer, slower, and saltier Atlantic  
562 influenced water.

563

#### 564 4.2. Patterns in biological and functional traits

565

566 Our two surveys in the Chukchi and Beaufort seas encompass most of Barrow Canyon, sharing  
567 some of the hydrographic characteristics, but they only share a portion of the biomass-dominant taxa.  
568 Because of this result, we asked if these two study areas were, in fact, functionally different or shared  
569 similarities. Although the regional comparison is somewhat biased by the different mesh size in the  
570 Beaufort Sea LN survey, we were able to shed light on the variability of the biological traits both within  
571 and adjacent to Barrow Canyon. The fact that there was not a biological trait or trait modality exclusive  
572 to either system infers that these two systems share similarities in their biological processes which may  
573 be surprising given the differences in taxonomy between the two study areas. This is one of the  
574 fundamental benefits to a biological traits analysis; even though the taxonomic composition and  
575 distribution is different, the underlying functional processes are similar.

576 Of the ten biological traits examined, however, four traits and their respective trait modalities  
577 were considered variable enough within their respective study area to further examine patterns. The  
578 four biological traits, Body Design, Body Form, Feeding Mechanism, and General Prey Type share some  
579 characteristics. For example, the trait modality “soft/protected” often coincides with the trait  
580 modalities “erect”, and “filter/suspension” feeding. Similar to the connection in water masses and  
581 taxonomic distribution, the variability we observed in trait distribution can in part be attributed to  
582 habitat heterogeneity and transitions (e.g. sediment, hydrography) that occur in this region. The  
583 Chukchi Sea survey area contained a high prominence of filter/suspension feeders in line with the  
584 convergence of the PWW and increased current velocities as this water mass accelerates north into

585 Barrow Canyon. High current velocities tend to contain high loads of suspended particles that serve as  
586 food for these filter feeders. These filter/suspension feeders maintain a presence in Barrow Canyon as it  
587 enters into the Beaufort and extends onto the shelf with the PWW transitioning into the Beaufort  
588 shelfbreak jet. The filter/suspension feeders do not extend to the Barrow Canyon slope or waters >200  
589 m where deposit feeders dominate. This is likely related to the lower suspended particle content in  
590 slowing waters and the fine-grained, less eroded sediment that is more suitable for deposit feeders.  
591 This supports the taxonomic distribution results and again highlights an important transition zone from  
592 the fast flowing Beaufort Sea shelf environment (<200 m) dominated by filter/suspension traits to one  
593 dominated by the deposit feeding trait within the deeper Atlantic water. These relationships between  
594 feeding mechanism and flow velocity match results of a study by Pisareva et al. (2015) that used the  
595 feeding modes of benthic fauna and sediment characteristics as indicators of hydrographic flow on  
596 varying time scales. They also concluded that, in general, benthic suspension feeders were associated  
597 with regions of stronger flow and deposit feeders with regions with weaker flow (Pisareva et al., 2015),  
598 and that these faunal patterns were reflective of the long-term flow velocities. Further, Pisareva et al.  
599 (2015) found that there was a higher proportion of suspension feeding fauna in the central Barrow  
600 Canyon and a higher proportion of deposit feeding taxa outside the Canyon based on flow speed and  
601 sediment grain size. This shift in both taxa and traits from the head of Barrow Canyon in the Chukchi  
602 Sea to the Beaufort Sea shelf occurs within an oceanographically complex region. The hydrography at  
603 the head of Barrow Canyon in the Chukchi Sea hosts both vertical and horizontal transition zones that  
604 include lateral fronts, vertical stratifications and the influence of swift flows interacting with steep  
605 bottom topography gradients (Fig. 2).

606           Some biological traits had little variability in their distribution within a survey but differed  
607 between surveys. For example, those traits representing reproduction modes and early life history  
608 stages (Propagule Dispersal and Larval Development) showed little to no variation within a survey. It is

609 possible that these traits are less influenced by currents, water mass properties, and sediment  
610 composition than morphological or feeding traits. In contrast to this result, between-survey differences  
611 included a high proportion of “direct” development in the Chukchi Sea survey that was observed to a  
612 lesser degree in the Beaufort Sea. This trait may contribute to some of the differences we observed in  
613 the taxonomy between the Chukchi and Beaufort parts of Barrow Canyon. The retention of “direct”  
614 developers (low dispersal) at the head of Barrow Canyon may cause these taxa to remain in the Chukchi  
615 Sea and not be advected into the Beaufort Sea. Whether the prominence of taxa with this Larval  
616 Development trait at the head of Barrow Canyon are fostered by conditions such as nutrients and  
617 upwelling, or whether these differences are driven by competitive interactions within the community  
618 itself, is difficult to determine. Although we do not quantitatively compare the absolute biomass of  
619 these traits between surveys (e.g. there is “more” of a trait in a survey), the fact that some of these trait  
620 modalities are evenly distributed within a survey is interesting. Life history strategies in marine benthic  
621 invertebrates, in particular reproduction, are especially complex processes with multiple tradeoffs that  
622 can translate into differences, for example, in fecundity among closely related species inhabiting  
623 different habitats (Llodra, 2002). This suggests the possibility that the processes affecting those taxa at  
624 the head of Barrow Canyon are not the same as those in the Beaufort Sea side of Barrow Canyon in  
625 depths less than 200 m, even though the water mass transport, bathymetry, and current velocities  
626 appear to be similar and given these sites are within only 60 km of each other.

627

#### 628 *4.3. Study limitations and recommendations for future studies*

629

630 The limitations of our functional traits analysis is that in the Arctic, life history and other  
631 information on benthic invertebrates is particularly sparse. In the absence of life history traits for many  
632 of these Arctic species, our approach was, therefore, to apply known trait modalities from those species

633 within the same genus or family. Given the lack of species-specific knowledge, we used traits that  
634 focused on the general functions of an organism, like Feeding Mechanism, rather than those traits  
635 describing complex processes like growth rates. We recommend that future studies on impacts of  
636 climate change and other human impacts also include those traits characteristic of Arctic fauna such as  
637 (slow) growth rates, (high) longevity and (late) age at maturity. Also, the focus of this study was on the  
638 top 90% by biomass of the epibenthic invertebrates; this eliminated 80-90% of the taxa that were  
639 captured in the surveys, shifting the focus to organisms that make up the largest biomass and for which  
640 information on biological traits could be gathered. The weakness in focusing on only a relatively small  
641 number of taxa, in this case <20 per survey area, is that information was lost on taxa or species that may  
642 have been common to all stations but comprised a very small fraction of the total biomass at that  
643 station and across the survey area. These taxa or species could be filling a small, but important,  
644 ecological niche in the overall function of a local community. The BTA approach could also be refined by  
645 using fuzzy instead of binary coding for the traits since many species exhibit more than one trait  
646 modality within a trait category. For example, most sea stars were placed in the “predator” modality as  
647 their primary method of feeding, but they can also be “opportunistic/scavengers” and “deposit  
648 feeders”; fuzzy coding would allow better resolution of the complexity of their functional contributions  
649 at the community level.

650

#### 651 *4.3 Conclusions and monitoring recommendations*

652

653 It is well documented that the effects of climate change are accelerated in the Arctic (Pithan and  
654 Mauritsen, 2014). What remains unclear, is the magnitude in which these rapidly changing conditions  
655 will affect marine life in the coming years. For example, Cross et al. (this issue) has shown that  
656 decreased saturation rates of calcium carbonate (e.g. ocean acidification) from anthropogenic changes

657 in atmospheric carbon dioxide, has fundamentally altered the duration and intensity of the PWW. Both  
658 in- and epi- faunal invertebrates are particularly vulnerable to changes in ocean acidification. Since the  
659 PWW is the primary source of transport from the Pacific to the Arctic Basin, through Barrow Canyon, a  
660 well-documented biological “hotspot” for micro- to macro- fauna (Moore et al., 2014; Moore and  
661 Stabeno, 2015; Grebmeier et al., 2015), it is an especially important region of the Pacific Arctic to  
662 monitor for the effects of climate change. A traits analysis, along with traditional taxonomic methods,  
663 has become a useful tool in ecosystem monitoring and management (Usseglio-Polatera et al., 2000;  
664 Doledec et al., 2006; Tomanova et al., 2008). In these studies, researchers used community composition  
665 analyses (taxonomic and/or traits) and changes therein as a direct reflection of ecosystem health.  
666 Although changes in taxonomic diversity can be indicative of change that is occurring, extending this to  
667 analyzing biological traits makes a direct connection between environmental processes and the  
668 ecological functioning of the systems organisms.

669         This study improved the knowledge of epibenthic communities in the Barrow Canyon area,  
670 which has previously not been well resolved nor their connections to the complex regional  
671 hydrodynamics. This effort contributes to the baseline data in terms of both species and functional  
672 diversity of the epibenthic invertebrate communities within this region. Monitoring the epibenthic  
673 invertebrate community at these “hotspots” is in line with the recently established Distributed  
674 Biological Observatory (Grebmeier et al. 2010, 2015), the US-wide Marine Biodiversity Observation  
675 Network (MBON) including its Arctic component and the Conservation of Arctic Flora and Fauna’s  
676 Circumpolar Biodiversity Monitoring Program. Benthic taxa can be excellent proxies for change over  
677 time because they are relatively long lived at high latitudes and can be indicative of changes in sediment  
678 characteristics and water mass influences due to warming, acidification, and the loss of sea ice (Kortsch  
679 et al., 2012; Grebmeier et al., 2015a; Cross et al., this issue). We recommend biological trait analysis  
680 approaches be included in such monitoring efforts.

681

682

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684

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918 Table 1 The taxa listed comprise 90% of the total biomass of epibenthic invertebrates, used in all  
 919 analyses, separated by survey and, within the Beaufort survey, by lined net (LN) or unlined net (UN). The  
 920 mean is the cube-root transformed CPUE kg/km<sup>2</sup> with the standard deviation kg/km<sup>2</sup>.  
 921

Species	Common name (class)	Survey	Mean kg/km <sup>2</sup>	Std dev kg/km <sup>2</sup>
<i>Beringius beringii</i>	sea snail (gastropod)	Chukchi	2.22	1.56
Bryozoa	bryozoa	Chukchi	1.42	2.15
<i>Crossaster papposus</i>	sea star (asteroidea)	Chukchi	3.52	1.27
<i>Ctenodiscus crispatus</i>	mud star	Chukchi	1.60	3.25
<i>Eualus</i> sp.	shrimp	Chukchi	0.57	1.82
<i>Gersemia rubiformis</i>	coral	Chukchi	2.26	3.08
<i>Gorgonocephalus</i> spp.	basket star (ophiuroid)	Chukchi	4.79	6.96
<i>Hyas coarctatus</i>	lyre star (crab)	Chukchi	2.34	2.40
<i>Musculus discors</i>	mussel	Chukchi	1.40	4.21
<i>Neptunea heros</i>	sea snail (gastropod)	Chukchi	3.61	2.65
<i>Neptunea ventricosa</i>	sea snail (gastropod)	Chukchi	1.84	2.05
<i>Pagurus trigonocheirus</i>	hermit crab	Chukchi	2.17	2.96
<i>Psolus peronii</i>	sea cucumber	Chukchi	3.00	6.76
<i>Pyrulofusus deformis</i>	sea snail (gastropod)	Chukchi	2.22	1.85
<i>Solaster dawsoni arcticus</i>	sea star (asteroidea)	Chukchi	4.21	2.98
<i>Strongylocentrotus droebachiensis</i>	sea urchin	Chukchi	1.73	3.25
<i>Urticina crassicornis</i>	sea anenome	Chukchi	1.76	2.77
Actiniaria	sea anenome	Beaufort LN	5.01	7.32
<i>Buccinum polare</i>	sea snail (gastropod)	Beaufort LN	5.86	5.30
<i>Chionoecetes opilio</i>	snow crab (crab)	Beaufort LN	16.16	9.57
<i>Ctenodiscus crispatus</i>	mud star	Beaufort LN	9.32	8.93
<i>Gorgonocephalus</i> spp.	basket star (ophiuroid)	Beaufort LN	2.79	5.61
<i>Musculus</i> sp.	mussel	Beaufort LN	5.97	11.32
<i>Neptunea</i> sp.	sea snail (gastropod)	Beaufort LN	6.89	3.12
* <i>Ophiura</i> sp.	brittle star (ophiuroid)	Beaufort LN	25.55	15.69
<i>Psolus peronii</i>	sea cucumber	Beaufort LN	5.31	6.89
<i>Strongylocentrotus</i> sp.	sea urchin	Beaufort LN	3.48	6.60
<i>Voluta middendorffii</i> and <i>Habevolutopsius</i>	sea snail (gastropod)	Beaufort LN	7.05	4.42
<i>Chionoecetes opilio</i>	snow crab (crab)	Beaufort UN	2.78	1.77
<i>Ctenodiscus crispatus</i>	mud star	Beaufort UN	3.48	4.21
<i>Halocynthia aurantium</i>	sea peach	Beaufort UN	6.53	5.79
<i>Hyas coarctatus</i>	lyre crab (crab)	Beaufort UN	4.16	2.04
<i>Neptunea heros</i>	sea snail (gastropod)	Beaufort UN	1.44	3.07
<i>Pagurus trigonocheirus</i>	hermit crab	Beaufort UN	4.72	2.06
<i>Polymastia</i> sp.	sponge (demosponge)	Beaufort UN	2.33	4.98
<i>Psolus peronii</i>	sea cucumber	Beaufort UN	4.25	4.65
<i>Pyrulofusus deformis</i>	sea snail (gastropod)	Beaufort UN	2.36	2.58
<i>Stomphia</i> sp.	sea anenome	Beaufort UN	4.31	1.67
<i>Strongylocentrotus</i> sp.	sea urchin	Beaufort UN	3.46	5.45
<i>Vulcanella</i> sp.	sponge (demosponge)	Beaufort UN	3.86	6.79
*95% of the <i>Ophiura</i> sp. was comprised of <i>Ophiura sarsi</i>				

922  
 923

924 Table 2 The biological traits for those taxa in Table 1 used in the FCA analysis. Within each Biological  
 925 Trait are several Trait Modalities; each unique combination of Trait and Modality is assigned a Trait  
 926 Code.  
 927

Biological Trait	Trait Modalities	Trait Code
Size	small (<10 g)	S1
	medium (10-50 g)	S2
	large (>50 g)	S3
Body Design	soft	BD1
	soft/protected	BD2
	endoskeleton	BD3
	hard exoskeleton	BD4
	hard shell	BD5
Body Form	erect	BF1
	round	BF2
	flat	BF3
General Prey Type	herbivore	PT1
	omnivore	PT2
	carnivore	PT3
Feeding Mechanism	deposit feeder	FM1
	filter/suspension	FM2
	opportunist/scavenger	FM3
	predator	FM4
Degree of attachment	none	DA1
	semi-permanent	DA2
	permanent	DA3
Mobility	sessile	M1
	motile	M2
Propagule Dispersal	pelagic	PD1
	substrate	PD2
Reproductive Mode	sexual/release eggs	RM1
	sexual/release larvae	RM2
	sexual/brood	RM3
Larval Development	direct	LD1
	planktotrophic	LD2
	lecithotrophic	LD3

928 Table 3 Results of the CCA analysis on species abundance constrained by environmental variables. The  
 929 observed variance accounted for by the variables are shown in percent for both axes CCA1 and CCA2.  
 930 Variables that were used in the CCA are listed under “Variables Full Model” and the corresponding  
 931 significance level from the ANOVA test are listed under “Significance (p<0.05)”; significant values are in  
 932 bold.

933

Survey	CCA 1	CCA 2	Variables Full Model	Significance (p<0.05)
Chukchi Survey	12%	5%	Bottom Hardness	<b>0.001</b>
			Bottom Depth	0.085
			East Velocity	0.140
Beaufort LN Survey	24%	22%	Bottom Temperature	<b>0.004</b>
			Bottom Depth	<b>0.004</b>
			Mean Year Speed	<b>0.010</b>
			North Velocity	0.279
Beaufort UN Survey	28%	20%	Bottom Depth	<b>0.020</b>
			Mean Year Speed Var	0.168
			North Velocity	<b>0.051</b>

934 Table 4 Correlation Ratios for the FCA ordination of biological traits. The proportion of variance on each  
 935 axis that can be explained by the Trait Modalities (Table 2) within each Biological Trait. Ratios greater  
 936 than 20% on axis 1 are in bold and less than 5% on axis 1 in italics. Biological Traits that are mapped in  
 937 Fig. 7 are shown in bold text. The respective eigenvalues for each survey are given for each axis. The  
 938 total inertia (in parentheses) represents the total variance accounted for in an ordination. The percent  
 939 of variance that can be explained by each axis is listed by survey and axis.

940

Survey	Biological Traits	Axis 1	Axis 2
Chukchi	Size	0.110	0.070
Chukchi	<b>Body Design</b>	<b>0.237</b>	0.030
Chukchi	<b>Body Form</b>	<b>0.218</b>	0.013
Chukchi	<b>General Prey Type</b>	<b>0.218</b>	0.102
Chukchi	<b>Feeding Mechanism</b>	0.143	0.193
Chukchi	Degree of attachment	<i>0.028</i>	0.083
Chukchi	Mobility	<i>0.028</i>	0.083
Chukchi	<b>Propagule Dispersal</b>	<i>0.033</i>	0.010
Chukchi	Reproductive Mode	0.079	0.007
Chukchi	<b>Larval Development</b>	<i>0.002</i>	0.051
Percent of Variance	(Total Inertia)	37%	21% (0.299)
Eigenvalues		0.109	0.064
Beaufort LN	Size	0.082	0.035
Beaufort LN	<b>Body Design</b>	<b>0.225</b>	0.072
Beaufort LN	<b>Body Form</b>	0.196	0.022
Beaufort LN	<b>General Prey Type</b>	<b>0.207</b>	0.054
Beaufort LN	<b>Feeding Mechanism</b>	<b>0.202</b>	0.025
Beaufort LN	Degree of attachment	0.172	0.022
Beaufort LN	Mobility	0.179	0.015
Beaufort LN	<b>Propagule Dispersal</b>	<i>0.000</i>	0.001
Beaufort LN	Reproductive Mode	<i>0.022</i>	0.130
Beaufort LN	<b>Larval Development</b>	<i>0.021</i>	0.178
Percent of Variance	(Total Inertia)	51%	22% (0.253)
Eigenvalues		0.130	0.055
Beaufort UN	Size	0.141	0.107
Beaufort UN	<b>Body Design</b>	0.067	0.119
Beaufort UN	<b>Body Form</b>	0.084	0.054
Beaufort UN	<b>General Prey Type</b>	0.120	0.036
Beaufort UN	<b>Feeding Mechanism</b>	<b>0.235</b>	0.077
Beaufort UN	Degree of attachment	0.151	0.003
Beaufort UN	Mobility	0.151	0.003
Beaufort UN	<b>Propagule Dispersal</b>	<i>0.025</i>	0.019
Beaufort UN	Reproductive Mode	<i>0.047</i>	0.020
Beaufort UN	<b>Larval Development</b>	<i>0.049</i>	0.018
Percent of Variance	(Total Inertia)	55%	24% (0.193)
Eigenvalues		0.107	0.045

941 Figure captions

942 Fig. 1 The catch-per-unit-effort (CPUE metric tons (MT) wet weight/km<sup>2</sup>) by hauls in and near Barrow  
943 Canyon. The Chukchi Sea survey was in 2013 (yellow) and the Beaufort Sea LN (green), and UN (orange)  
944 surveys were in 2008; The Beaufort Sea LN refers to hauls sampled with a net liner and UN refers to  
945 those hauls sampled with no net liner. All hauls are labeled in white text for reference. The CPUE scale  
946 is different for the Beaufort Sea LN hauls; the lowest and highest CPUE estimate for the Beaufort UN and  
947 Chukchi hauls also varies. Note: Haul 22, Beaufort Sea UN survey, is masked by haul 10, Beaufort Sea LN  
948 survey due to a lower CPUE estimate.

949 Fig. 2 Average near bottom current velocities; results were produced by a 3-dimensional ocean and ice  
950 circulation numerical hindcast model, which was integrated over 2005 to 2011 with the Regional Ocean  
951 Modeling System (ROMS) framework. Large arrows were overlaid to show general current trajectories.

952 Fig. 3 Benthic invertebrate species composition for the top 90% by biomass (CPUE kg/km<sup>2</sup>) for the  
953 Chukchi Sea, Beaufort Sea LN (pie charts are shown with thicker outline), and Beaufort Sea UN hauls.  
954 The Beaufort Sea LN refers to hauls sampled with a net liner and UN refers to those hauls sampled with  
955 no net liner. Each pie chart represents one haul. Several taxa were lumped together under a common  
956 name for better map interpretation (e.g., sea stars).

957 Fig. 4 Results of the canonical correspondence analysis (CCA) on species biomass (CPUE kg/km<sup>2</sup>) for the  
958 Chukchi Sea (a), Beaufort Sea LN, and Beaufort Sea UN surveys. The Beaufort Sea LN refers to hauls  
959 sampled with a net liner and UN refers to those hauls sampled with no net liner. The hauls (numbered  
960 black dots) and environmental variables (arrows) are shown on each plot. Species associated with the  
961 hauls are in light gray text. Significant variables are in bold text. The label "Bot" refers to "bottom". The  
962 percentages refer to the amount of variance explained by each axis.

963 Fig. 5 Results of the fuzzy correspondence analysis (FCA) on the biological traits for the Chukchi Sea (a  
964 and b) (asterisk), Beaufort Sea LN (c and d) (black dots), and Beaufort Sea UN (d and e) (triangles)  
965 surveys. The Beaufort Sea LN refers to hauls sampled with a net liner and UN refers to those hauls  
966 sampled with no net liner. Figures 5a, 5c, and 5e are the ordination results by haul and Figures 5b, 5d,  
967 and 5f are the ordination results by traits (in light gray text) and aids in the interpretation of the results  
968 in the first column. Hauls that are grouped can be considered similar in the biological traits they exhibit.  
969 Trait codes are written out in full black text; some trait codes are truncated, refer to Table 2 for full



970 listing of traits. Hauls in the black circle indicated significance with bottom hardness in the Chukchi Sea  
971 (5a) and hauls >200 m depth in the Beaufort Sea LN (5c).

972 Fig. 6 Traits score results from the fuzzy correspondence analysis (FCA) on the biological traits for the  
973 Chukchi Sea (asterisk), Beaufort Sea LN hauls (black dots), and Beaufort Sea UN hauls (triangles) surveys.  
974 The Beaufort Sea LN refers to hauls sampled with a net liner and UN refers to those hauls sampled with  
975 no net liner. This figure is and alternative representation of Figures 5b, 5d, and 5f and is a visual  
976 comparison of the variation for each trait, in each survey, with vertical grouping by the Biological Trait  
977 and subsequent Trait Modalities. Note: some trait codes are truncated (e.g., Opp/Scavenger), refer to  
978 Table 2 for full listing of traits.

979 Fig. 7 Biological traits with correlations ratios above 0.20 (a-d) and correlation ratios below 0.05 (e and f)  
980 are shown for hauls in the Chukchi Sea, Beaufort Sea LN (outlined in black), and Beaufort Sea UN  
981 surveys. The Beaufort Sea LN refers to hauls sampled with a net liner and UN refers to those hauls  
982 sampled with no net liner. Each pie chart represents one haul. Note: to illustrate all hauls on one map  
983 some pie charts two hauls from the Beaufort Sea UN survey are slightly displaced from the actual haul  
984 location but a line connecting the chart to the location is shown.

985 Fig. 8 Map of the Chukchi Sea survey area overlaid with the acoustic transects for bottom hardness and  
986 the PacMARS Surface Sediment Parameters (Grebmeier, J., and L. Cooper. 2016. PacMARS Surface  
987 Sediment Parameters. Version 2.0. UCAR/NCAR-Earth Observing Laboratory.  
988 <https://doi.org/10.5065/D6416V3G>). The measure of bottom hardness is from vessel acoustics and is  
989 unitless; higher values imply harder bottom. “Modal Phi Size” refers to the sediment grain size mode.  
990 This figure illustrates the transition from finer to coarser sediment from offshore (lower current velocity)  
991 into Barrow Canyon and onto the shelf, where current velocities are greater.

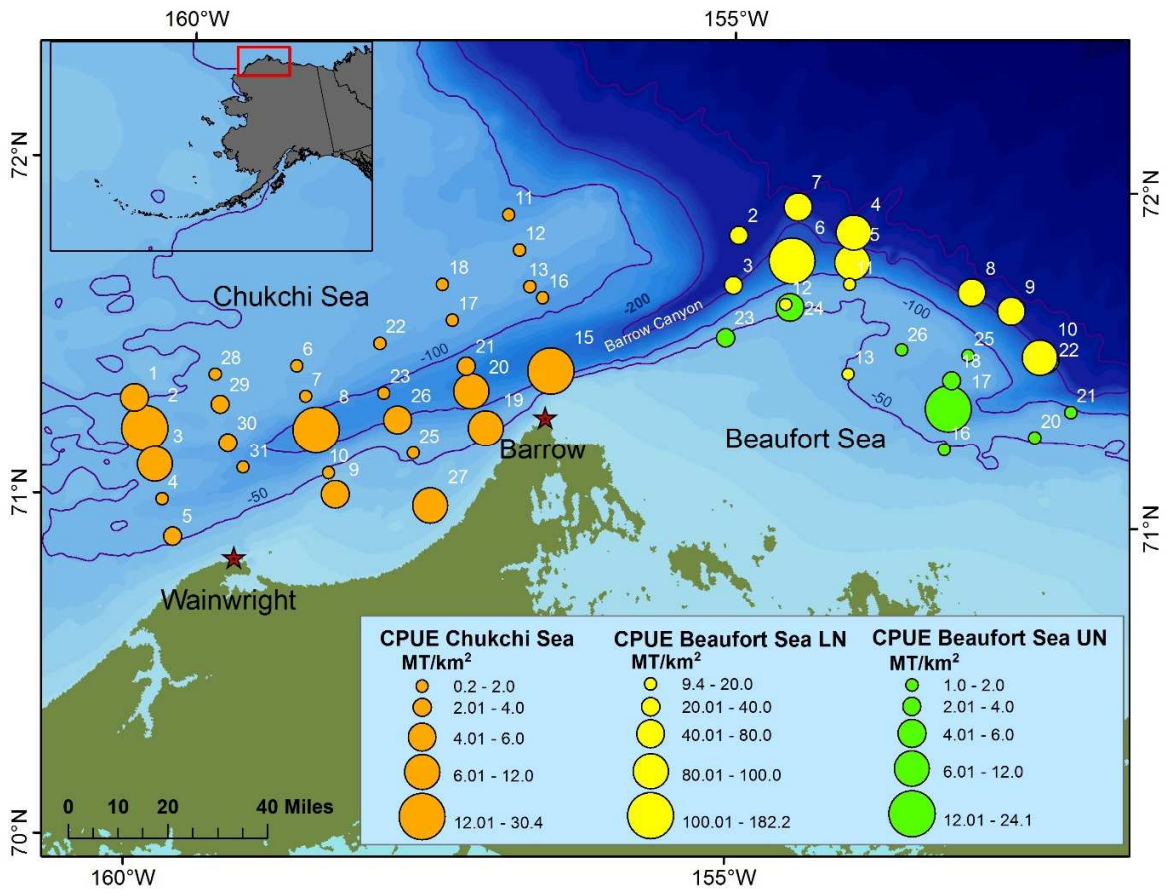


Fig. 1

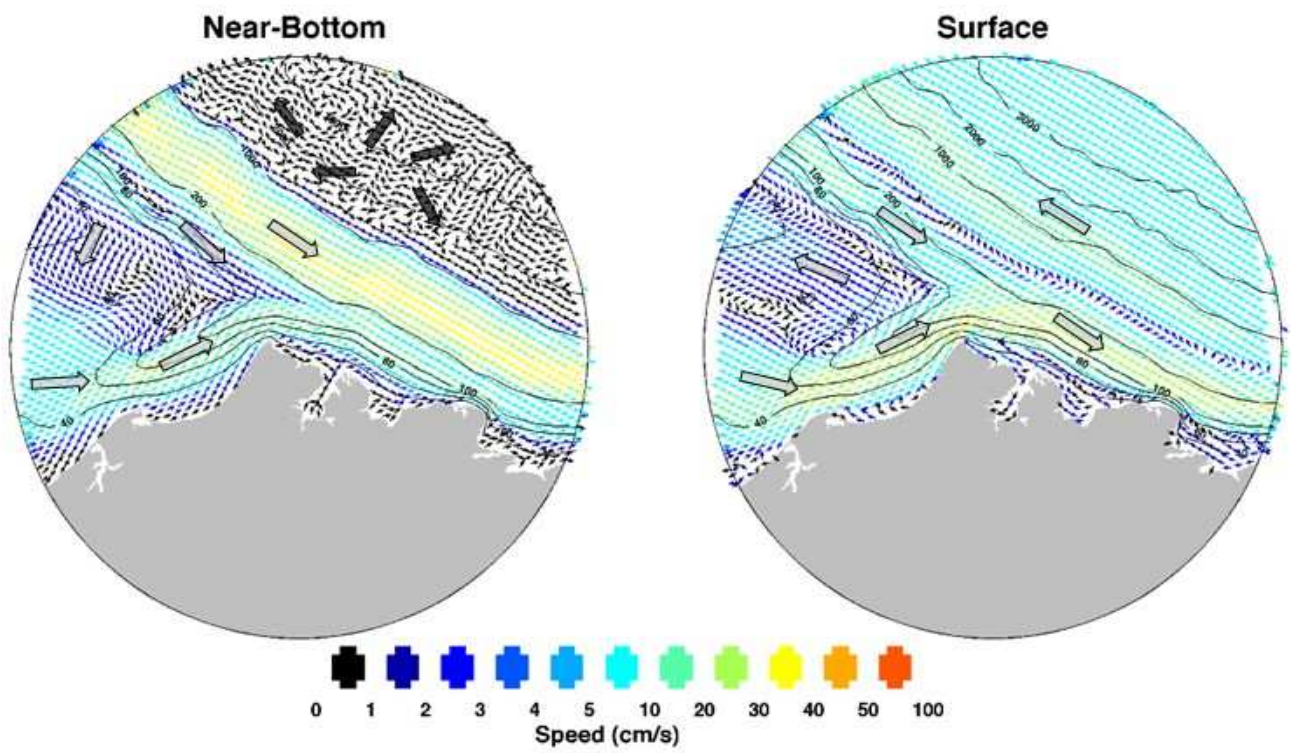


Fig. 2

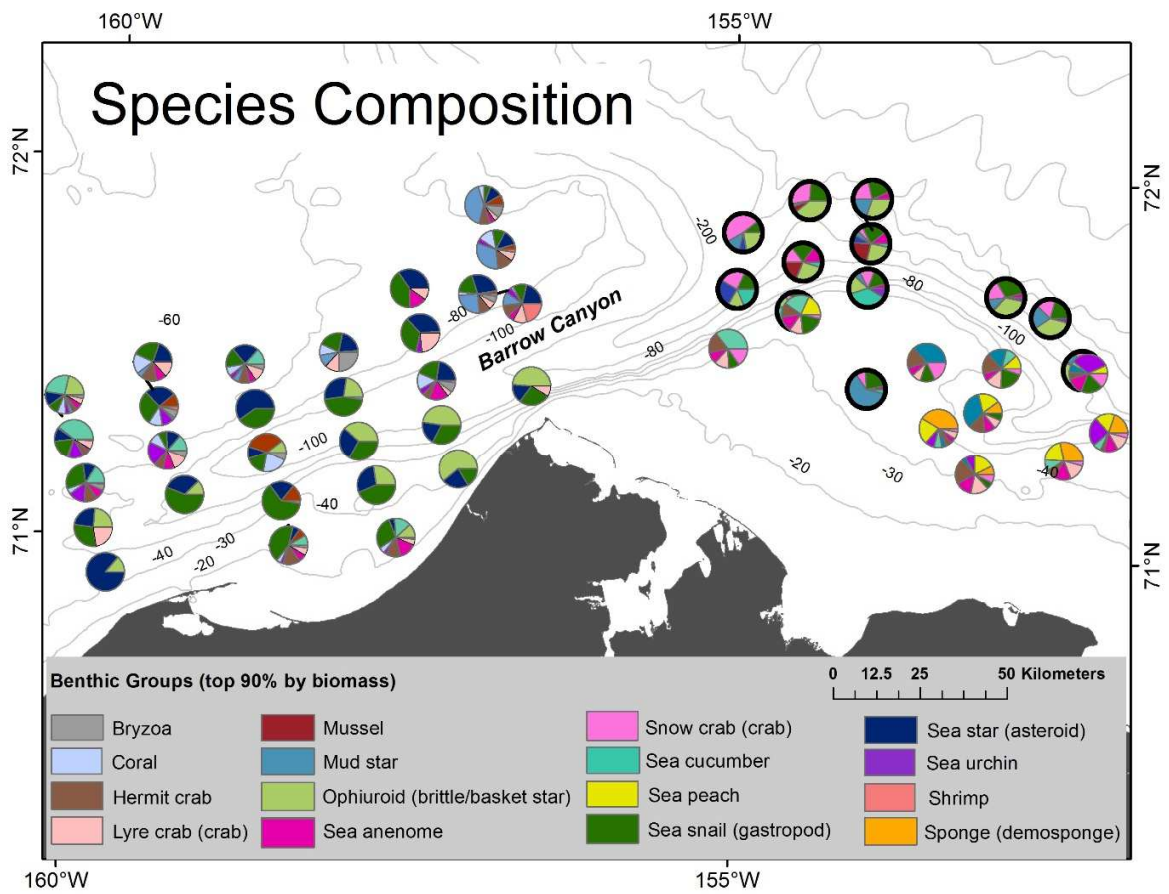


Fig. 3

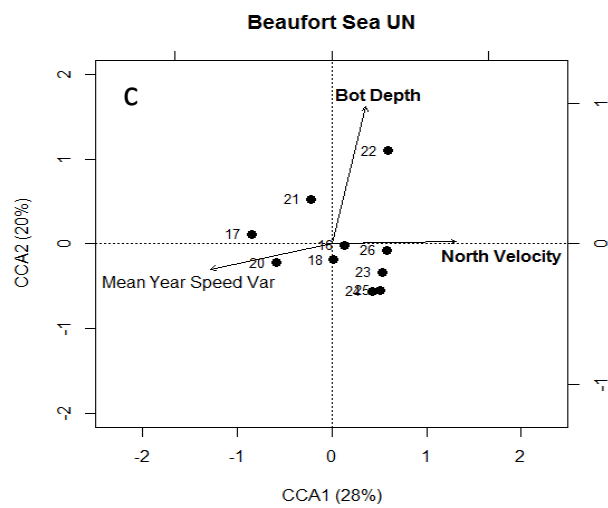
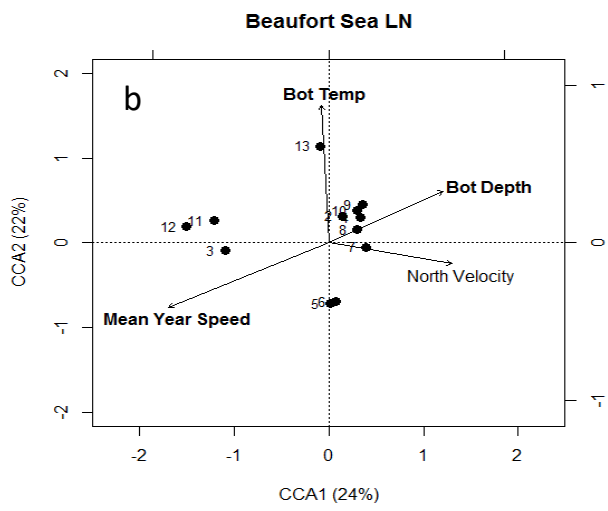
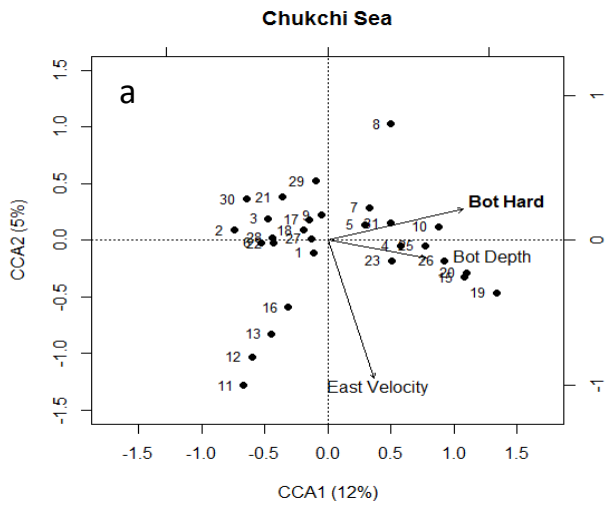


Fig. 4a-c

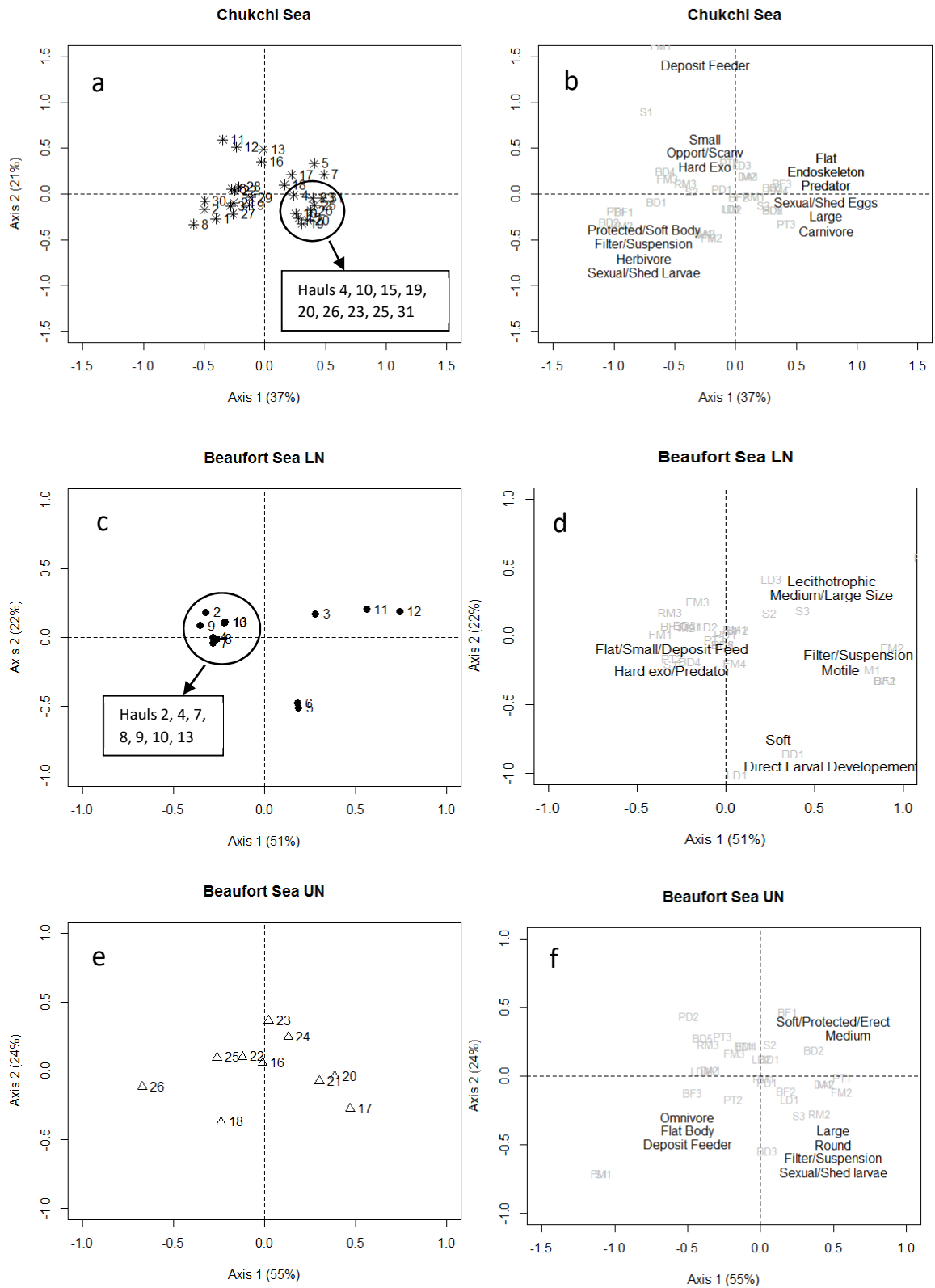


Fig. 5a-f

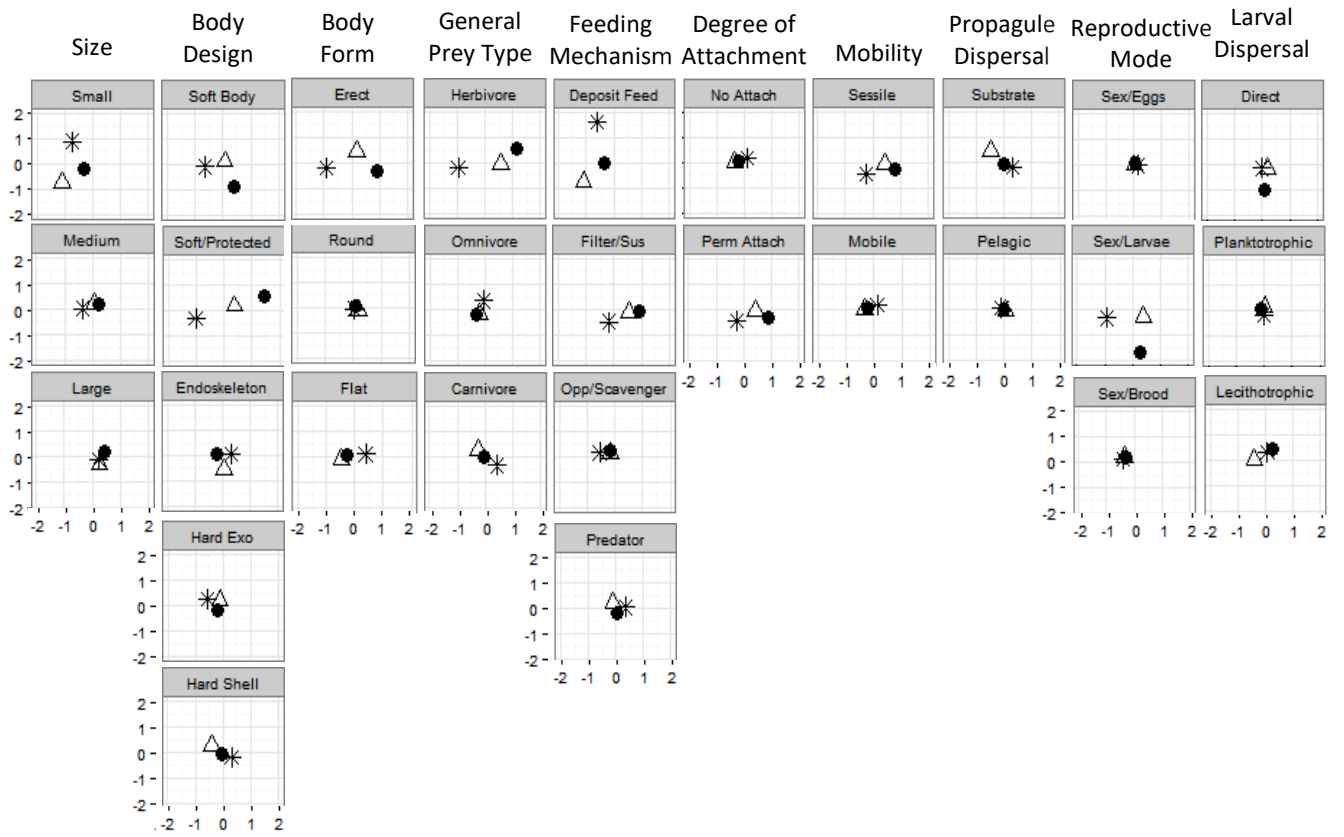


Fig. 6



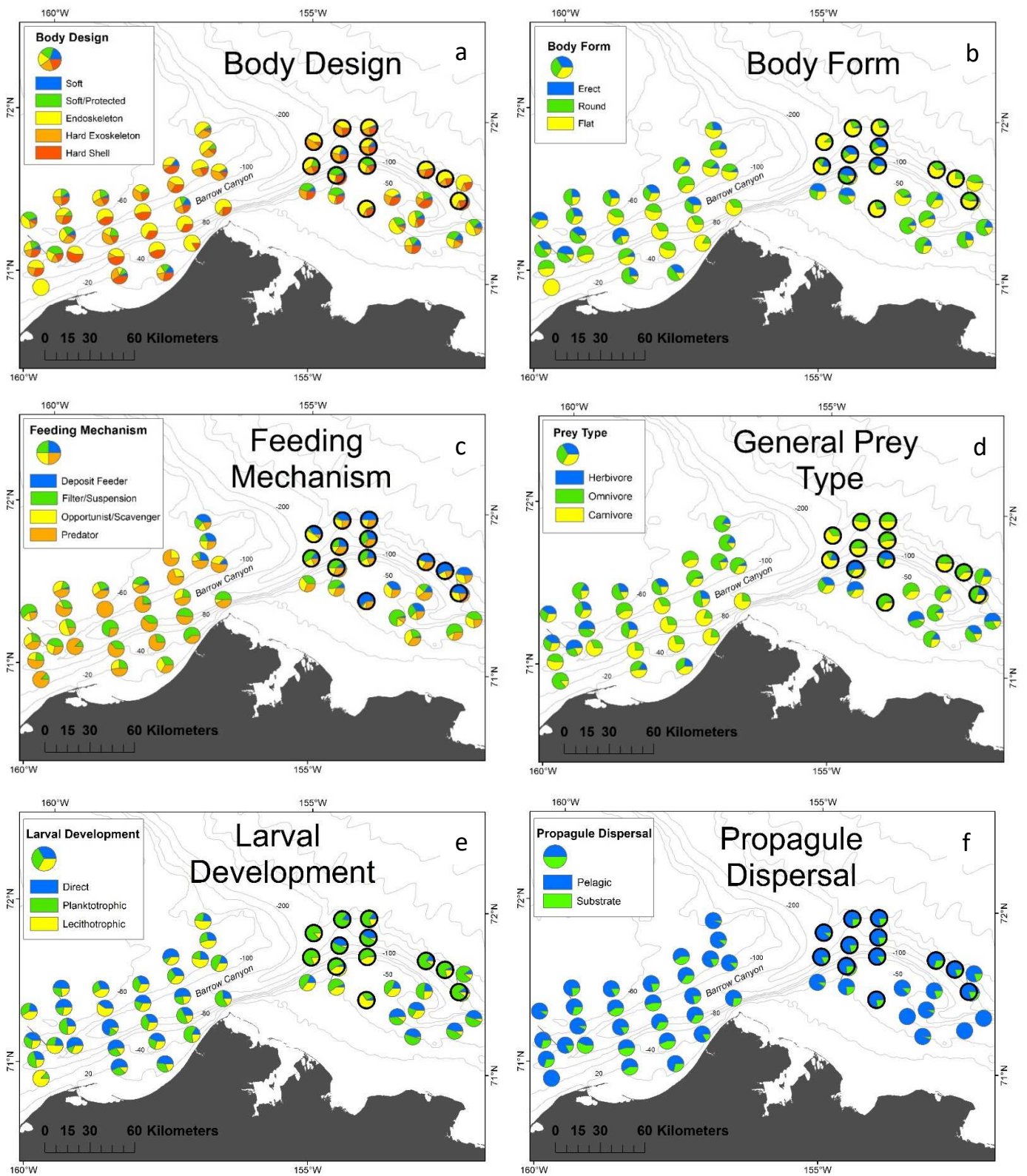


Fig. 7



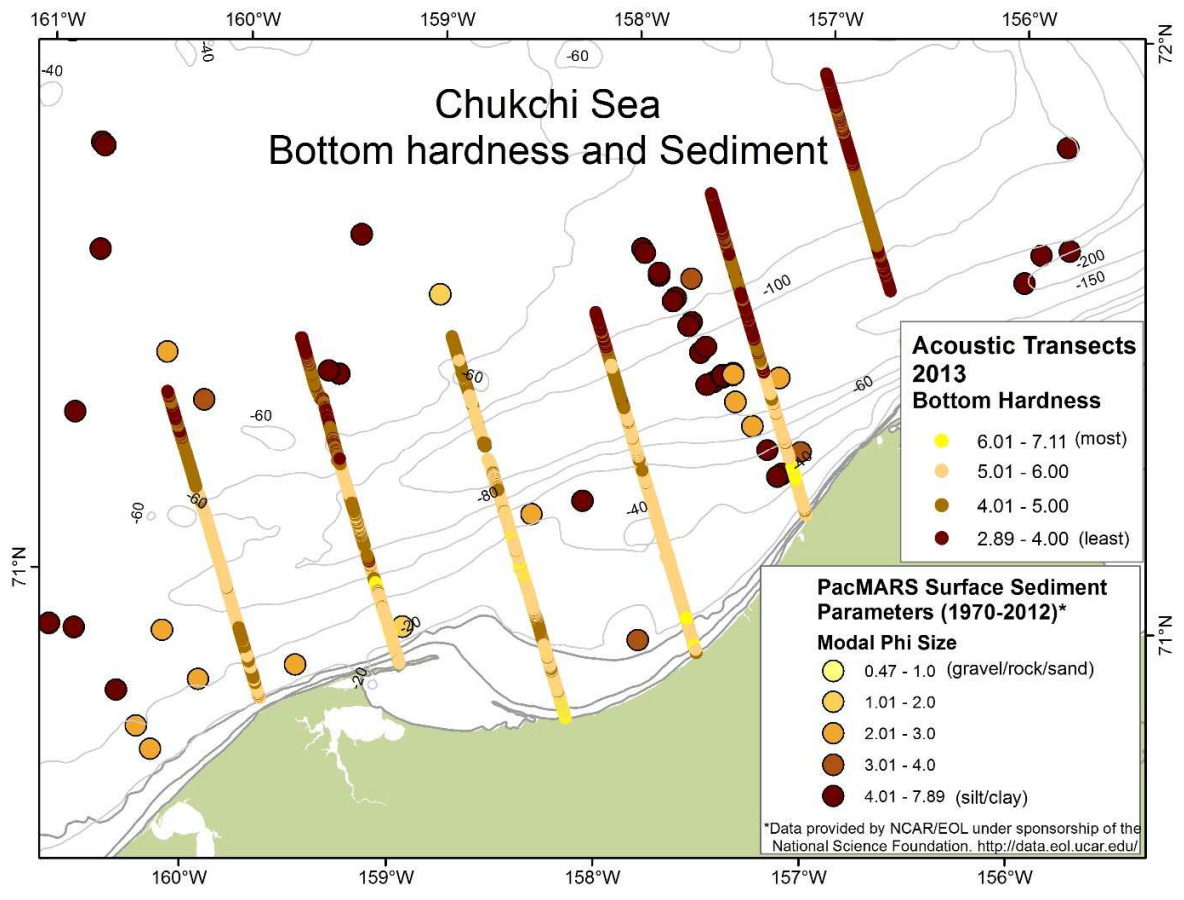


Fig. 8