

1 **Title** Biogeography of epibenthic assemblages in the central Beaufort Sea

2 **Authors** Alexandra M Ravelo<sup>1</sup>, Bodil A. Bluhm<sup>1,2</sup>, Nora Foster<sup>3</sup>, Katrin Iken<sup>1</sup>

3 **Affiliations** <sup>1</sup>College of Fisheries and Ocean Sciences, University of Alaska Fairbanks, Alaska USA

4 <sup>2</sup>Institute of Arctic and Marine Biology, UiT - The Arctic University of Norway, 9037 Tromsø,  
5 Norway, ORCID 0000-0002-4584-7796

6 <sup>3</sup>NRF Taxonomic Services, Fairbanks Alaska USA

7 **Communicating author** Alexandra M Ravelo [amravelo@alaska.edu](mailto:amravelo@alaska.edu), +1 907-738-7039

## 8 **Abstract**

9 Benthic communities change drastically in both biomass and community structure with increasing water  
10 depth on a global scale, attributed to a combination of food supply, environmental drivers, as well as  
11 physiological and competitive capacities. In the Arctic, benthic biogeographic patterns are additionally  
12 thought to be a result of the region's glaciation history. Here, we investigate gross epibenthic biomass  
13 and assemblage structure turnover with water mass from coastal to bathyal depths from 136 beam  
14 trawl samples collected in the Beaufort Sea. We test whether Pacific Boreal Arctic species have their  
15 core distribution in shelf water masses while Atlantic Boreal Arctic species have wider depth ranges.  
16 Gross biomass estimates differed statistically among water masses, with high values mostly under the  
17 influences of the Polar Mixed Layer and Arctic Halocline (outer shelf and upper slope, respectively).  
18 Stations in the Coastal Zone and Canada Basin Deep Water had the lowest biomass. Epibenthic  
19 assemblages also differed significantly among water masses, with high taxon richness in shelf water  
20 masses that decreased considerably with depth. Biomass of benthic taxa with Pacific Boreal Arctic  
21 affinity was essentially limited to the shelf, while Atlantic Boreal Arctic taxa occurred across a broad  
22 depth range, though their biomass increased in deeper water masses for mollusks and echinoderms, but  
23 not for decapods/isopods. Our results confirm earlier evidence of a strong Atlantic-Arctic deep-water  
24 connectivity reaching into the Pacific Arctic region and suggest new arrivals of species from the boreal  
25 Pacific are likely to settle on Pacific Arctic shelves, but are unlikely to invade continental slope and basin  
26 waters in the foreseeable future.

## 27 **Keywords**

28 Arctic, epibenthos, water mass, biomass, biogeography, boreal Arctic taxa

29

## 30 Introduction

31 On a global scale, benthic communities change with increasing water depth in both biomass  
32 (Rex et al. 2006; Wei et al. 2010; Bluhm et al. 2010) as well as community composition patterns (Brandt  
33 1997; Nephin et al. 2014; Ravelo et al. 2015). Food availability, mediated through vertical flux of surface-  
34 produced particles and flux attenuation with depth, is thought to be the primary reason for the  
35 observed biomass decrease with depth (Wei et al. 2010). Change in community composition with depth  
36 is interpreted in the context of a combination of factors rather than merely a direct result of food supply  
37 (Mayer and Piepenburg 1996; Piepenburg 2005). Species-specific depth ranges and underlying reasons  
38 for broad (eurybathic) versus narrow (stenobathic) depth distribution ranges are generally not well-  
39 understood for benthic organisms; however, they are thought to be modulated by local or regional  
40 environmental conditions such as current regimes in concert with physiological constraints, biological  
41 interactions, and a region's history (Gaylord and Gaines 2000; Clarke 2003). Physical properties of water  
42 masses such as temperature influence physiological rates and, hence, distributions patterns of species  
43 (Clarke 1983, 2003). Particular water masses occurring at certain depths also drive propagule supply and  
44 can influence biogeographic distribution of species (Kinlan et al. 2005; Cowen and Sponaugle 2009). In  
45 the Arctic, depth-dependent turnover of species and resulting community composition is likely a  
46 combination of such water mass-related factors, the geological history of the formation of the Arctic  
47 shelves and basins, and the Arctic glaciation history (summarized by Renaud et al. 2015).

48 Biogeography deals with patterns in the distribution of species across spatial gradients and must  
49 be discussed within defined temporal scales (Hedgpeth 1957, Golikov et al. 1990). Specifically, here we  
50 are concerned with the biogeographic affinity of species, which relates to a species' climatic tolerances,  
51 defined by the earth's climatic history in combination with its evolutionary niche conservatism (Harrison  
52 and Grace, 2007). Critical time periods for interpreting today's Arctic biogeography include 'the great  
53 trans-Arctic interchange' and the glaciation history. The great interchange occurred around 3.5 Ma years  
54 ago when Bering Strait opened sufficiently to allow a large number of shallow-water boreal species to  
55 migrate into the then cold-temperate Arctic and North Atlantic and resulted in mixing of different  
56 faunas (Briggs 2003). Many more Pacific species invaded the Arctic than did Atlantic species during this  
57 period (Briggs 2003). This unequal establishment is attributed to either a competitive advantage of  
58 Pacific species and unequal extinction rates or to species loss in the Atlantic fauna (Vermeij 1991).  
59 Repeated northern hemisphere glaciation since about 1.8 Ma years ago and until ~6000 years ago in  
60 both the Pacific and the Atlantic sectors of the Arctic caused a drastic reduction in the amount of boreal

61 species that inhabited the Arctic shelves after the great interchange (Vermeij 1991; Briggs 2003).  
62 Although the exact extent of the ice sheets at the height of various glaciated periods is debated (Maggs  
63 et al. 2008 and references therein), re-expansion onto Arctic shelves apparently occurred by species  
64 remaining in unglaciated pockets around the Arctic or from the deeper ocean (Maggs et al. 2008). The  
65 re-expansion from either glacial shelf refugia or the deep ocean appeared to have been asymmetric  
66 between the Pacific and Atlantic sides. Because shelf refugia were present on the Pacific Arctic shelves,  
67 and the Pacific boreal fauna invaded the Arctic through the shallow Bering Strait connection, today's  
68 benthic communities on the Pacific Arctic shelves are thought to be dominated by shallow-water and  
69 stenobathic species. In contrast, benthic communities on the Atlantic Arctic side tend to be more  
70 eurybathic (Dunton 1992 and references therein), in part stemming from deeper-water faunal  
71 connections with the Atlantic boreal regions and re-expansion onto the shelves from the deep ocean  
72 after glaciation events. This concept was tested on the Beaufort Sea shelf with the available published  
73 marine data of shallow Arctic fauna and flora from 1965-1988 (Dunton 1992), but over larger depth  
74 ranges has only been tested for polychaetes and bivalves (Bilyard and Carey 1980, Krylova et al. 2013). A  
75 larger dataset containing additional taxa and spanning the upper continental slope has recently become  
76 available, affording us the ability to perform a more in-depth biogeographic analysis.

77         The Alaskan Beaufort Sea is an ideal setting to study assemblage patterns along nearshore-to-  
78 slope depth gradients. Situated in the Pacific Arctic, this interior shelf sea (c.f., Carmack and Wassmann  
79 2006) receives surface water from the Pacific after it transits through the Chukchi Sea, while its steep  
80 slope meets Atlantic-origin water masses at about ~250 m depth (summarized in Majewski et al. 2017).  
81 As a consequence of this hydrographic situation and the above-mentioned Arctic glaciation history, the  
82 Beaufort Sea shelf and slope contain a combination of Pacific and Atlantic boreal Arctic and Arctic  
83 species (Nesis 1984; Dunton 1992). Over the continental slope, increasing water depth itself modulates  
84 carbon fluxes with degradation processes during sedimentation reducing the amount and quality of food  
85 with increasing depth (Lalande et al. 2009; Bell et al. 2016), thus influencing overall benthic biomass  
86 and, to some extent, community composition with depth (Nephtin et al. 2014; Roy et al. 2014, 2015). In  
87 addition, the layering of waters of different origins over the Beaufort Sea slope influences biogeography  
88 (see Smoot and Hopcroft 2017 for zooplankton), and thus, may also play a role in the benthic species  
89 turnover with depth. The characteristic oceanographic, hydrographic and geographic characteristics of  
90 the Beaufort Sea allows for the distinction of a number of geographic domains, defined by one or  
91 several of these features.

92           Epibenthic organisms in the Arctic tend to be long-lived and many have relatively low mobility;  
93 thus, we pose that the distribution of epibenthic species reflect time-integrated environmental  
94 conditions along the shelf and slope. In this study, we used data collected along a steep depth gradient  
95 with distinct water masses to understand the distribution of epibenthic communities in an Arctic sea.  
96 The goal of this analysis is two-fold, first, to understand how water masses, with distinct oceanographic  
97 features, may influence changes in epibenthic community diversity and composition; second, do inspect  
98 how the distribution of biogeographic affinities changes amongst water masses. First, we describe  
99 depth- and water mass-associated epibenthic assemblage structure. Second, we analyze assemblage  
100 patterns based on biogeographic affinities of four biomass-dominant taxa, echinoderms, decapods,  
101 isopods, and mollusks across water masses. We tested two hypotheses: 1) Epibenthic biomass and  
102 assemblage structure change in synchrony with water mass from coastal to bathyal depths, and 2)  
103 Pacific Boreal Arctic species have their core distribution on the shelf where Pacific origin waters prevail,  
104 while Atlantic Boreal Arctic species have wider depth distribution ranges.

## 105 **Materials and Methods**

### 106 *Study area*

107           The combination of hydrography, depth and land-ocean interactions was used to define the  
108 following five water masses for the study region in the central Beaufort Sea: the Coastal Zone (CZ) water  
109 (recognizing this is a dynamic mixture of waters, Weingartner et al. 2017), the Polar Mixed Layer (PML),  
110 the Arctic Halocline (AH), the Atlantic Water (AW), and the Canadian Basin Deep Water (CBDW) (Table  
111 1). The Coastal Zone of the Beaufort Sea (0-~35 m) is the most land-ocean –influenced region, reaching  
112 from shore to about 10 m by riverine influx that carries terrestrial run-off consisting of freshwater,  
113 inorganic sediment and terrestrial carbon into the marine system (Carmack et al. 2015). To about the 20  
114 m isobath, the Coastal Zone is characterized by landfast sea ice that persists for about 8 months of the  
115 year (Mahoney et al. 2007). The Stamukhi zone, an area of pressure ridges created by the collision of  
116 landfast ice and offshore pack-ice with keels reaching the seafloor and keeping low salinity water  
117 inshore of this zone, ranges from ~18 - 35 m depth on the Beaufort Sea shelf (Reimnitz and Kempema  
118 1984). The conjunction of the diverse environmental features characterize the Coastal Zone as an area  
119 of high disturbances for benthic fauna and, as a result, depauperate faunal communities (Ravelo et al.  
120 2015). Beyond the Coastal Zone, the Polar Mixed Layer is the ocean surface layer, formed by the upper  
121 part of the boundary current that enters the Beaufort Sea through Barrow Canyon, mixed with  
122 freshwater inputs in the Beaufort Sea itself (Carmack et al. 1989). The summer configuration of this

123 water mass is predominantly derived from the fresher Alaska Coastal water with a smaller fraction of  
124 Chukchi/Bering summer water (Weingartner et al. 2017). While the water column of the Polar Mixed  
125 Layer is well mixed in winter, a seasonal pycnocline can separate the Polar Mixed Layer from the  
126 underlying colder, and highly nutrient-rich and structured Arctic Halocline in the summer months at  
127 around 100 m depth (Shimada et al. 2001). The Arctic Halocline varies widely in its depth distribution  
128 throughout the Beaufort Sea, ranging from 50 – 170 m, depending on latitude (Shimada et al. 2005). On  
129 the Beaufort Sea upper slope, this water layer can extend down to 250 m depth (Shimada et al. 2005).  
130 Below approximately 250 m, the bottom of the Beaufort Sea slope is covered by the warmer and more  
131 saline Atlantic Water (Shimada et al. 2004). This water mass is flowing eastward along the continental  
132 slope as part of a large-scale cyclonic boundary current system within the Arctic Ocean (Coachman et al.  
133 1975). The Atlantic Water, characterized by temperatures greater than 0° C, originates in the Barents  
134 Sea and travels through the Arctic (Coachman and Barns 1963). The temperature maximum of the  
135 Atlantic Water in the central Beaufort Sea occurs at a depth of about 450 m, reaching up to 0.5° C in this  
136 area (Coachman and Barns 1963). Heat loss and freshening of the Atlantic Water occurs as the water  
137 mass approaches the Canadian Basin, from interacting with the over- and underlying colder and fresher  
138 water masses, forming the Canadian Basin Deep Water (Rudels et al. 1994). The transition of Atlantic  
139 Water into the cold Canadian Basin Deep Water is at 750-800 m depth in the Canadian Basin (Rudels et  
140 al. 1994; Lansard et al. 2012). We included stations sampled at 750 m in the Canadian Basin Deep Water  
141 designation. We refer to the epibenthos as occurring in the described water masses where those water  
142 masses meet the seafloor, while recognizing that these benthic communities are indirectly influenced by  
143 the entire water mass assembly above.

#### 144 *Biogeographic affinities classification*

145         Based on compilations from published biogeographic classifications (e.g. MacPherson 1971,  
146 Vassilenko and Petryashov 2009, Buzhinskaja 2011) and geographic distributions of species, we used the  
147 following five classification categories to describe biogeographic affinities (for detailed references and a  
148 detailed list of species included in this classification see ESM 2). Arctic species are here defined to be  
149 limited to the shelves of the marginal Arctic seas, and they may extend to the continental slope of the  
150 Arctic basin. These species have an uninterrupted (circumpolar) or interrupted range and do not occur in  
151 boreal regions. In the category ‘Pacific Boreal Arctic and Pacific Boreal species’ we combine species that  
152 occur as far south as in temperate waters to 33° - 38° N in the Pacific Ocean and also occur in either large  
153 or limited parts of the Arctic, but do not occur in the Atlantic. In the group ‘Atlantic Boreal Arctic and

154 Atlantic Boreal species' we combine species that are found in the North Atlantic (generally north of ~38°  
155 N) and also occur in often large parts of the Arctic or just penetrate into the Arctic. Given few truly  
156 boreal species occur in our study area, we use the terms 'Pacific Boreal Arctic' and 'Atlantic Boreal  
157 Arctic' in the remaining text. In the group 'Boreal Arctic and Amphiboreal species' we include species  
158 that are found in temperate waters of *both* the North Atlantic and North Pacific and are either wide-  
159 spread in the Arctic or only extend into parts of the Arctic mostly near inflow shelves. For brevity, we  
160 refer to this group as 'Boreal Arctic' in the remainder of the paper. Bathyal species here are species  
161 restricted to waters deeper than ~200 m and occurring on the slope either only in the Arctic or also  
162 beyond (Vassilenko and Petryashov 2009). Because of the scarcity of information on the biogeographic  
163 affinity of certain taxa sampled in this study, we limited the analysis of biogeographic affinity  
164 distribution across water masses to taxa within the phyla Echinodermata, Mollusca, and taxa within the  
165 orders Decapoda and Isopoda (both in the phylum Arthropoda).

#### 166 *Data collection*

167 Epibenthos were sampled from a modified 3-m plumb-staff beam trawl with 7 mm mesh and 4 mm cod  
168 end liner and bottom roller gear that avoids penetration of the foot rope into the typically soft, muddy  
169 sediment on the Beaufort Sea shelf and slope. Start and end times of the bottom contact, recorded by a  
170 time-depth recorder (Star Oddi) affixed to the net, were taken to be matched with specific latitudes and  
171 longitudes from the ship records. Area swept was calculated from trawl width, trawling time on the  
172 bottom, and trawling speed (Holme and McIntyre 1984) and standardized to catch-per-unit-effort  
173 (CPUE) calculations as biomass per 1000 m<sup>2</sup>. These commonly used estimates are considered semi-  
174 quantitative because of variable trawl performance across bottom types, net avoidance behavior of  
175 some taxa and difficulties in precisely weighting the gear to obtain ideal bottom contact; hence, we  
176 refer to these data as gross estimates (Eleftherious & MacIntyre 2005). Haul duration was approximately  
177 3–15 minutes depending on the substrate and the real-time display on the SIMRAD depth sensor at a  
178 current speed of approximately 1–2 knots (ESM 1). For detail of trawling procedures see Norcross et al.  
179 (2010).

180 Epibenthic invertebrates from whole trawl catches or a defined, well-mixed subsample were  
181 sorted to the lowest taxonomic level possible. We excluded taxa that were clearly pelagic (specifically  
182 jellyfish, hyperiid amphipods and euphausiids) or clearly infaunal (specifically infaunal clams and many,  
183 mostly sedentary polychaete families) because they are not caught quantitatively with the trawl and  
184 represent accidental captures. We consulted Degen and Faulwetter (2019) and where in doubt, we

185 included taxa; very few hyperbenthic taxa were encountered and they were included. Voucher samples  
186 were preserved to later confirm questionable field identifications in consultation with taxonomic  
187 experts listed in the acknowledgments. Several taxa within the groups Nemertea, Porifera, Bryozoa and  
188 Sipuncula remained at a higher taxon level because of lacking available expertise. Taxon names were  
189 standardized to the World Register of Marine Species as the most widely accepted standard for current  
190 names of marine species. Weight per taxon was determined on board the ship using digital hanging  
191 scales.

192 A total of 136 stations on the central Beaufort Sea shelf and slope were included in this study  
193 ranging from 3 m to 1163 m depth (Figure 1). Stations sampled as part of the US-Canada Transboundary  
194 Fish and Lower Trophic Communities project in 2013 (44 stations) and 2014 (48 stations) occurred along  
195 transects perpendicular to shore at target sampling depths of 20 m, 50 m, 100 m, 200 m, 350 m, 500 m,  
196 750 m, and 1000 m. Stations sampled as a part of the Arctic Nearshore Impact Monitoring in  
197 Development Area (ANIMIDA) III project in 2014 (26 stations) and 2015 (18 stations) were placed  
198 following a random tessellated grid design and ranged from 3 m to 302 m. The stations were assigned to  
199 the above-mentioned water masses based on their water depth (Table 1). Bottom water temperature  
200 and salinity data collected at 2 – 5 m above bottom at each station, with larger distances on the slope of  
201 up to 10 m, from Conductivity Temperature Depth (CTD) deployments were used to explore how closely  
202 our predetermined water mass affiliations matched with groupings based on actual physical  
203 measurements (Figure 2). Overall, we found a good match between the two metrics, with some scatter  
204 especially in the Coastal Zone and the Polar Mixed Layer, likely due to the highly spatio-temporal  
205 heterogeneous nature of these zones (Weingartner et al. 2017). We deemed our *a priori* assignment  
206 appropriate to represent the water masses of the region and used those for all further analyses (Figure  
207 3a).

#### 208 *Data Analysis*

209 Epibenthic biomass was the metric used for all analyses because it included colonial taxa such as  
210 Porifera, Hydrozoa, Bryozoa, colonial Ascidiacea, etc., which cannot be enumerated as individuals,  
211 would be excluded from count-based assessments, reducing by 14%, on average, the taxon richness per  
212 station. Hence, biomass patterns present a more complete picture of epibenthic assemblages.  
213 Significant differences of total biomass, taxon richness (number of taxa) and evenness (Pielou's  
214 evenness  $J' = H'/\log(S)$ ) among water masses were tested with one-way ANOVAs and pairwise

215 comparisons of means using R ([www.r-project.org](http://www.r-project.org), V3.5.0). All maps were produced using ArcGIS  
216 (ArcMap 13.0) and assemblage value breaks were determined by Jenks' natural breaks.

217 All multivariate statistical analyses of epibenthic assemblage patterns were done in Primer-e V7.  
218 Biomass data were square-root transformed to reduce the influence of taxa with very large biomass  
219 while still maintaining the overall dominance structure of the assemblage. To test the significance of  
220 station groupings based on a Bray-Curtis similarity matrix by water mass affiliation, a Permutational  
221 multivariate analysis of variance (PERMANOVA) was used with "water mass" as a fixed factor. As an  
222 exploratory tool we used a non-metric Multidimensional Scaling (nMDS) plot to depict differences  
223 among assemblages classified by water mass. In support of the nMDS, a cluster diagram based on a  
224 Bray-Curtis similarity matrix was also conducted (ESM 3). The taxa that contribute most to characterizing  
225 epibenthic assemblages by water mass were identified with a Similarity percentages (SIMPER) routine (),  
226 which provides the similarity contribution of each taxon (Contribution, %) and their combination  
227 (Cumulative, %). We chose to represent here only those taxa that individually contributed 5% or more to  
228 similarity within a water mass.

229 Differences in biogeographic affinities among water masses were explored qualitatively through  
230 relative percentage (number of taxa and biomass) graphs and shade plots (provided in ESM 4-7).

## 231 **Results**

### 232 *Epibenthic assemblage structure*

233 The mean biomass for the study region was 377 g ww/1000 m<sup>2</sup> ( $\pm$  576 (sd)). The biomass varied  
234 by three orders of magnitude across all stations from 4 to 3,968 g ww/1000 m<sup>2</sup> (Figure 3b). Stations with  
235 higher biomass were mostly located on the outer shelf and upper slope of the central study area,  
236 corresponding predominantly to the Polar Mixed Layer and Arctic Halocline abutting the seafloor.  
237 Stations under the influence of the Coastal Zone and the Canada Basin Deep Water typically had the  
238 lowest biomass (Figure 3b). By phylum, Echinodermata accounted for 67% of the total biomass across all  
239 stations, followed by Arthropoda (10%), Mollusca (9%), Cnidaria (7%), Annelida (3%), and Porifera (2%).  
240 All other phyla combined accounted for only 1.4% of the total biomass (Bryozoa (0.6%), Chordata (0.5%),  
241 Nemertea (0.2%), Sipuncula (0.1%), Platyhelminthes (< 0.1%), and Brachiopoda (< 0.1%)). Across all  
242 stations, three echinoderm taxa accounted for 38% of the total biomass, the sea cucumber *Psolus*  
243 *peronii* (22%), and the brittle stars *Ophiocten sericeum* (10%) and *Ophiopleura borealis* (6%). The mean



244 epibenthic abundance of the study region was 5,985 ind./1000 m<sup>2</sup> ( $\pm$  10,092 (sd)). The abundance per  
245 station varied largely from 12 to 5,641 ind. /1000 m<sup>2</sup>.

246 The mean number of taxa per station in the study region was 30 ( $\pm$  11), with a total of 332 taxa  
247 found during the study. The distribution of number of taxa varied by one order of magnitude across all  
248 stations, from 5 to 65 taxa per station (Figure 3c). By phylum, Arthropoda contained the greatest  
249 number of taxa (114), followed by Mollusca (81), Annelida (44), and Echinodermata (39) across the  
250 study region. Taxon richness within Bryozoa (22), Cnidaria (20), Porifera (9), Brachiopoda (1), Nemertea  
251 (1), and Platyhelminthes (1) was underestimated because of a lack of taxonomic resolution in those  
252 phyla. Number of taxa was highly variable under the Coastal Zone with some of the highest and some of  
253 the lowest value stations corresponding to this water mass. High taxon richness also occurred under the  
254 Polar Mixed Layer but typically decreased in deeper water masses (Figure 3c).

255 The mean biomass, taxon richness and evenness varied significantly across water masses  
256 (ANOVAs,  $p$ -values  $<$  0.05) (Tables 2 and 3). Biomass and taxon richness in the Polar Mixed Layer (47% of  
257 total biomass and 29% of total taxa) were significantly higher than those in both the Atlantic Water (8%  
258 biomass and 14% taxa) and the Canadian Basin Deep Water (5% of biomass and 12% of taxa) (Tables 2  
259 and 3). Biomass and taxon richness were significantly different between The Arctic Halocline and the  
260 Canadian Basin Deep Water, and biomass was significantly different between the Arctic Halocline and  
261 the Atlantic Water (Tables 2 and 3). Coastal Zone epibenthic biomass (7%) was significantly lower than in  
262 the Arctic Halocline (33%), and lower in taxon richness (23% for Coastal Zone) than in the Polar Mixed  
263 Layer (29% of taxa) (Tables 2 and 3). In terms of taxa evenness (Pielou's evenness index), the values  
264 across water masses were intermediate and showed little variation (ranging from 0.55 to 0.65). Though  
265 evenness was significantly across water masses, the pairwise comparison of means revealed that the  
266 differences between communities by water mass were only significant between the Polar Mixed Layer  
267 and the Arctic Halocline communities (Tables 2 and 3). Epibenthic square-root transformed abundance  
268 did not vary significantly across water masses.

269 Epibenthic assemblage composition significantly differed among water masses (PERMANOVA  
270 Pseudo-F = 19.11,  $P$ (perm) = 0.0001; Table 4), with significant pairwise comparisons across all water  
271 masses ( $P$ (perm) = 0.001; Table 5). Epibenthic assemblages under the Canadian Basin Deep Water were  
272 the most dissimilar to assemblages under the Polar Mixed Layer and the least dissimilar to those in the  
273 Atlantic Water (Table 5). These relationships were also well reflected in multi-dimensional space, where  
274 assemblages under the same water mass affiliation clearly grouped together (Figure 4, ESM 3).

275           With the exception of the Coastal Zone, taxa that contributed most to assemblage similarity  
276 within each water mass belonged to the phylum Echinodermata (Table 6). Similarity within the Coastal  
277 Zone assemblages was mostly driven by members of the Arthropoda. The number of taxa contributing  
278  $\geq 5\%$  to similarity within each of the water masses ranged from four to six taxa. Several species were  
279 characteristic across multiple water masses, e.g., the brittle star *Ophiocten sericeum* across the three  
280 upper water masses, and the sea star *Pontaster tenuispinus* in the deeper three water masses (Table 6).

281           Comparing across water masses, the distribution of biomass differed at the phylum level (Figure  
282 5). Within the Echinodermata, 45% of all taxa had more than 50% of their biomass concentrated in the  
283 Arctic Halocline (Figure 5a). Many echinoderm taxa also had a high proportion of their biomass  
284 concentrated in the upper slope area of the Polar Mixed Layer but only a low number of taxa had high  
285 biomass in the Coastal Zone (Figure 5a). Arthropoda and Mollusca both had high numbers of taxa with  
286 high biomass ( $>50\%$ ) in the Coastal Zone (25% of all arthropod and 31% of all mollusk taxa) and in the  
287 Polar Mixed Layer (35% of all arthropod and mollusk taxa) (Figures 5b and 5c). Among Arthropoda and  
288 Mollusca, fewer taxa with high biomass were present in the three deeper water masses. Across all phyla,  
289 the Atlantic Water and the Canadian Basin Deep Water had the fewest taxa with high biomass  
290 concentrated in these water masses. Differences in the distribution of biomass of individual taxa among  
291 water masses are visualized in shade plots (ESM 4 – 7.pdf).

### 292 *Biogeographic patterns*

293           Some biogeographic patterns were consistent across Echinodermata, Mollusca, and  
294 Decapoda/Isopoda (Figures 6 and 7). Common trends across all groups were the virtually zero biomass  
295 of Pacific Boreal Arctic taxa in the Atlantic Water and the Canadian Basin Deep Water, e.g., only 0.002%  
296 of echinoderm and 0.4% of decapod/isopod biomass with Boreal Pacific Arctic biogeographic affinity  
297 occurred in the Canadian Basin Deep Water. Also, Bathyal species biomass was exclusively found in the  
298 Atlantic Water and the Canadian Basin Deep Water (Figures 6 and 7). In addition, consistent across all  
299 taxonomic groups was the presence of Atlantic Boreal Arctic, Boreal Arctic and Arctic taxa in all water  
300 masses; however, biomass or taxon proportion of these biogeographic affinities across water masses  
301 differed for the different taxonomic groups (Figures 6 and 7).

302           The proportion of epibenthic biomass within the various biogeographic affinities showed some  
303 differences between Echinodermata, Mollusca, and Decapoda/Isopoda. For mollusks and echinoderms,  
304 there was a clear increase in biomass of Atlantic Boreal Arctic taxa with depth, particularly in the

305 Atlantic Water and Canadian Basin Deep Water, while this was not the case for decapods/isopods  
306 (Figures 7a and 7b). Boreal Arctic taxa biomass was lowest in the Atlantic Water and Canadian Basin  
307 Deep Water in Mollusca and Echinoderm, but not in Decapoda/Isopoda (Figure 7a and 7b). However,  
308 these patterns did not hold true for decapods-isopods, for neither Atlantic Boreal Arctic nor boreal Arctic  
309 taxa biomass (Figure 7c). The distribution of biomass of Arctic taxa among water masses did not show a  
310 consistent pattern across taxonomic target groups (Figure 7). Most of the Arctic affinity mollusk biomass  
311 was concentrated in the Polar Mixed Layer and Coastal Zone, while Arctic affinity echinoderms biomass  
312 was higher in the Arctic Halocline water mass, albeit being overall very low. In contrast,  
313 decapods/isopods with Arctic affinity had maximum biomass proportion in the Atlantic Water. In terms  
314 of number of taxa, there was a relatively uniform distribution of biogeographic affinities across water  
315 masses for all taxonomic target groups (Figure 7).

## 316 **Discussion**

### 317 *Epibenthic assemblage structure*

318 We hypothesized that epibenthic biomass as well as assemblage structure change in accordance  
319 with water masses from coastal to bathyal depths, and overall, our results supported this hypothesis. In  
320 the Coastal Zone, at depths shallower than 35 m, overall biomass was low. Biomass-dominant taxa in  
321 the Coastal Zone, including highly mobile decapod shrimps (*Eualus gaimardii*, *Sabinea septemcarinata*),  
322 the ophiuroid *Ophiocten sericeum*, amphipods (e.g., *Anonyx* sp.), and the isopod *Saduria entomon*, have  
323 in common that they are tolerant to the dynamic shallow-water habitat (Hagerman and Szaniawska  
324 1988; Steffens et al. 2006). This coastal habitat is strongly affected by freshwater discharge from the  
325 multiple rivers draining into the Beaufort Sea (Dunton et al. 2006; Macdonald and Yu 2006; Mahoney et  
326 al. 2014), and is characterized by mobile sediments (often sandy bottoms) and strong ice scour,  
327 disturbances that limit the development of high benthic biomass (Conlan and Kvitek 2005). The mobile  
328 taxa typical for the Coastal Zone can either avoid larger disturbances by moving away, or they have large  
329 tolerance windows towards environmental conditions such as low salinity. While biomass of these  
330 coastal assemblages was typically low, species richness was occasionally surprisingly high, especially  
331 within the amphipods. Perhaps the reason is that the disturbance regime in the Coastal Zone enhances  
332 coexistence of species because of their differing responses to the disturbance-induced variability in  
333 resources and environmental conditions (Roxburgh et al. 2004). Most taxa in this zone have omnivorous  
334 and highly plastic feeding habits that allow them to capitalize on the large variety of food sources

335 available in the Coastal Zone, such as the mix of terrestrial and marine organic matter (Dunton et al.  
336 2006; Divine et al. 2015; Bell et al. 2016; Harris et al. 2018).

337 Total biomass was generally highest in the Polar Mixed Layer and the Arctic Halocline,  
338 approximately between 35 – 200 m depth. Epibenthic assemblages in this depth range are exposed to  
339 more stable environmental conditions than in the shallower, disturbed Coastal Zone, and receive a  
340 stronger flux of more labile food particles from surface production (Roy et al. 2015; Bell et al. 2016).  
341 Dominant taxa in the shelf zone vary in relation to oceanographic conditions and sediment grain size  
342 structure (Ravelo et al. 2015). One character species of the Polar Mixed Layer was the sea cucumber  
343 *Psolus peronii*, which occurred mostly between 35 – 50 m depth within the seafloor underlying the Polar  
344 Mixed Layer. This species has an extremely patchy distribution, often contributing >50% to biomass at  
345 those stations where it occurs but being rare at other stations. At that depth range, a previous study  
346 highlighted the presence of shell hash, gravel and boulders interspersed within the soft sediment  
347 (Ravelo et al 2015). The restricted depth distribution and *P. peronii*'s typical association with coarse  
348 substrates (Glud et al. 2010) may indicate this filter-feeding species requires a combination of sufficient  
349 food particle concentrations and water movement plus hard substrate for attachment. Another highly  
350 abundant character species of the Polar Mixed Layer and the Arctic Halocline was the brittle star  
351 *Ophiecten sericeum*; however, with its small size, it contributed typically less to overall biomass than  
352 some less abundant but larger species. High densities of this brittle star species are common in many  
353 Arctic shelf regions, such as on the Barents, Kara and Laptev Sea shelves (Piepenburg and Schmid 1996,  
354 1997; Steffens et al. 2006; Galkin et al. 2015) and in the Canadian Arctic (Roy et al. 2014), where it is  
355 known to play important roles in nutrient recycling (Piepenburg et al. 1997). In the Chukchi Sea and on  
356 the Beaufort Sea shelf west to our study region (west of ~150°W), the dominant brittle star species shifts  
357 from *O. sericeum* to the larger-bodied brittle star *Ophiura sarsii* (Bluhm et al. 2009; Ravelo et al. 2015).  
358 We previously hypothesized that *O. sarsii* may have the ability to outcompete *O. sericeum* in areas  
359 influenced by nutrient-rich water masses, with higher primary production and strong pelagic-benthic  
360 coupling (Ravelo et al. 2016). Another ophiuroid, *Ophiacantha bidentata*, became prominent in the  
361 deeper Arctic Halocline, which is consistent with patterns in the adjacent Canadian Beaufort Sea (Nephin  
362 et al. 2014) and other regions of the Arctic where *O. bidentata* starts to replace *O. sericeum* at  
363 intermediate shelf break depths (Mayer and Piepenburg 1996; Piepenburg and Schmid 1996).

364 Epibenthic biomass precipitously declined in the deeper water masses of the Atlantic Water and  
365 the Canadian Basin Deep Water. This decline was mostly due to lower densities at greater depth, which

366 is similar to patterns found in deeper waters of the Canadian Beaufort Sea (Nepkin et al. 2014) and likely  
367 less to decreasing body size. In fact, some of the most dominant taxa at these deeper water masses  
368 were large-bodied sea stars (e.g., *Pontaster tenuispinus*, *Bathybiaster vexillifer*, *Icasterias panopla*) and  
369 ophiuroids (*Ophiopleura borealis*). This seems contrary to previous observations that Arctic (and global)  
370 benthic deep-sea fauna gets increasingly smaller-bodied with depth (Rex et al. 2006; Wei et al. 2006),  
371 but both these studies in fact show body size decrease is less obvious in epibenthic megafauna than in  
372 macro-infauna and in the upper 1000 m. The maximum depth sampled here (1162 m) is still located on  
373 the Beaufort slope and is likely exposed to more dynamic food supply from downward shelf transport or  
374 upwelling (Bell et al. 2016) than the fauna in the deep-sea plain, where limited food supply is thought to  
375 drive arctic benthic communities and their food webs (Iken et al. 2005; Bluhm et al. 2010; Roy et al.  
376 2015).

377         At the greater depth of the Atlantic Water and the Canadian Basin Deep Water, species  
378 composition was quite different from the shallower water masses, instead of simply a shift in relative  
379 abundances of the same species. This agrees with patterns found in the adjacent Canadian Beaufort Sea  
380 where species turnover ( $\beta$  diversity) was particularly high on the mid-slope (Nepkin et al. 2014). Among  
381 the sea stars characteristic of the epibenthic assemblages in these deeper water masses, *Pontaster*  
382 *tenuispinus* started to occur regularly, or to even dominate, below 250 m in the Atlantic Water, which is  
383 shallower than the common depth range for this sea star reported in areas located in the Amerasian and  
384 Eurasian basins (Smirnov 1994). While *P. tenuispinus* remained common into the Canadian Basin Deep  
385 Water, the more prominent sea star of this deeper water assemblage was the scavenging/predatory  
386 *Bathybiaster vexillifer*. This deep-sea species obtains food from both phyto-detrital and microbial  
387 sources (Howell et al. 2004), which supports our recent inference that microbial processing of organic  
388 material is an essential component of the slope food web of the Beaufort Sea (Bell et al. 2016). The  
389 dominant ophiuroid in these deep water masses (750 – 1000 m) was *Ophiopleura borealis*, which is also  
390 known from deep waters (500 m) in the Kara Sea (Galkin et al. 2015) and in Northeast Greenland  
391 (Starmans et al. 1999), although the species' distribution can be shallower (< 100 m) in cold, arctic water  
392 masses (Aitken and Fournier 1993; Piepenburg and Schmid 1996). This distinct depth zonation in brittle  
393 stars, and the dominant role these different brittle star species play within the epibenthic assemblages  
394 of each of the water masses, showcase the overall importance of brittle stars in Arctic benthic systems  
395 and may indicate resource partitioning among these species (Graeve et al. 1997; Piepenburg 2003).

396           Although we only catalogued 332 epifaunal taxa of the estimated >750 combined macro- and  
397 megafaunal benthic invertebrate species occurring on the Beaufort shelf (Piepenburg et al. 2011),  
398 characteristic taxa for the Beaufort Sea shelf and slope were common to other Arctic regions, as  
399 discussed above. Most species similarities, especially in shallower water masses, are with other interior  
400 shelf systems (c.f. Carmack et al. 2015) that are strongly freshwater-influenced, like the Kara Sea (Galkin  
401 et al. 2015). In contrast, some notable species differences occurred to the adjacent Chukchi Sea inflow  
402 shelf, such as the above-mentioned transition of the dominant brittle star species (also see Ravelo et al.  
403 2015). Another noteworthy difference to Arctic inflow shelves was the extremely low abundance of  
404 brachyuran and anomuran crabs, such as the snow crab *Chionoecetes opilio* and the lyre crab *Hyas*  
405 *coarctatus*, which can be epibenthic assemblage dominants in the adjacent Chukchi Sea (Bluhm et al.  
406 2009; Ravelo et al. 2014). We encountered appreciable numbers of snow crab only in the western and  
407 deeper part of our study region, mostly in the Atlantic Water, where individuals were large compared  
408 with the smaller crab size prominent on the adjacent Chukchi Sea shelf (Konar et al. 2014). We also  
409 encountered high abundances of pycnogonids, especially at greater depths  $\geq 750$  m in the Canadian  
410 Basin Deep Water in our Beaufort Sea study region, which are reported as common also in the Barents  
411 Sea (Jørgensen et al. 2015), but can otherwise often be a rare group in the Arctic.

412           In summary, epibenthic assemblage structure was strongly associated with the layers of water  
413 masses along the depth gradient from the shallow coastal shelf to the deep slope of the Beaufort Sea, as  
414 also found for the Canadian Beaufort Sea (Nephtin et al. 2014). This is similar to water mass-associated  
415 community structures of zooplankton (Smoot and Hopcroft 2017) and fishes (Majewski et al. 2017) in  
416 the Beaufort Sea. Such patterns may be driven by physiological constraints associated with depth, the  
417 availability and quality of food mediated by surface production, the influences of midwater grazing and  
418 degradation processes on food particle quality, and sinking velocities (e.g., Roy et al. 2015; Bell et al.  
419 2016; Stasko et al. 2018), and/or by biogeographic affinities to water masses.

#### 420 *Biogeographic patterns*

421           This study confirmed our hypothesis that benthic taxa with Pacific Boreal Arctic affinity were  
422 essentially limited to the shelf, primarily to areas under the Coastal Zone and Polar Mixed Layer waters.  
423 The virtual absence of Pacific Boreal Arctic taxa from deep waters confirms findings from earlier studies  
424 (Menzies 1973, Bilyard and Carey 1979), hence showing these earlier conclusions were not simply an  
425 artifact of sparse knowledge of the deep fauna during these earlier years. A recent study on epifaunal  
426 communities in the Chukchi Borderland area confirms the pattern (Zhulay et al. 2019). The underlying

427 causes that limit vertical distribution of Boreal Pacific Arctic species are not entirely clear, but appear to  
428 be strongly driven by a combination of today's propagule supply and Arctic glaciation history.

429 Propagule supply in the Pacific Arctic is a combination of larvae advected from the south  
430 through Bering Strait and of local reproduction (Parada et al. 2010). Advective inflow transports Pacific  
431 water containing benthic taxa propagules across the Chukchi Sea into the Beaufort Sea, where this  
432 water contributes primarily to the Polar Mixed Layer and Arctic Halocline waters (McLaughlin et al.  
433 1996). This propagule inflow agrees with our observations of Pacific Boreal Arctic species distribution  
434 records in the Polar Mixed Layer water on the Beaufort Sea shelf. Wind-mediated Pacific water  
435 pathways including upwelling events can transport this water to the coastal zone (Okkonen et al. 2009),  
436 which may explain the Pacific Boreal Arctic taxon occurrences in Coastal Zone water. Pacific water that  
437 moves offshore into the Canada Basin's Polar Mixed Layer and Pacific Halocline also carries some Pacific  
438 holozooplankton and meroplankton (larvae of benthic invertebrates) species (Kosobokova et al. 2011;  
439 Smoot and Hopcroft 2017), but at least the Pacific holozooplankton species do not reproduce there  
440 (Kosobokova et al. 2011). The meroplankton in those studies could not be identified to species, but if  
441 they were Pacific Boreal species they apparently did not successfully settle to the deep seafloor off the  
442 shelf break. Exceptions were the Pacific Boreal hermit crab *Pagurus capillatus* and the Pacific Boreal  
443 brittle star *Amphiodia craterodmeta*, which we interestingly also found in the Canadian Basin Deep  
444 Water and believe to be first reports from these depths on the Beaufort Sea slope. The lower depth  
445 range of *P. capillatus* is given as ~500 m (Vassilenko and Petryashev 2009), while *A. craterodmeta* does  
446 occur to depths of 1000 m, but so far only on the Pacific and not the Arctic slope (Smirnov, ZIN, 2014  
447 unpubl. manuscript). Along the Beaufort Sea shelf, the Pacific water influence is most strongly seen in  
448 the benthic fauna until ~ 150° W where a biogeographic shift in benthic (Ravelo et al. 2015) and also  
449 pelagic communities (Smoot and Hopcroft 2016) is obvious. This distribution shift agrees with long-term  
450 mooring measurements tracking Pacific waters along the shelf (Pickart et al. 2013).

451 Processes during and after glaciation events in the Arctic also likely contributed to the  
452 restriction of Pacific Boreal and Pacific Boreal Arctic taxa to the shelf water masses. Pockets of  
453 unglaciated shelf refugia remained in the Pacific Arctic during the arctic glaciation and allowed Pacific  
454 fauna to persist on shelf areas during glaciated times rather than going extinct or being pushed down  
455 the slope (Maggs et al. 2008). In contrast to boreal Atlantic Boreal Arctic and Atlantic boreal taxa,  
456 eurybathy did not seem to have been a biological trait selected for in Pacific Boreal and Pacific Boreal  
457 Arctic taxa during recolonization, as confirmed by the virtual absence of these taxa in deeper water

458 masses in our study. Also, the shallow depth of the Bering Strait would have limited the colonization of  
459 Pacific deep-water species into the deep Arctic during the trans-Arctic interchange, certainly for adults  
460 and deep-dwelling larvae both after deglaciation and today. Shelf-dwelling Pacific Boreal and Pacific  
461 Boreal Arctic taxa may be ill-adapted to migrate to and occupy deeper waters. Some Pacific Boreal  
462 invertebrate and fish species such as the crab *Telmessus cheiragonus* and Bering Flounder are  
463 documented and predicted to increasingly move northward and into the Arctic with warming waters  
464 (Cheung et al. 2009; Sirenko and Gagaev 2007; Mueter and Litzow 2008; Hollowed et al. 2013), but the  
465 currently scarce occurrence of Pacific Boreal and Pacific Boreal Arctic taxa deeper than the shelf break  
466 (Bilyard and Carey 1979; Menzies 1973; Zhulay et al. 2019; this study) suggests new immigrant species  
467 from the Pacific will probably settle on the Chukchi and Beaufort Sea shelves rather than invade the  
468 continental slope and basin waters in the foreseeable future.

469           Low temperature, often invoked as a driver of species distribution limits through physiological  
470 and other constraints (Peck et al 2004; Hoegh-Guldberg and Bruno 2010), seems an unlikely depth-  
471 limiting force for Pacific Boreal Arctic taxa given that water temperature can be lower on large parts of  
472 the Beaufort Sea shelf where these species occur compared with the deeper Atlantic Layer encountered  
473 at the Beaufort Sea slope. Rather, low temperatures prolong larval duration and survival and, thus,  
474 would allow farther dispersal of propagules (Hoegh-Guldberg and Bruno 2010), which may help explain  
475 the occurrence of Boreal Pacific Arctic and Boreal Pacific species on shelf areas far from the Bering  
476 Strait inflow.

477           Atlantic Boreal Arctic taxa, in contrast, occurred in all water masses across the full depth range  
478 of our sampling, again confirming our hypothesis of their broad vertical distribution ranges. The  
479 proportion of these taxa of total biomass in deeper water masses (especially Atlantic Water and  
480 Canadian Basin Deep Water) increased substantially for mollusks and echinoderms, albeit not for  
481 decapods and isopods and agrees with the dominance of Atlantic taxa in the Arctic Basins (Krylova et al.  
482 2013; Mironov et al. 2013). A similar although less dramatic increase with deeper water masses was  
483 observed for Atlantic Boreal Arctic taxon richness in all taxon groups. Our results stress the high  
484 connectivity of the North Atlantic's and Arctic's faunas in shelf waters and beyond the shelf break. This  
485 finding agrees with a series of recent molecular studies across different taxa demonstrating this strong  
486 Atlantic-Arctic connectivity (polychaetes: Carr et al. 2011; echinoderms: Hardy et al. 2011; bivalves:  
487 Krylova et al. 2013; bryozoans: Kuklinski et al. 2013; amphipods: Tempestini et al. 2018). In today's  
488 setting, this connectivity is facilitated through the massive inflow of an annual ~ 9-10 Sv of Atlantic



489 water into the Arctic (Schauer et al. 2004). In contrast to the Pacific inflow, the Atlantic connection is not  
490 limited to surface waters but extends through much of the water column in Fram Strait (Schauer et al.  
491 2004). This inflow provides ample opportunity for propagules of deep-water or eurybathic species to  
492 spread into the Arctic. Highest faunal similarity between the North Atlantic and Arctic occurs in the  
493 Barents Sea region and extending to Svalbard's west coast (Krylova et al. 2013), but over geological time  
494 North Atlantic species have clearly dispersed all the way into the Canada Basin and the adjacent  
495 Beaufort Sea slope with the flow of the Atlantic Water and Arctic Deep Water (Bilyard and Carey 1979;  
496 Krylova et al. 2013; this study). Notably, however, Atlantic Boreal Arctic taxa also occur, and in some  
497 cases even dominate, the shallower water masses on the Beaufort shelf, such as some echinoderm taxa  
498 in the Coastal Zone. Alongside, Atlantic Boreal Arctic decapod and isopod biomass represented an  
499 important fraction of the total biomass of the Coastal Zone, the Polar Mixed Layer and the Arctic  
500 Halocline. This documents that Atlantic Boreal Arctic taxa can compete with species of other  
501 biogeographic affinities on Pacific shelves (Krylova et al. 2013; this study).

502           Increasing expansions of Atlantic boreal species are being observed and predicted and are  
503 related to documented stronger inflow and/or warming of Atlantic water (Polyakov et al. 2017). Such  
504 species range extensions include, for example, increasing amounts of Atlantic cod north of Svalbard  
505 (Haug et al. 2017), the establishment of the boreal amphipod *Gammarus oceanicus* off the west and  
506 north coast of Spitsbergen over the past decades (Węśławski et al. 2018), and northward spreading of  
507 the crab *Chionoecetes opilio* and the Atlantic fish community in the Barents Sea (Fossheim et al. 2015;  
508 Renaud et al., 2015). Underlying the warming of recent decades and related species expansions is,  
509 however, the still-ongoing recolonization of the Arctic after glacial extinctions, a process that has  
510 resulted in terming Arctic fauna 'immature' (Zenkevitch 1963, Knox and Lowry 1977, Hardy et al. 2011).

511           Like Atlantic Boreal Arctic taxa, Boreal Arctic taxa occurred in all water masses, with relatively  
512 little variation in taxon numbers among water masses, but with decreasing biomass proportions in the  
513 deeper water masses (Atlantic Water, Canadian Basin Deep Water). These observations generally agree  
514 with findings for other taxa in the Beaufort Sea, specifically polychaetes (Bilyard and Carey 1979) and  
515 bivalves (Krylova et al. 2013). The high proportion of shelf echinoderms being of Pacific affinity agrees  
516 with Mironov and Dilman's (2010) finding for that group. Mostly, Boreal Arctic taxa derive from  
517 northward spreading during warmer times from either the Atlantic or the Pacific, and subsequent  
518 persistence in both boreal regions as well as parts of the Arctic (Laakkonen 2015). Future proportion of  
519 Boreal Arctic taxa may decline given large genetic breaks occurring between Pacific and Atlantic-Arctic

520 lineages (e.g., for polychaetes), supporting the notion of long-term separation (Carr et al. 2011). The  
521 classification of some species as ‘Amphiboreal’ may, hence, be limited by both our ability to delineate  
522 species based on morphology or molecular divergence thresholds (Hebert et al. 2003) and by ongoing  
523 speciation.

524 Arctic and Bathyal taxa were the least represented biogeographic affinities in terms of number  
525 of taxa. However, Arctic taxa contributed substantially to biomass in the Coastal Zone and Polar Mixed  
526 Layer (Mollusca) and Atlantic water (Decapoda/Isopoda). Example species of Arctic affinity included the  
527 bivalve *Similipecten greenlandicus*, the gastropod *Colus sabini* and the decapod *Eualus gamardii* (Table  
528 6) which represented as much as 32-40% of the total biomass at stations where they were present. On  
529 the one hand this dichotomy of low taxon number of Arctic affinity but high biomass of these few taxa  
530 documents a current co-existence pattern of Arctic with Boreal Arctic species, in which few Arctic species  
531 managed to establish proportionally large biomass. On the other hand, the fact that it is *few* Arctic  
532 epibenthic species that maintain currently strong presence in the Arctic shelf systems stresses the need  
533 for a better understanding of the fate of Arctic species in a rapidly changing Arctic environment. In  
534 contrast, not only were there few taxa representing the Bathyal biogeographic affinity, they also added  
535 very little to the overall biomass of the deeper stations. The taxa with Bathyal affinity included two  
536 decapods (*Bythocaris biruli* and *Bythocaris irene*) and two echinoderms (the sea star *Bathybiaster*  
537 *vexillifer* and the sea cucumber *Kolga* sp.).

### 538 *Conclusions and Outlook*

539 Here we demonstrated that gross biomass estimates and community structure differed among  
540 water masses and that Pacific Boreal Arctic and Pacific Boreal taxa were essentially limited to the shelf,  
541 while Atlantic Boreal Arctic and Atlantic Boreal taxa occurred across a broad depth range. The potential  
542 for northward range extensions of boreal marine species and transarctic biotic interchange between the  
543 Atlantic and the Pacific is gaining renewed interest related to climate warming scenarios. We show  
544 Atlantic taxa are already on the Beaufort Sea shelf with little distance left to the boreal Pacific region,  
545 though both the primary northward current flow from the Pacific into the Arctic and competition may  
546 keep them from spreading southward into boreal areas of the opposing ocean. While few very recent  
547 Arctic transgressions have been documented so far (but see diatom *Neodenticula seminae*, Reid et al.  
548 2007), several relatively recent post-glacial transgressions suggest present-day trans-Arctic exchange is  
549 conceivable. The mussel *Mytilus trossulus* in Greenland, for example, is suggested to originate from the  
550 Pacific as a consequence of postglacial long-distance dispersal through Bering Strait (Bach et al. 2018).

551 Given the documented increasing warming of Arctic waters, in particular in inflow shelves (Polyakov et  
552 al. 2017), such exchange seems increasingly likely though we consider it less likely that new arrivals of  
553 Boreal Pacific taxa expand to continental slope and basin waters in the foreseeable future. Probably  
554 more likely, however, is quick dispersal across the Arctic in both directions related to increasing ship  
555 traffic, given that ballast water is a well-documented vector for unplanned and undesired transport of  
556 species and such human-aided trans-Arctic transports are considered increasingly likely (Chan et al.  
557 2013). Such upcoming changes in climate and human activities will complicate disentangling  
558 biogeographic patterns in the future, providing some urgency for biogeography mapping as done in the  
559 present work, which could be enhanced through the combination of fossil morphological and modern  
560 molecular tools.

### 561 **Acknowledgments**

562 We thank C. Coon, D. Holiday and K. Wedemeyer for their support as BOEM Project managers. Project  
563 management support was tirelessly provided by Olgoonik Fairweather (OF) (M13PC00019), especially S.  
564 Wisdom, J. Blank, W. Hetrick, W. Thorsen, and PI B. Norcross (M12AC00011) with support by L.  
565 Edenfield and B. Holladay (all University of Alaska Fairbanks, UAF). We also thank the chief scientists and  
566 captains during many cruises on the R/V Norseman II for mastering trawling in the poorly charted and  
567 muddy waters of the Beaufort Sea with an incredibly positive attitude. Invaluable help on deck was  
568 provided by the wonderful Norseman II crew, and admirable support with trawl sorting was kindly  
569 provided by D. Holiday and K. Wedemeyer (BOEM), J. Blank (OF), L. Bell, R. Décoteaux, K. Dilliplaine, L.  
570 Edenfield, T. Schollmeier, C. Serratos, K. Walker, and J. Weems (all UAF). We are very thankful for  
571 taxonomic support by K. Coyle (Amphipoda) and M. Hoberg (Polycyhaeta; both UAF), G. Hendler  
572 (Holothuroidea, Ophiuroide; National History Museum of Los Angeles County), C. Mah (Asteroidea) and  
573 L. Cole (Asciacea; both Smithsonian Institution), and R. Melzer (Pycnogonida; Zoologische  
574 Staatssammlung München). The views and conclusions contained in this document are those of the  
575 authors and should not be interpreted as representing the opinions or policies of the U.S. Government.  
576 Voucher material of many of the species used in this study was archived at the Smithsonian Institution.  
577 Dr. A Vedenin and two anonymous reviewers are thanked for improving an earlier draft of the  
578 manuscript.

### 579 **Funding**

580 This study was made possible by contracts from the U.S. Department of the Interior, Bureau of Ocean  
581 Energy Management (BOEM), Alaska Outer Continental Shelf Region, Anchorage, Alaska by as part of

582 the BOEM Environmental Studies Program; Contract Number M13PC00019 (Arctic Nearshore Impact  
583 Monitoring in Development Area (ANIMIDA) III: Contaminants, Sources, and Bioaccumulation) and  
584 Cooperative Agreement No. M12AC00011 (US–Canada Transboundary Fish and Lower Trophic  
585 Communities).

#### 586 **Conflict of Interest**

587 The authors declare that they have no conflict of interest.

#### 588 **Ethical approval**

589 All applicable international, national, and/or institutional guidelines for the care and use of animals were  
590 followed by the authors.

#### 591 **Sampling and field studies**

592 All necessary permits for sampling and observational field studies have been obtained by the authors  
593 from the competent authorities.

#### 594 **Data availability**

595 The datasets generated during and/or analyzed during the current study are available from the  
596 corresponding author on reasonable request.

597

#### 598 **References**

- 599 Aitken AE, Fournier J (1993) Macrobenthos communities of Cambridge, McBeth and Itirbilung fiords,  
600 Baffin Island, Northwest Territories, Canada. *Arctic* 46:60-71
- 601 Anisimova NA (1989) Distributional patterns of echinoderms in the Eurasian sector of the Arctic Ocean.  
602 In Herman Y (ed), *The Arctic Seas*. Springer, Boston, pp 281-301
- 603 Bach L, Zbawicka M, Strand J, Wenne R (2018) *Mytilus trossulus* in NW Greenland is genetically more  
604 similar to North Pacific than NW Atlantic populations of the species. *Mar Biodiv*  
605 [doi.org/10.1007/s12526-018-0870-0](https://doi.org/10.1007/s12526-018-0870-0)
- 606 Bell LE, Bluhm BA, Iken K (2016) Influence of terrestrial organic matter in marine food webs of the  
607 Beaufort Sea shelf and slope. *Mar Ecol Prog Ser* 550:1–24. doi: 10.3354/meps11725
- 608 Bluhm BA, Iken K, Mincks Hardy S, Sirenko BI, Holladay BA (2009) Community structure of epibenthic  
609 megafauna in the Chukchi Sea. *Aquat Biol* 7:269–293. doi: 10.3354/ab00198

- 610 Bluhm BA, Iken K, Hopcroft RR (2010) Deep-Sea Research II Observations and exploration of the Arctic's  
611 Canada Basin and the Chukchi Sea: The Hidden Ocean and RUSALCA expeditions. *Deep-Sea Res Part II*  
612 57:1–4. doi.org/10.1016/j.dsr2.2009.08.001
- 613 Bilyard GR, Carey AG (1979) Distribution of western Beaufort Sea polychaetous annelids. *Mar Biol*  
614 54:329–339. doi.org/10.1007/BF00395439
- 615 Brandt A (1997) Abundance, diversity and community patterns of epibenthic-and benthic-boundary  
616 layer peracarid crustaceans at 75 N off East Greenland. *Polar Biol* 17:159-174
- 617 Briggs JC (2003) Marine centers of origin as evolutionary engines. *J Biogeogr* 30:1-18.
- 618 Buzhinskaya GN (ed) (2011) Illustrated keys to free-living invertebrates of Eurasian Arctic Seas and  
619 adjacent Arctic deep waters. Vol. 2. Nemertea, Cephalorhyncha, Oligochaeta, Hiridunida, Pogonophora,  
620 Echiura, Sipuncula, Phoronida, and Brachiopoda. Alaska Sea Grant, University of Alaska Fairbanks.
- 621 Carmack EC, Macdonald RW, Papadakis JE (1989) Water mass structure and boundaries in the  
622 Mackenzie shelf estuary. *J Geophys Res Oceans* 94:18043-18055
- 623 Carmack EC, Wassmann P (2006) Food webs and physical–biological coupling on pan-Arctic shelves:  
624 Unifying concepts and comprehensive perspectives. *Prog Oceanogr* 71:446–477  
625 doi.org/10.1016/j.pocean.2006.10.004
- 626 Carmack E, Winsor P, Williams W (2015) The contiguous panarctic Riverine Coastal Domain: A unifying  
627 concept. *Prog Oceanogr* 139:13–23 [doi.org/10.1016/j.pocean.2015.07.014](https://doi.org/10.1016/j.pocean.2015.07.014)
- 628 Carr CM, Hardy SM, Brown TM, Macdonald TA, Hebert PD (2011) A tri-oceanic perspective: DNA  
629 barcoding reveals geographic structure and cryptic diversity in Canadian polychaetes. *PLoS One*  
630 6:e22232
- 631 Chan FT, Bailey SA, Wiley CJ, MacIsaac HJ (2013) Relative risk assessment for ballast-mediated invasions  
632 at Canadian Arctic ports. *Biol Invasions* 15:295-308
- 633 Cheung WWL, Lam VW, Sarmiento JL, Kearney K, Watson R, Pauly D (2009) Projecting global marine  
634 biodiversity impacts under climate change scenarios. *Fish Fish* 10:235-51
- 635 Clarke A (1983) Life in cold water: the physiological ecology of polar marine ectotherms. *Oceanogr Mar*  
636 *Biol Ann Rev* 21:341-453
- 637 Clarke A (2003) Costs and consequences of evolutionary temperature adaptation. *Trends Ecol Evol*  
638 18:573-581.
- 639 Clarke A, Johnston NM (2003) Antarctic marine benthic diversity. In: Gibson RN, Atkinson RJA (eds)  
640 *Oceanogr Mar Biol* 41, London, 55-57
- 641 Coachman LK, Aagaard K, Tripp RB (1975) Bering Strait: the regional physical oceanography. University  
642 of Washington Press, Seattle
- 643 Coachman LK, Barnes CA (1963) The movement of Atlantic Water in the Arctic Ocean. *Arctic* 16:1–80  
644 [doi.org/10.14430/arctic3517](https://doi.org/10.14430/arctic3517)

- 645 Conlan KE, Kvitek RG (2005) Recolonization of soft-sediment ice scours on an exposed Arctic coast. *Mar*  
646 *Ecol Prog Ser* 286:21-42
- 647 Cowen RK, Sponaugle S (2009) Larval dispersal and marine population connectivity. *Annu Rev Mar Sci*  
648 1:443-466
- 649 Degen R, Faulwetter S (2019) The Arctic Traits database – a repository of Arctic benthic invertebrate  
650 traits. *Earth Syst Sci Data* 11:301-322.
- 651 Divine LM, Iken K, Bluhm BA (2015) Regional benthic food web structure on the Alaska Beaufort Sea  
652 shelf. *Mar Ecol Prog Ser* 531:15-32
- 653 Dunton K (1992) Arctic biogeography: the paradox of the marine benthic fauna and flora. *Trends Ecol*  
654 *Evol* 7:183–189
- 655 Dunton KH, Weingartner T, Carmack EC (2006) The nearshore western Beaufort Sea ecosystem:  
656 Circulation and importance of terrestrial carbon in arctic coastal food webs. *Prog Oceanogr* 71:362–378  
657 [https://doi: 10.1016/j.pocean.2006.09.011](https://doi.org/10.1016/j.pocean.2006.09.011)
- 658 Fossheim M, Primicerio R, Johannesen E, Ingvaldsen RB, Aschan MM, Dolgov AV (2015) Recent warming  
659 leads to a rapid borealization of fish communities in the Arctic. *Nat Clim Change* 5:673-677
- 660 Gaylord B, Gaines SD (2000) Temperature or transport? Range limits in marine species mediated solely  
661 by flow. *Am Nat* 155:769-89
- 662 Galkin SV, Vedenin AA, Minin KV, Rogacheva AV, Molodtsova TN, Rajskiy AK, Kucheruk NV (2015)  
663 Macrobenthos of the southern part of St. Anna trough and the adjacent Kara Sea shelf. *Oceanology*  
664 55:614-22
- 665 Glud RN, Berg P, Hume A, Batty P, Blicher ME, Lennert K, Rysgaard S (2010) Benthic O<sub>2</sub> exchange across  
666 hard-bottom substrates quantified by eddy correlation in a sub-Arctic fjord. *Mar Ecol Prog Ser* 417:1-12
- 667 Golikov AN, Dolgolenko MA, Maximovich NV, Scarlato OA (1990) Theoretical approaches to marine  
668 biogeography. *Mar Ecol Prog Ser* 63:289-301
- 669 Graeve M, Kattner G, Piepenburg D (1997) Lipids in Arctic benthos: does the fatty acid and alcohol  
670 composition reflect feeding and trophic interactions? *Pol Biol* 18:53-61
- 671 Hagerman L, Szaniawska A (1988) Respiration, ventilation and circulation under hypoxia in the  
672 glacial relict *Saduria (Mesidotea) entomon*. *Mar Ecol Prog Ser* 47: 55-63
- 673 Hardy SM, Carr CM, Hardman M, Steinke D, Corstorphine E, Mah C (2011) Biodiversity and  
674 phylogeography of Arctic marine fauna: insights from molecular tools. *Mar Biodiv* 41:195-210
- 675 Harris CM, McTigue ND, McClelland JW, Dunton KH (2018) Do high Arctic coastal food webs rely on a  
676 terrestrial carbon subsidy? *Food Webs*. [doi.org/10.1016/j.fooweb.2018.e00081](https://doi.org/10.1016/j.fooweb.2018.e00081)
- 677 Haug T, Bogstad B, Chierici M, Gjørseter H, Hallfredsson EH, Høines ÅS, Hoel AH, Ingvaldsen RB,  
678 Jørgensen LL, Knutsen T, Loeng H (2017) Future harvest of living resources in the Arctic Ocean north of  
679 the Nordic and Barents Seas: a review of possibilities and constraints. *Fish Res* 188:38-57

- 680 Hebert PD, Cywinska A, Ball SL (2003) Biological identifications through DNA barcodes. *P Roy Soc Lond B:*  
681 *Biol Sci* 270:313-21
- 682 Hedgpeth JW (1957) Marine biogeography. *Geol Soc Am Mem* 67:359–382
- 683 Herman Y (1989) *The Arctic Sea. Climatology, sedimentology and biology.* New York
- 684 Hollowed AB, Planque B, Loeng H (2013) Potential movement of fish and shellfish stocks from the sub-  
685 Arctic to the Arctic Ocean. *Fish Oceanogr* 22:355-70
- 686 Hoegh-Guldberg O, Bruno JF (2010) The impact of climate change on the world's marine ecosystems.  
687 *Science* 328:1523-8
- 688 Holme NA, McIntyre A (1984) *Methods for the study of marine benthos. International Biological*  
689 *Programme Handbook.* 2<sup>nd</sup> edition Blackwell, Oxford
- 690 Howell KL, Billett DS, Tyler PA (2002) Depth-related distribution and abundance of seastars  
691 (Echinodermata: Asteroidea) in the Porcupine Seabight and Porcupine Abyssal Plain, NE Atlantic. *Deep*  
692 *Sea Res I* 49:1901–1920
- 693 Howell KL, Billett DSM, Tyler PA, Davidson R (2004) Feeding ecology of deep-sea seastars  
694 (Echinodermata: Asteroidea): a pigment biomarker approach. *Mar Ecol Prog Ser* 266:103–110  
695 [https://doi: 10.3354/meps266103](https://doi.org/10.3354/meps266103)
- 696 Iken K, Bluhm B, Gradinger R (2005) Food web structure in the high Arctic Canada Basin: evidence  
697 from  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  analysis. *Polar Biol* 28:238–249 <https://doi.org/10.1007/s00300-004-0669-2>
- 698 Jørgensen LL, Archambault P, Blicher M, Denisenko N, Gudmundsson G, Iken K, Roy V, Sørensen J,  
699 Anisimova N, Behe C, Bluhm B, Metcalf V, Olafsdottir S, Schiøtte T, Tendal O, Piepenburg D, Ravelo AM,  
700 Kedra M (2017). 3.3. Benthos. In: CAFF (ed) *State of the Arctic marine biodiversity.* Arctic Council,  
701 *Circumpolar Biodiversity Monitoring Program - Conservation of Arctic Flora and Fauna, International*  
702 *Secretariat, Akureyri, Iceland.* 978-9935-431-63-9. pp 85-104, <http://hdl.handle.net/11374/1955>
- 703 Kinlan BP, Gaines SD, Lester SE (2005) Propagule dispersal and the scales of marine community process.  
704 *Divers Distrib* 11:139-148
- 705 Knox GA, Lowry JK (1977) A comparison between the benthos of the Southern Ocean and the North  
706 Polar Ocean with special reference to the Amphipoda and the Polychaeta. *Polar oceans.* Arctic Institute  
707 of North America, Calgary, pp 423-62
- 708 Konar B, Ravelo A, Grebmeier J, Trefry JH (2014) Size frequency distributions of key epibenthic  
709 organisms in the eastern Chukchi Sea and their correlations with environmental parameters. *Deep-Sea*  
710 *Res Part II* 102:107–118 <https://doi.org/10.1016/j.dsr2.2013.07.015>
- 711 Kosobokova KN, Hopcroft RR, Hirche HJ (2011) Patterns of zooplankton diversity through the depths of  
712 the Arctic's central basins. *Mar Biodiv* 41:29-50
- 713 Krylova EM, Ivanov DL, Mironov AN (2013) The ratio of species of Atlantic and Pacific origin in modern  
714 Arctic fauna of bivalve mollusks. *Invert Zool* 10:89-126

- 715 Kuklinski P, Taylor PD, Denisenko NV, Berning B (2013) Atlantic origin of the Arctic biota? Evidence from  
716 phylogenetic and biogeographical analysis of the cheilostome bryozoan genus *Pseudoflustra*. PLoS one  
717 8:e59152
- 718 Laakkonen H (2015) Phylogeography of amphi-boreal marine fauna. Helsingin yliopisto. Helsinki, pp 48
- 719 Lalande C, Forest A, Barber DG, Gratton Y, Fortier L (2009) Variability in the annual cycle of vertical  
720 particulate organic carbon export on Arctic shelves: Contrasting the Laptev Sea, Northern Baffin Bay and  
721 the Beaufort Sea. Cont Shelf Res 29:2157-2165
- 722 Lansard B, Mucci A, Miller LA, Macdonald RW, Gratton Y (2012) Seasonal variability of water mass  
723 distribution in the southeastern Beaufort Sea determined by total alkalinity and  $\delta^{18}O$ . J Geophys Res:  
724 Oceans (1978–2012) 117:C03003
- 725 MacPherson E (1971) The marine mollusks of Arctic Canada. National Museum of Canada Publications in  
726 Biological Oceanography No. 3
- 727 Macdonald RW, Yu Y (2006) The Mackenzie estuary of the Arctic Ocean. In: Wangersky PJ (eds)  
728 Estuaries. Springer, Berlin, pp 91–120
- 729 Maggs CA, Castilho R, Foltz D, Henzler C, Jolly MT, Kelly J, Olsen J, Perez KE, Stam W, Väinölä R, Viard F  
730 (2008) Evaluating signatures of glacial refugia for North Atlantic benthic marine taxa. Ecology 89:S108-  
731 S122. [doi.org/10.1890/08-0257.1](https://doi.org/10.1890/08-0257.1)
- 732 Mahoney A, Eicken H, Gaylord AG, Shapiro L (2007) Alaska landfast sea ice: Links with bathymetry and  
733 atmospheric circulation. J Geophys Res 112:C02001. <https://doi.org/10.1029/2006JC003559>
- 734 Mahoney AR, Eicken H, Gaylord AG, Gens R (2014) Landfast sea ice extent in the Chukchi and Beaufort  
735 Seas: The annual cycle and decadal variability. Cold Reg Sci Technol 103:41–56  
736 [doi.org/10.1016/j.coldregions.2014.03.003](https://doi.org/10.1016/j.coldregions.2014.03.003)
- 737 Majewski AR, Atchison S, MacPhee S, Eert J, Niemi A, Michel C, Reist JD (2017) Marine fish community  
738 structure and habitat associations on the Canadian Beaufort shelf and slope. Deep-Sea Res I 121:169–  
739 182. [doi.org/10.1016/j.dsr.2017.01.009](https://doi.org/10.1016/j.dsr.2017.01.009)
- 740 Mayer M, Piepenburg D (1996) Epibenthic community patterns on the continental slope off East  
741 Greenland at 75° N. Mar Ecol Prog Ser 143:151–164. [doi.org/10.3354/meps143151](https://doi.org/10.3354/meps143151)
- 742 McLaughlin FA, Carmack EC, Macdonald RW, Bishop JK (1996) Physical and geochemical properties  
743 across the Atlantic/Pacific water mass front in the southern Canadian Basin. J Geophys Res: Oceans  
744 101:1183-1197
- 745 Menzies RJ (1973) Biological history of the Mediterranean Sea with reference to the abyssal benthos.  
746 Rapports de la Commission Internationale pour l'Exploration Scientifique de la Mer Méditerranée 1:717-  
747 23
- 748 Mironov AN, Dilman AB (2010) Effect of the East Siberian barrier on the echinoderm dispersal in the  
749 Arctic Ocean. Oceanology 50:342-55
- 750 Mironov AN, Dilman AB, Krylova EM (2013) Global distribution pattern of genera occurring in the Arctic  
751 Ocean deeper than 2000 m. Invertebrate Zool 10(1):167-194



- 752 Mueter FJ, Litzow MA (2008) Sea ice retreat alters the biogeography of the Bering Sea continental shelf.  
753 Ecol Appl 18:309-20
- 754 Nephin J, Juniper SK, Archambault P (2014) Diversity, abundance and community structure of benthic  
755 macro-and megafauna on the Beaufort shelf and slope. PLoS One 9:e101556
- 756 Nesis KN (1984) A hypothesis on the origin of western and eastern Arctic distribution area of marine  
757 bottom animals. Soviet J Mar Biol 9:235-243
- 758 Norcross BL, Holladay BA, Busby MS, Mier KL (2010) Demersal and larval fish assemblages in the Chukchi  
759 Sea. Deep-Sea Res II 57:57-70
- 760 Okkonen SR, Ashjian CJ, Campbell RG, Maslowski W, Clement-Kinney JL, Potter R (2009) Intrusion of  
761 warm Bering/Chukchi waters onto the shelf in the western Beaufort Sea. J Geophys Res 114:C00A11  
762 [doi.org/10.1029/2008JC004870](https://doi.org/10.1029/2008JC004870)
- 763 Parada C, Armstrong DA, Ernst B, Hinckley S, Orensanz JM (2010) Spatial dynamics of snow crab  
764 (*Chionoecetes opilio*) in the eastern Bering Sea—putting together the pieces of the puzzle. B Mar Sci  
765 86:413-437
- 766 Peck LS, Webb KE, Bailey DM (2004) Extreme sensitivity of biological function to temperature in  
767 Antarctic marine species. Fun Ecol 18:625-630
- 768 Pickart RS, Schulze LM, Moore GWK, Charette MA, Arrigo KR, van Dijken G, Danielson SL (2013) Long-  
769 term trends of upwelling and impacts on primary productivity in the Alaskan Beaufort Sea. Deep Sea  
770 Res. Part I 79:106–121 [doi.org/10.1016/j.dsr.2013.05.003](https://doi.org/10.1016/j.dsr.2013.05.003)
- 771 Piepenburg D, Schmid MK (1996) Brittle star fauna (Echinodermata: Ophiuroidea) of the Arctic  
772 northwestern Barents Sea: composition, abundance, biomass and spatial distribution. Polar Biol 16:383-  
773 392
- 774
- 775 Piepenburg D, Schmid MK (1997) A photographic survey of the epibenthic megafauna of the Arctic  
776 Laptev Sea shelf: Distribution, abundance, and estimates of biomass and organic carbon demand. Mar  
777 Ecol Prog Ser 147:63-75
- 778 Piepenburg D, Voss J, Gutt J (1997) Assemblages of sea stars (Echinodermata: Asteroidea) and brittle  
779 stars (Echinodermata: Ophiuroidea) in the Weddell Sea (Antarctica) and off Northeast Greenland  
780 (Arctic): A comparison of diversity and abundance. Polar Biol 17:305-322
- 781 Piepenburg D (2003) Arctic brittle stars (Echinodermata: Ophiuroidea). Oceanogr Mar Biol 38:189-256
- 782 Piepenburg D (2005) Recent research on Arctic benthos: common notions need to be revised. Polar Biol  
783 28:733–755 doi: 10.1007/s00300-005-0013-5
- 784 Piepenburg D, Archambault P, Ambrose WG, Blanchard AL, Bluhm BA, Carroll ML, Conlan KE, Cusson M,  
785 Feder HM, Grebmeier JM, Jewett SC (2011) Towards a pan-Arctic inventory of the species diversity of  
786 the macro- and megabenthic fauna of the Arctic shelf seas. Mar Biodiv 41:51–70. doi: 10.1007/s12526-  
787 010-0059-7

- 788 Polyakov IV, Pnyushkov AV, Alkire MB, Ashik IM, Baumann TM, Carmack EC, Goszczko I, Guthrie J, Ivanov  
789 VV, Kanzow T, Krishfield R (2017) Greater role for Atlantic inflows on sea-ice loss in the Eurasian Basin of  
790 the Arctic Ocean. *Science* 356:285-291
- 791 Ravelo AM, Konar B, Trefry JH, Grebmeier JM (2014) Epibenthic community variability in the  
792 northeastern Chukchi Sea. *Deep Res Part II* 102:119–131 doi: 10.1016/j.dsr2.2013.07.017
- 793 Ravelo AM, Konar B, Bluhm BA (2015) Spatial variability of epibenthic communities on the Alaska  
794 Beaufort Shelf. *Polar Biol* 38:1783–1804 [doi.org/10.1007/s00300-015-1741-9](https://doi.org/10.1007/s00300-015-1741-9)
- 795 Ravelo AM, Konar B, Bluhm B, Iken K (2016) Growth and production of the brittle stars *Ophiura sarsii*  
796 and *Ophiocten sericeum* (Echinodermata: Ophiuroidea). *Cont Shelf Res* 139:9-20
- 797 Reid PC, Johns DG, Edwards M, Starr M, Poulin M, Snoeijs P (2007) A biological consequence of reducing  
798 Arctic ice cover: arrival of the Pacific diatom *Neodenticula seminae* in the North Atlantic for the first time  
799 in 800 000 years. *Glob Change Biol* 13:1910-1921
- 800 Reimnitz E, Kempema EW (1984) Pack ice interaction with Stamukhi Shoal, Beaufort Sea, Alaska. In:  
801 Barnes PW, Reimnitz E, Schell DM (eds) *The Alaskan Beaufort Sea: ecosystems and environments*.  
802 Academic Press Inc, Orlando, pp 159–181
- 803 Renaud PE, Sejr MK, Bluhm BA, Sirenko B, Ellingsen IH (2015) The future of Arctic benthos: Expansion,  
804 invasion, and biodiversity. *Prog Oceanogr* 139:244-257
- 805 Rex MA, Etter RJ, Morris JS, Crouse J, McClain CR, Johnson NA, Stuart CT, Deming JW, Thies R, Avery R  
806 (2006) Global bathymetric patterns of standing stock and body size in the deep-sea benthos. *Mar Ecol*  
807 *Prog Ser* 317:1-8
- 808 Roxburgh SH, Shea K, Wilson JB (2004) The intermediate disturbance hypothesis: patch dynamics and  
809 mechanisms of species coexistence. *Ecology* 85:359-371
- 810 Roy V, Iken K, Archambault P (2014) Environmental drivers of the Canadian Arctic megabenthic  
811 communities. *PLoS One* 9:e100900 doi:10.1371/journal.pone.0100900
- 812 Roy V, Iken K, Archambault P (2015) Regional variability of megabenthic community structure across the  
813 Canadian Arctic. *Arctic* 68:180–192
- 814 Rudels B, Jones EP, Anderson LG, Kattner G (1994) On the intermediate depth waters of the Arctic  
815 Ocean. In: Johannessen OM, Muench RD, Overland JE (eds) *The Polar Oceans and Their Role in Shaping*  
816 *the Global Environment*, Washington DC, pp 33-46 [doi.org/10.1029/GM085](https://doi.org/10.1029/GM085)
- 817 Schauer U, Fahrbach E, Osterhus S, Rohardt G (2004) Arctic warming through the Fram Strait: Oceanic  
818 heat transport from 3 years of measurements. *J Geophys Res* 109:C06026
- 819 Shimada K, Carmack EC, Hatakeyama K, Takizawa T (2001) Varieties of shallow temperature maximum  
820 waters in the western Canadian Basin of the Arctic Ocean. *Geophys Res Lett* 28:3441-3444
- 821 Shimada K, McLaughlin F, Carmack E, Proshutinsky A, Nishino S, Itoh M (2004) Penetration of the 1990s  
822 warm temperature anomaly of Atlantic water in the Canada basin. *Geophys Res Lett* 31:L20301  
823 [doi.org/10.1029/2004GL020860](https://doi.org/10.1029/2004GL020860)

- 824 Shimada K, Itoh M, Nishino S, McLaughlin F, Carmack E, Proshutinsky A (2005) Halocline structure in the  
825 Canada Basin of the Arctic Ocean. *Geophys Res Lett* 32:L03605 [doi.org/10.1029/2004GL021358](https://doi.org/10.1029/2004GL021358)
- 826 Sirenko BI, Gagaev SY (2007) Unusual abundance of macrobenthos and biological invasions in the  
827 Chukchi Sea. *Russ J Mar Biol* 33:335-364
- 828 Smirnov AV (1994) Arctic echinoderms: composition, distribution and history of the fauna. In: David B,  
829 Guille A, Féral JP, Roux M (eds) *Echinoderms through time (Echinoderms Dijon)*. Balkema, Rotterdam, pp  
830 135–143
- 831 Smoot CA, Hopcroft RR (2016) Cross-shelf gradients of epipelagic zooplankton communities of the  
832 Beaufort Sea and the influence of localized hydrographic features. *J Plankton Res* 39:65-78
- 833 Smoot CA, Hopcroft RR (2017) Depth-stratified community structure of Beaufort Sea slope zooplankton  
834 and its relations to water masses. *J Plankton Res* 39:79-91
- 835 Starmans A, Gutt J, Arntz WE (1999) Mega-epibenthic communities in Arctic and Antarctic shelf areas.  
836 *Mar Biol* 135:269-280
- 837 Stasko AD, Bluhm BA, Michel C, Archambault P, Majewski A, Reist JD, Swanson H, Power M (2018)  
838 Benthic-pelagic trophic coupling in an Arctic marine food web along vertical water mass and organic  
839 matter gradients. *Mar Ecol Progr Ser* 594:1-9
- 840 Steffens M, Piepenburg D, Schmid MK (2006) Distribution and structure of macrobenthic fauna in the  
841 eastern Laptev Sea in relation to environmental factors. *Polar Biol* 29:837-848
- 842 Tempestini A, Rysgaard S, Dufresne F (2018) Species identification and connectivity of marine  
843 amphipods in Canada's three oceans. *PLoS One* 13:e0197174
- 844 Vassilenko SV, VV Petryashov (eds.) (2009) *Illustrated Keys to Free-Living Invertebrates of Eurasian Arctic*  
845 *Seas and Adjacent Deep Waters, Vol. 1. Rotifera, Pycnogonida, Cirripedia, Leptostraca, Mysidacea,*  
846 *Hyperiidia, Caprellidea, Euphausiacea, Dendrobranchiata, Pleocyemata, Anomura, and Brachyura.*  
847 Alaska Sea Grant, University of Alaska Fairbanks
- 848 Vermeij GT (1991) Anatomy of an invasion: the trans-Arctic interchange. *Paleobiol* 17:281-307
- 849 Wei MA, Etter RJ, Morris JS, Crouse J, McClain CR, Johnson NA, Stuart CT, Deming JW, Thies R, Avery R  
850 (2006) Global bathymetric patterns of standing stock and body size in the deep-sea benthos. *Mar Ecol*  
851 *Prog Ser* 317:1-8
- 852 Wei CL, Rowe GT, Escobar-Briones E, Boetius A, Soltwedel T, Caley MJ, Soliman Y, Huettmann F, Qu F, Yu  
853 Z, Pitcher CR et al. (2010) Global patterns and predictions of seafloor biomass using random forests.  
854 *PLoS One* 5:e15323
- 855 Weingartner TJ, Danielson SL, Potter RA, Trefry JH, Mahoney A, Savoie M, Irvine C, Sousa L (2017)  
856 Circulation and water properties in the landfast ice zone of the Alaskan Beaufort Sea. *Cont Shelf Res*  
857 148:185-198
- 858 Węśławski JM, Dragańska-Deja K, Legeżyńska J, Walczowski W (2018) Range extension of a boreal  
859 amphipod *Gammarus oceanicus* in the warming Arctic. *Ecol Evol* 8:7624-32

- 860 Zenkevitch L (1963) *Biology of the Seas of the USSR*. Interscience Publishers, New York
- 861 Zhulay I, Iken K, Renaud P, Bluhm BA (2019) Epifaunal community across marine landscapes of the deep  
862 Chukchi Borderland (Pacific Arctic). *Deep-Sea Research I* [doi.org/10.1016/j.dsr.2019.06.011](https://doi.org/10.1016/j.dsr.2019.06.011)

863 **Tables**

864 Table 1: Beaufort Sea study region water mass classification used in the present study. Published depth  
 865 ranges corresponding to each water mass category, the depth range of the sample station and the  
 866 number of stations assigned to each water mass are given. For relevant references see methods text.

Water mass category (abbreviation)	Literature-based depth range (m)	Station depth range (m)	Number of stations
Coastal Zone (CZ)	0 - 35	3 - 35	33
Polar Mixed Layer (PML)	36 - <100	36 - 75	31
Arctic Halocline (AH)	>50 - 250	96 - 230	28
Atlantic Water (AW)	<250 - <750	302 - 702	23
Canadian Basin Deep Water (CBDW)	750 - 1000	750 - 1163	21

867

868

869 Table 2: Distribution of epibenthic mean biomass (g ww/1000 m<sup>2</sup>), abundance (ind./1000 m<sup>2</sup>), richness  
 870 (number of taxa) and evenness (calculated using Pielou's evenness formula) among water masses in the  
 871 central Beaufort Sea study region. sd: standard deviation. Coastal Zone (CZ), Polar Mixed Layer (PML),  
 872 Arctic Halocline (AH), Atlantic Water (AW), Canadian Basin Deep Water (CBDW). For description of water  
 873 mass categories see methods text.

Water mass category	mean biomass (sd)		mean abundance (sd)		mean richness (sd)		mean evenness (sd)	
CZ	1,122	(1,213)	2,491	(3,190)	29.2	(15.1)	0.63	(0.1)
PML	7,789	(7,802)	14,491	(14,539)	37.9	(8.9)	0.55	(0.2)
AH	5,999	(7,081)	8,882	(10,681)	32.6	(7.6)	0.65	(0.1)
AW	1,745	(1,656)	700	(555)	25.4	(5.2)	0.57	(0.1)
CBDW	1,248	(2,199)	843	(971)	22.9	(5.2)	0.56	(0.1)

874

875

876 Table 3: Significant differences of epifaunal communities in the Beaufort Sea among water mass  
 877 categories for biomass, taxon richness and evenness. Only significant values for Tukey's test (95%  
 878 confidence level) are shown for each comparison of means. df: degrees of freedom, SS: sum of squares.  
 879 Coastal Zone (CZ), Polar Mixed Layer (PML), Arctic Halocline (AH), Atlantic Water (AW), Canadian Basin  
 880 Deep Water (CBDW). For description of water mass categories see methods text.

881

Response variable	water mass category		df	SS	F-value	p-value
Biomass			4	1,099,000	10.6	0.0001
	CZ	vs AH				0.0025
	PML	vs AW				0.0010
	PML	vs CBDW				0.0010
	AH	vs AW				0.0282
	AH	vs CBDW				0.0130
Taxon Richness			4	3,658	9.7	0.0001
	CZ	vs PML				0.0046
	PML	vs AW				0.0010
	PML	vs CBDW				0.0010
	AH	vs CBDW				0.0064
Evenness			4	0.2028	3.549	0.0089
	PML	vs AH				0.0218

882

883 Table 4: Multi-variate test results showing significant differences in epifaunal community biomass  
 884 composition among water masses in the Beaufort Sea. PERMANOVA design used “water mass” as fixed  
 885 factor. df: degrees of freedom, SS: sums of squares, MS: mean squares, Pseudo-F: pseudo-*F* ratio,  
 886 P(perm): permutation *P*-value and perms: unique permutations.

Source	df	SS	MS	Pseudo-F	P(perm)	perms
Water mass	4	176,790	44,199	19.11	0.0001	9,845
Residuals	131	303,060	2,313			
Total	135	479,860				

887

888



889 Table 5: Significant differences among epifaunal communities in different water masses. Shown are  
 890 results from pairwise comparisons from PERMANOVA analysis. P(perm) was 0.001 across all groups and  
 891 number of unique permutations ranged from 997-999. Water mass labels correspond to Coastal Zone  
 892 (CZ), Polar Mixed Layer (PML), Arctic Halocline (AH), Atlantic Water (AW), and Canadian Basin Deep  
 893 Water (CBDW). df: degrees of freedom, t: *t statistic*. For description of water mass categories see  
 894 methods text.

895

Water mass Group comparisons	t	df
CBDW – PML	6.26	50
AW – PML	5.47	52
AH – CBDW	5.27	47
CBDW - CZ	4.73	52
CZ – AW	4.17	54
AH – AW	3.88	49
AW – PML	3.72	57
AH – CZ	3.72	59
CZ – PML	3.47	62
CBDW – AW	2.66	42

896

897

898 Table 6: Taxa that contributed most to the similarity (%) among stations within epibenthic communities  
 899 in each water mass. The total community similarity within each water mass is presented in parenthesis  
 900 in the water mass column. The individual contribution to within-group similarity of each taxon is  
 901 presented in percentage (Contribution, %) as well as their cumulative contribution (Cumulative, %). Only  
 902 taxa individually contributing  $\geq 5\%$  similarity are presented here. A: Arthropoda, C: Cnidaria, E:  
 903 Echinodermata, M: Mollusca.

Water mass (Similarity)	Taxa (Phylum)	Av. Similarity	Contribution (%)	Cumulative (%)
Coastal Zone (21%)	<i>Eualus gaimardii</i> (A)	3.7	17.4	17.4
	<i>Sabinea septemcarinata</i> (A)	1.7	8.2	25.6
	<i>Saduria entomon</i> (A)	1.6	7.6	33.2
	<i>Ophiecten sericeum</i> (E)	1.4	6.5	39.7
	<i>Anonyx</i> sp. (A)	1.2	5.7	45.4
Polar Mixed Layer (37%)	<i>Psolus peronii</i> (E)	7.9	21.4	21.4
	<i>Ophiecten sericeum</i> (E)	5.5	15.0	36.4
	<i>Similipecten greenlandicus</i> (M)	4.6	12.5	48.9
	<i>Sabinea septemcarinata</i> (A)	2.7	7.4	56.3
Arctic Halocline (34%)	<i>Ophiacantha bidentata</i> (E)	5.6	16.6	16.6
	<i>Ophiecten sericeum</i> (E)	4.9	14.5	31.1
	<i>Florometra</i> sp. (E)	3.0	9.0	40.1
	<i>Pontaster tenuispinus</i> (E)	2.5	7.4	47.5
	<i>Allantactis parasitica</i> (C)	2.0	5.9	53.4
	<i>Argis</i> spp. (A)	1.7	5.0	58.4
Atlantic Water (37%)	<i>Pontaster tenuispinus</i> (E)	8.4	22.9	22.9
	<i>Ophiopleura borealis</i> (E)	5.7	15.5	38.4
	<i>Bathybiaster vexillifer</i> (E)	3.4	9.3	47.7
	<i>Icasterias panopla</i> (E)	3.0	8.3	56.0
	<i>Eualus gaimardii</i> (A)	2.9	7.9	63.8
Canadian Basin Deep Water (45%)	<i>Ophiopleura borealis</i> (E)	13.8	30.5	30.5
	<i>Bathybiaster vexillifer</i> (E)	6.2	13.8	44.3
	<i>Pontaster tenuispinus</i> (E)	6.1	13.4	57.7
	<i>Saduria sabini</i> (A)	2.9	6.4	64.1
	Zoantharia (C)	2.3	5.0	69.1

904

905

906 **Figure Captions**

907 **Fig 1** Beaufort Sea study region, stations are color coded by sampling year. Colored arrows represent the  
908 major oceanographic features in the region

909 **Fig 2** Distribution of stations in the Beaufort Sea study region in a salinity versus temperature (°C) plot.  
910 Stations are color coded according to *a priori* assigned water masses based on their depth distribution  
911 (see text and references for details). Coastal Zone (CZ), Polar Mixed Layer (PML), Arctic Halocline (AH),  
912 Atlantic Water (AW), Canadian Basin Deep Water (CBDW)

913 **Fig 3** Beaufort Sea study region stations. a. Distribution of stations color coded by *a priori* designated  
914 water masses. b. Total epibenthic biomass (g ww/1000 m<sup>2</sup>), represented by the size of the circle at each  
915 station. c. Taxon richness, represented by the size of the circle at each station. Coastal Zone (CZ), Polar  
916 Mixed Layer (PML), Arctic Halocline (AH), Atlantic Water (AW), Canadian Basin Deep Water (CBDW)

917 **Fig 4** Epibenthic assemblage similarity on the central Beaufort Sea shelf and slope, shown in an nMDS  
918 plot based on square-root transformed epibenthic biomass data. Stations are symbolized by water mass  
919 (see text for details). Coastal Zone (CZ), Polar Mixed Layer (PML), Arctic Halocline (AH), Atlantic Water  
920 (AW), Canadian Basin Deep Water (CBDW)

921 **Fig 5** Number of taxa represented in sampled trawls in the Beaufort Sea study region for Mollusca (a),  
922 Echinodermata (b) and Arthropoda (c), color coded by the proportions of their biomass occurring in  
923 each water mass shown in shades black (100-75% of biomass), red (75-50%), pink (50-25%) and light  
924 pink (25-0.1%). Coastal Zone (CZ), Polar Mixed Layer (PML), Arctic Halocline (AH), Atlantic Water (AW),  
925 Canadian Basin Deep Water (CBDW)

926 **Fig 6** Proportion of epibenthic biomass (a) and number of taxa (b) by biogeographic affinity in each  
927 water mass domain in the Beaufort Sea study area for Mollusca (M), Echinodermata (E), and  
928 Decapoda/Isopoda (D-I). Coastal Zone (CZ), Polar Mixed Layer (PML), Arctic Halocline (AH), Atlantic  
929 Water (AW), Canadian Basin Deep Water (CBDW). For biogeographic affinity designation, see methods  
930 text and ESM 2.

931 **Fig 7** Biogeographic affinity of the proportion of epibenthic biomass (left) and number of taxa (right) in  
932 each water mass domain in the Beaufort Sea study area for Mollusca (a), Echinodermata (b) and  
933 Decapoda/Isopoda (c). Coastal Zone (CZ), Polar Mixed Layer (PML), Arctic Halocline (AH), Atlantic Water  
934 (AW), Canadian Basin Deep Water (CBDW). For biogeographic affinity designation, see methods text and  
935 ESM 2.

936

937 ESM 1: Station table. Station number corresponds to those featured in Figure 1, Figure 3 and ESM 3.

938 Station name corresponds to station identification assigned during field collections.

Station number	Station name	Year sampled	Latitude (decimal degree N)	Longitude (decimal degree West)	Depth (m)	Water mass category
1	A1-100	2013	70.34	-141.12	100	Arctic Halocline
2	A1-1000	2013	70.60	-141.04	1008	Canadian Basin Deep Water
3	A1-20	2013	69.72	-141.14	20	Coastal Zone
4	A1-200	2013	70.37	-141.19	210	Arctic Halocline
5	A1-350	2014	70.41	-141.05	350	Atlantic Water
6	A1-50	2013	70.04	-141.08	50	Polar Mixed Layer
7	A1-500	2013	70.47	-141.02	500	Atlantic Water
8	A1-750	2013	70.53	-141.03	752	Canadian Basin Deep Water
9	A2-100	2013	70.49	-141.94	100	Arctic Halocline
10	A2-1000	2013	70.63	-142.07	988	Canadian Basin Deep Water
11	A2-20	2013	69.92	-142.23	20	Coastal Zone
12	A2-200	2013	70.50	-141.91	230	Arctic Halocline
13	A2-350	2013	70.54	-142.00	352	Atlantic Water
14	A2-50	2013	70.12	-142.26	50	Polar Mixed Layer
15	A2-500	2013	70.56	-141.98	506	Atlantic Water
16	A2-750	2013	70.62	-141.95	757	Canadian Basin Deep Water
17	A6-100	2013	70.82	-146.06	100	Arctic Halocline
18	A6-1000	2013	71.02	-146.13	1004	Canadian Basin Deep Water
19	A6-20	2013	70.43	-146.11	34	Coastal Zone
20	A6-200	2014	70.89	-146.08	200	Arctic Halocline
21	A6-350	2013	70.93	-146.07	350	Atlantic Water
22	A6-50	2013	70.68	-146.09	50	Polar Mixed Layer
23	A6-750	2013	70.97	-146.03	782	Canadian Basin Deep Water
24	A6-mid PSBT	2013	70.33	-146.06	30	Coastal Zone
25	GRY-100 PSBT	2013	70.09	-137.77	100	Arctic Halocline
26	GRY-1000 PSBT	2013	70.52	-139.23	960	Canadian Basin Deep Water
27	GRY-20	2014	69.70	-136.67	20	Coastal Zone
28	GRY-200	2013	70.14	-137.98	200	Arctic Halocline
29	GRY-350 PSBT	2013	70.25	-138.36	350	Atlantic Water
30	GRY-50	2013	69.88	-137.22	50	Polar Mixed Layer
31	GRY-500 PSBT	2013	70.30	-138.49	505	Atlantic Water
32	GRY-750 PSBT	2013	70.44	-138.95	756	Canadian Basin Deep Water

33	MAC-100	2013	69.63	-137.97	100	Arctic Halocline
34	MAC-1000 PSBT	2013	70.59	-139.78	980	Canadian Basin Deep Water
35	MAC-200	2013	69.83	-138.40	200	Arctic Halocline
36	MAC-50	2014	69.46	-137.66	50	Polar Mixed Layer
37	MAC-500 PSBT	2013	70.30	-139.26	500	Atlantic Water
38	TBS-100	2014	70.24	-140.26	100	Arctic Halocline
39	TBS-1000 PSBT	2013	70.60	-140.37	1007	Canadian Basin Deep Water
40	TBS-200	2014	70.27	-140.30	200	Arctic Halocline
41	TBS-350 PSBT	2013	70.34	-140.39	361	Atlantic Water
42	TBS-50	2014	70.16	-140.40	50	Polar Mixed Layer
43	TBS-500 PSBT	2013	70.42	-140.36	505	Atlantic Water
44	TBS-750 PSBT	2013	70.56	-140.45	750	Canadian Basin Deep Water
45	A1-100	2014	70.33	-141.07	102	Arctic Halocline
46	A1-1000	2014	70.62	-141.15	1000	Canadian Basin Deep Water
47	A1-20	2013	69.72	-141.15	20	Coastal Zone
48	A1-200	2014	70.37	-141.21	205	Arctic Halocline
49	A1-350	2013	70.41	-141.05	350	Atlantic Water
50	A1-50	2013	70.03	-141.02	50	Polar Mixed Layer
51	A1-500	2014	70.46	-140.99	501	Atlantic Water
52	A1-750	2014	70.53	-141.06	702	Atlantic Water
53	A2-100	2014	70.48	-141.92	100	Arctic Halocline
54	A2-1000	2014	70.63	-142.05	1043	Canadian Basin Deep Water
55	A2-10-13	2014	69.92	-142.23	13	Coastal Zone
56	A2-20	2014	69.98	-142.22	22	Coastal Zone
57	A2-200	2014	70.50	-141.93	213	Arctic Halocline
58	A2-350	2014	70.54	-142.06	354	Atlantic Water
59	A2-40-13	2014	70.13	-142.30	43.3	Polar Mixed Layer
60	A2-50	2014	70.29	-142.14	52.5	Polar Mixed Layer
61	A2-500	2014	70.56	-141.98	505	Atlantic Water
62	A2-750	2014	70.61	-141.95	750	Canadian Basin Deep Water
63	A4-100	2014	70.58	-144.16	100	Arctic Halocline
64	A4-20	2014	70.20	-144.09	22	Coastal Zone
65	A4-35	2014	70.30	-144.07	37	Polar Mixed Layer
66	A4-50	2014	70.46	-144.07	53	Polar Mixed Layer
67	A5-100	2014	70.72	-145.08	103	Arctic Halocline
68	A5-1000	2014	70.99	-145.02	1075	Canadian Basin Deep Water
69	A5-20	2014	70.12	-145.10	20	Coastal Zone
70	A5-200	2014	70.75	-145.07	200	Arctic Halocline
71	A5-35	2014	70.33	-145.10	35	Coastal Zone
72	A5-350	2014	70.84	-145.08	350	Atlantic Water
73	A5-50	2013	70.55	-145.06	50	Polar Mixed Layer
74	A5-500	2014	70.94	-145.09	500	Atlantic Water

75	A5-750	2014	70.97	-145.02	753	Canadian Basin Deep Water
76	A6-100	2014	70.82	-146.04	102	Arctic Halocline
77	A6-1000	2014	71.01	-146.08	973	Canadian Basin Deep Water
78	A6-1500	2014	71.03	-146.13	1163	Canadian Basin Deep Water
79	A6-20	2014	70.27	-146.11	23	Coastal Zone
80	A6-200	2013	70.89	-146.02	200	Arctic Halocline
81	A6-350	2014	70.92	-145.97	355	Atlantic Water
82	A6-37	2014	70.45	-146.11	37	Polar Mixed Layer
83	A6-50	2014	70.64	-146.09	51	Polar Mixed Layer
84	A6-500	2014	70.96	-146.06	500	Atlantic Water
85	A6-750	2014	70.97	-146.04	750	Canadian Basin Deep Water
86	TBS-100	2013	70.25	-140.31	100	Arctic Halocline
87	TBS-1000	2014	70.60	-140.42	1000	Canadian Basin Deep Water
88	TBS-200	2013	70.27	-140.33	200	Arctic Halocline
89	TBS-350	2014	70.34	-140.36	347	Atlantic Water
90	TBS-50	2014	70.15	-140.37	50	Polar Mixed Layer
91	TBS-500	2014	70.40	-140.32	500	Atlantic Water
92	TBS-750	2014	70.56	-140.45	753	Canadian Basin Deep Water
93	AN14-1	2014	71.32	-152.10	64	Polar Mixed Layer
94	AN14-1.05	2014	71.08	-152.56	16	Coastal Zone
95	AN14-10	2014	70.71	-148.79	24	Coastal Zone
96	AN14-11	2014	70.88	-148.14	44	Polar Mixed Layer
97	AN14-12	2014	70.67	-147.60	39	Polar Mixed Layer
98	AN14-15	2014	70.64	-146.69	40	Polar Mixed Layer
99	AN14-8	2014	70.74	-149.45	19	Coastal Zone
100	AN14-1C	2014	70.15	-144.80	24	Coastal Zone
101	AN14-20	2014	70.35	-144.45	39	Polar Mixed Layer
102	AN14-21	2014	70.27	-143.88	39	Polar Mixed Layer
103	AN14-22	2014	70.19	-142.89	35	Coastal Zone
104	AN14-23	2014	70.01	-141.97	35	Coastal Zone
105	AN14-24	2014	70.26	-141.75	52	Polar Mixed Layer
106	AN14-25	2014	69.85	-141.70	23	Coastal Zone
107	AN14-5	2014	70.95	-151.37	19	Coastal Zone
108	AN14-T3	2014	70.44	-145.82	38	Polar Mixed Layer
109	AN14-5B (29)	2014	70.58	-148.93	17	Coastal Zone
110	AN14-6	2014	71.28	-151.56	54	Polar Mixed Layer
111	AN14-6D	2014	70.75	-150.48	19	Coastal Zone
112	71-145	2015	70.67	-144.91	96	Arctic Halocline
113	AN14-7	2014	70.85	-150.06	25	Coastal Zone
114	AN14-7C (23)	2014	70.92	-152.01	10	Coastal Zone
115	AN14-16	2014	70.74	-145.92	61	Polar Mixed Layer
116	71-146	2015	70.96	-145.74	399	Atlantic Water
117	AN14-L250-5	2014	70.36	-146.11	31	Coastal Zone
118	143W-2	2015	70.44	-143.61	45	Polar Mixed Layer

119	143W-1	2015	70.26	-143.60	37	Polar Mixed Layer
120	AN14-5(5)	2014	70.44	-147.34	19	Coastal Zone
121	143W-3	2015	70.55	-143.54	100	Arctic Halocline
122	143W-4	2015	70.57	-143.60	151	Arctic Halocline
123	143W-5	2015	70.63	-143.58	302	Atlantic Water
124	149-200	2015	71.21	-149.35	200	Arctic Halocline
125	152W0	2015	71.00	-152.38	13	Coastal Zone
126	152W1	2015	71.19	-152.25	36	Coastal Zone
127	3A	2015	70.28	-147.07	3	Coastal Zone
128	5A	2015	70.50	-148.77	9	Coastal Zone
129	70-142	2015	70.46	-142.38	62	Polar Mixed Layer
130	70-143	2015	70.36	-142.82	54	Polar Mixed Layer
131	70-145	2015	70.49	-144.95	43	Polar Mixed Layer
132	AN14-6F (21)	2014	70.67	-151.21	13	Coastal Zone
133	AN14-9	2014	70.96	-149.00	36	Coastal Zone
134	71-147	2015	70.97	-147.40	107	Arctic Halocline
135	71-149	2015	71.15	-148.41	75	Polar Mixed Layer
136	71-150	2015	70.94	-151.00	15	Coastal Zone

939

940

941

942 ESM2: Biogeographic affinity and source for taxa included in biogeographic analysis.

<b>Mollusca taxa</b>	<b>Class</b>	<b>Biogeographic affinity</b>	<b>Reference</b>
<i>Bathyarca glacialis</i>	Bivalvia	Atlantic Boreal Arctic	Coan et al. (2000)
<i>Ciliatocardium ciliatum</i>	Bivalvia	Boreal Arctic	Coan et al. (2000)
<i>Hiatella arctica</i>	Bivalvia	Boreal Arctic	Coan et al. (2000)
<i>Lyonsia arenosa</i>	Bivalvia	Boreal Arctic	Coan et al. (2000)
<i>Musculus discors</i>	Bivalvia	Boreal Arctic	Coan et al. (2000)
<i>Musculus glacialis</i>	Bivalvia	Boreal Arctic	Coan et al. (2000)
<i>Pandora glacialis</i>	Bivalvia	Boreal Arctic	Coan et al. (2000)
<i>Serripes groenlandicus</i>	Bivalvia	Boreal Arctic	Coan et al. (2000)
<i>Similipecten greenlandicus</i>	Bivalvia	Arctic	Coan et al. (2000)
<i>Bathypolypus arcticus</i>	Cephalopoda	Atlantic Boreal Arctic	<a href="http://eol.org/pages/492845/maps">http://eol.org/pages/492845/maps</a>
<i>Benthoctopus sibiricus</i>	Cephalopoda	Arctic	<a href="http://www.biodiversitylibrary.org/name/Benthoctopus_sibiricus#">http://www.biodiversitylibrary.org/name/Benthoctopus_sibiricus#</a>
<i>Adalaria proxima</i>	Gastropoda	Boreal Arctic	Behrens (1991)
<i>Admete regine</i>	Gastropoda	Boreal Arctic	MacGinitie (1959)

<i>Admete solida</i>	Gastropoda	Boreal Arctic	MacGinitie (1959)
<i>Admete viridula</i>	Gastropoda	Boreal Arctic	Bouchet & Waren (1993)
<i>Anomalisipho verkruezeni</i>	Gastropoda	Atlantic Boreal Arctic	Bouchet & Waren (1993)
<i>Ariadnaria borealis</i>	Gastropoda	Boreal Arctic	MacPherson (1971)
<i>Aulacofusus brevicauda</i>	Gastropoda	Boreal Arctic	Bouchet & Waren (1993)
<i>Beringius behringi</i>	Gastropoda	Pacific Boreal Arctic	MacPherson (1971)
<i>Buccinum angulosum</i>	Gastropoda	Pacific Boreal Arctic	MacPherson (1971)
<i>Buccinum ciliatum</i>	Gastropoda	Boreal Arctic	MacPherson (1971)
<i>Buccinum glaciale</i>	Gastropoda	Boreal Arctic	MacPherson (1971)
<i>Buccinum hydrophanum</i>	Gastropoda	Boreal Arctic	MacPherson (1971)
<i>Buccinum plectrum</i>	Gastropoda	Boreal Arctic	MacGinitie (1959)
<i>Buccinum polare</i>	Gastropoda	Pacific Boreal Arctic	MacPherson (1971)
<i>Buccinum scalariforme</i>	Gastropoda	Boreal Arctic	MacPherson (1971)
<i>Buccinum solenum</i>	Gastropoda	Pacific Boreal Arctic	Dall (1921)
<i>Calycidoris geuntheri</i>	Gastropoda	Pacific Boreal Arctic	Kantor & Sysoev (2006)
<i>Colus pubescens</i>	Gastropoda	Arctic	Bouchet & Waren (1993)
<i>Colus sabini</i>	Gastropoda	Atlantic Boreal Arctic Atlantic Boreal Arctic	Bouchet & Waren (1993)
<i>Cryptonatica affinis</i>	Gastropoda	Boreal Arctic	MacGinitie (1959)
<i>Curtitoma decussata</i>	Gastropoda	Boreal Arctic	MacPherson (1971)
<i>Curtitoma novajasemljensis</i>	Gastropoda	Arctic	MacPherson (1971)
<i>Curtitoma violacea</i>	Gastropoda	Boreal Arctic	MacPherson (1971)
<i>Cylichna alba</i>	Gastropoda	Boreal Arctic	Behrens (1991)
<i>Cylichnoides occultus</i>	Gastropoda	Boreal Arctic	Kantor & Sysoev (2006)
<i>Diaphana hiemalis</i>	Gastropoda	Boreal Arctic	Kantor & Sysoev (2006)
<i>Euspira pallida</i>	Gastropoda	Boreal Arctic	MacGinitie (1959)
<i>Granotoma albrechti</i>	Gastropoda	Pacific Boreal Arctic	Kantor & Sysoev (2006)
<i>Iphinopsis sp.</i>	Gastropoda	Atlantic Boreal Arctic	Bouchet & Waren (1993)
<i>Lacuna crassior</i>	Gastropoda	Boreal Arctic	Kantor & Sysoev (2006)
<i>Lepeta caeca</i>	Gastropoda	Boreal Arctic	MacPherson (1971)
<i>Limneria undata</i>	Gastropoda	Boreal Arctic	MacPherson (1971)
<i>Margarites costalis</i>	Gastropoda	Boreal Arctic	MacPherson (1971)
<i>Margarites groenlandicus</i>	Gastropoda	Boreal Arctic	MacPherson (1971)
<i>Margarites helycinus</i>	Gastropoda	Boreal Arctic	MacPherson (1971)
<i>Neophinoe kroeyeri</i>	Gastropoda	Boreal Arctic	Kantor & Sysoev (2006)
<i>Neptunea communis</i>	Gastropoda	Pacific Boreal Arctic	MacPherson (1971)
<i>Neptunea heros</i>	Gastropoda	Pacific Boreal Arctic	MacPherson (1971)
<i>Neptunea ventricosa</i>	Gastropoda	Pacific Boreal Arctic	MacPherson (1971)
<i>Nodulotrophon coronatus</i>	Gastropoda	Pacific Boreal Arctic	Kantor & Sysoev (2006)



<i>Obesotoma japonica</i>	Gastropoda	Boreal Arctic	MacGinitie (1959)
<i>Obesotoma laevigata</i>	Gastropoda	Arctic	Kantor & Sysoev (2006)
<i>Obesotoma simplex</i>	Gastropoda	Boreal Arctic	MacGinitie (1959)
<i>Obesotoma tenuilirata</i>	Gastropoda	Boreal Arctic	MacGinitie (1959)
<i>Oenopota harpa</i>	Gastropoda	Pacific Boreal Arctic	MacGinitie (1959)
<i>Oenopota impressa</i>	Gastropoda	Pacific Boreal Arctic	MacGinitie (1959)
<i>Oenopota pingelii</i>	Gastropoda	Atlantic Boreal Arctic ArcticAtlantic Boreal Arctic	Kantor & Sysoev (2006)
<i>Oenopota pyramidalis</i>	Gastropoda	Boreal Arctic	MacGinitie (1959)
<i>Plicifusus kroeyeri</i>	Gastropoda	Boreal Arctic	MacPherson (1971)
<i>Propebela arctica</i>	Gastropoda	Boreal Arctic	MacPherson (1971)
<i>Propebela nobilis</i>	Gastropoda	Boreal Arctic	MacPherson (1971)
<i>Pyrulofusus deformis</i>	Gastropoda	Pacific Boreal Arctic	MacPherson (1971)
<i>Retifusus roseus</i>	Gastropoda	Pacific Boreal Arctic	MacPherson (1971)
<i>Stenosemus albus</i>	Gastropoda	Boreal Arctic Atlantic Boreal	MacPherson (1971)
<i>Turrisipho lachensis</i>	Gastropoda	Arctic ArcticAtlantic Boreal Arctic	Bouchet & Waren (1993)
<i>Velutina coriacea</i>	Gastropoda	Pacific Boreal Arctic	Kantor & Sysoev (2006)
<i>Velutina laevigata</i>	Gastropoda	Boreal Arctic	MacGinitie (1959)
<i>Velutina velutina</i>	Gastropoda	Boreal Arctic	MacPherson (1971)
<i>Volutopsius</i> sp.	Gastropoda	Pacific Boreal Arctic	Kantor & Sysoev (2006)
<i>Amicula vestita</i>	Polyplacophora	Boreal Arctic	MacGinitie (1959)
<b>Echinodermata taxa</b>	<b>Class</b>	<b>Biogeographic affinity</b>	<b>Reference</b>
<i>Bathybiaster vexillifer</i>	Asteroidea	Bathyal Atlantic Boreal Arctic ArcticAtlantic	Smirnov (2014a)
<i>Crossaster papposus</i>	Asteroidea	Boreal Arctic	Smirnov (2014a)
<i>Ctenodiscus crispatus</i>	Asteroidea	Boreal Arctic Atlantic Boreal Arctic ArcticAtlantic	Smirnov (2014a)
<i>Henricia sanguinolenta</i>	Asteroidea	Boreal Arctic	Smirnov (2014a)
<i>Hymenaster pellucidus</i>	Asteroidea	Arctic	Smirnov (2014a)
<i>Icasterias panopla</i>	Asteroidea	Arctic	Smirnov (2014a)
<i>Leptasterias arctica</i>	Asteroidea	Pacific Boreal Arctic	Smirnov (2014a)
<i>Leptasterias groenlandica</i>	Asteroidea	Boreal Arctic	Smirnov (2014a)
<i>Leptasterias polaris</i>	Asteroidea	Boreal Arctic Atlantic Boreal	Smirnov (2014a)
<i>Lophaster furcifer</i>	Asteroidea	Arctic Atlantic Boreal	Smirnov (2014a)
<i>Pontaster tenuispinus</i>	Asteroidea	Arctic	Smirnov (2014a)
<i>Poraniomorpha tumida</i>	Asteroidea	Arctic	Smirnov (2014a)

<i>Pteraste jordani</i>	Asteroidea	Boreal Arctic	Smirnov (2014a)
<i>Pteraste militaris</i>	Asteroidea	Boreal Arctic Atlantic Boreal	Smirnov (2014a)
<i>Pteraster obscurus</i>	Asteroidea	Arctic Atlantic Boreal	Smirnov (2014a)
<i>Urasterias lincki</i>	Asteroidea	Arctic	Smirnov (2014a)
<i>Strongylocentrotus pallidus</i>	Echinoidea	Boreal Arctic	Smirnov (2014b)
<i>Kolga</i> sp.	Holothuroidea	Bathyal Atlantic Boreal	Smirnov (2014c)
<i>Molpadia borealis</i>	Holothuroidea	Arctic	Smirnov (2014c)
<i>Myriotrochus rinkii</i>	Holothuroidea	Pacific Boreal Arctic	Smirnov (2014c)
<i>Ocnus glacialis</i>	Holothuroidea	Pacific Boreal Arctic	Smirnov (2014c)
<i>Psolus peronii</i>	Holothuroidea	Pacific Boreal Arctic	Smirnov (2014c)
<i>Eupyrigus scaber</i>	Holothuroidea	Arctic	Smirnov (2014c)
<i>Amphiodia craterodmeta</i>	Ophiuroidea	Pacific Boreal Arctic	Martynov and Smirnov (2014)
<i>Amphiura sundevalli</i>	Ophiuroidea	Boreal Arctic	Martynov and Smirnov (2014)
<i>Gorgonocephalus</i> sp.	Ophiuroidea	Boreal Arctic	Martynov and Smirnov (2014)
<i>Ophiacantha bidentata</i>	Ophiuroidea	Boreal Arctic	Martynov and Smirnov (2014)
<i>Ophiocten sericeum</i>	Ophiuroidea	Boreal Arctic	Martynov and Smirnov (2014)
<i>Ophiopholis aculeata</i>	Ophiuroidea	Boreal Arctic Atlantic Boreal	Martynov and Smirnov (2014)
<i>Ophiopleura borealis</i>	Ophiuroidea	Arctic Atlantic Boreal	Martynov and Smirnov (2014)
<i>Ophioscolex glacialis</i>	Ophiuroidea	Arctic Atlantic Boreal	Martynov and Smirnov (2014)
<i>Ophiura robusta</i>	Ophiuroidea	Arctic	Martynov and Smirnov (2014)
<i>Ophiura sarsii</i>	Ophiuroidea	Boreal Arctic	Martynov and Smirnov (2014)
<i>Stegophiura nodosa</i>	Ophiuroidea	Pacific Boreal Arctic	Martynov and Smirnov (2014)

Arthropoda taxa	Order	Biogeographic affinity	Reference
<i>Bythocaris biruli</i>	Decapoda	Bathyal	Vassilenko and Petryashov (2009)
<i>Bythocaris irene</i>	Decapoda	Bathyal	Vassilenko and Petryashov (2009)
<i>Chionoecetes opilio</i>	Decapoda	Boreal Arctic	Vassilenko and Petryashov (2009)
<i>Eualus gaimardii</i>	Decapoda	Arctic	Vassilenko and Petryashov (2009)
<i>Eualus macilentus</i>	Decapoda	Boreal Arctic	Vassilenko and Petryashov (2009)
<i>Hyas coarctatus</i>	Decapoda	Boreal Arctic	Vassilenko and Petryashov (2009)
<i>Labidochirus splendescens</i>	Decapoda	Pacific Boreal Arctic	Vassilenko and Petryashov (2009)
<i>Lebbeus groenlandicus</i>	Decapoda	Boreal Arctic	Vassilenko and Petryashov (2009)
<i>Lebbeus polaris</i>	Decapoda	Boreal Arctic	Vassilenko and Petryashov (2009)
<i>Pagurus capillatus</i>	Decapoda	Pacific Boreal Arctic	Vassilenko and Petryashov (2009)
<i>Pagurus trigonocheirus</i>	Decapoda	Pacific Boreal Arctic	Vassilenko and Petryashov (2009)
<i>Pandalus goniurus</i>	Decapoda	Pacific Boreal Arctic	Vassilenko and Petryashov (2009)
<i>Pandora glacialis</i>	Decapoda	Atlantic Boreal	Vassilenko and Petryashov (2009)

<i>Sabinea septemcarinata</i>	Decapoda	Arctic Atlantic Boreal Arctic	Vassilenko and Petryashov (2009)
<i>Sclerocrangon ferox</i>	Decapoda	Atlantic Boreal Arctic	Vassilenko and Petryashov (2009)
<i>Saduria entomon</i>	Isopoda	Boreal Arctic	<a href="http://www.eol.org/pages/128509/maps">http://www.eol.org/pages/128509/maps</a>
<i>Saduria sabini</i>	Isopoda	Boreal Arctic	<a href="http://www.eol.org/data_objects/21428319">http://www.eol.org/data_objects/21428319</a>
<i>Saduria sibirica</i>	Isopoda	Pacific Boreal Arctic	<a href="http://www.eol.org/pages/345079/maps">http://www.eol.org/pages/345079/maps</a>
<i>Synidotea bicuspidata</i>	Isopoda	Boreal Arctic	<a href="http://www.eol.org/pages/343135/maps">http://www.eol.org/pages/343135/maps</a>
<i>Munnopsis typica</i>	Isopoda	Atlantic Boreal Arctic	<a href="http://www.eol.org/pages/325664/details">http://www.eol.org/pages/325664/details</a>
<i>Munnospsurus giganteus</i>	Isopoda	Atlantic Boreal Arctic	<a href="http://www.eol.org/pages/325458/maps">http://www.eol.org/pages/325458/maps</a>

## 943 **References**

- 944 Behrens DW (1991) Pacific coast nudibranchs. A guide to the opisthobranchs Alaska to Baja California.  
945 Sea Challengers, pp 107.
- 946 Bouchet P, Warén A (1985) Revision of the Northeastern Atlantic bathyal and Abyssal Neograstropoda  
947 excluding Turridae (Mollusca: Gastropoda). Societa Italiana di Malacologia Bollettina Malacologica  
948 Supplemento 1, pp 296.
- 949 Coan E, Paul V, Scott V, Bernard RF (2000) Bivalve Seashells of Western North America. Marine Bivalve  
950 Mollusks from Arctic Alaska to Baja California. Santa Barbara Museum of Natural History Monographs  
951 Number 2, Studies in Biodiversity number 2, pp 764.
- 952 Dall WH (1921) Summary of the marine shellbearing mollusca of the northwest coast of America, from  
953 San Diego, California, to the Polar Sea, mostly contained in the collection of the United States National  
954 Musuem, with illustrations of hitherto unfigured species. Bull. U. S, Nat. Mus. 112:1-127.
- 955 Kantor Yu. I, Sysoev AV (2006) Marine and brackish water Gastropoda of Russia and adjacent countries:  
956 an illustrated catalogue. KMK Scientific Press, Moscow, pp 372.
- 957 MacGinite N (1959) Marine mollusca of Point Barrow, Alaska. Proceedings of the U.S. national Museum  
958 109:59-208.
- 959 MacPherson E (1971) The marine mollusks of arctic Canada. National Museum of Canada Publications in  
960 Biological Oceanography No. 3.
- 961 Martynov AV, Smirnov IS (2014) Ophiura (brittle stars) of the Eurasian seas and adjacent deep regions of  
962 the Arctic. Unpublished manuscript
- 963 Smirnov AV (2014a) Sea stars (Asteroidea) of the Eurasian seas and adjacent deep regions of the Arctic.  
964 Unpublished manuscript

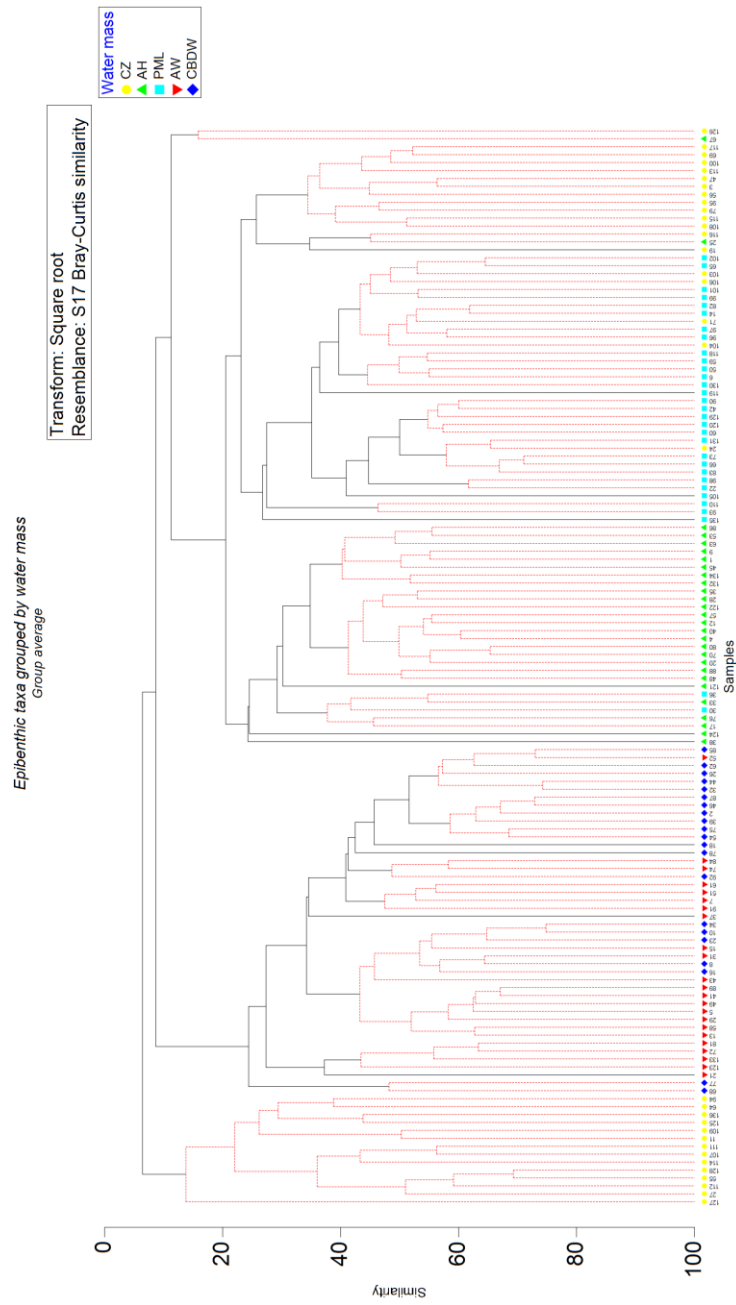
965 Smirnov AV (2014b) Sea urchins (Echinoidea) of the European seas and adjacent deep regions of the  
966 Arctic. Unpublished manuscript

967 Smirnov AV (2014c) Holothurians (Holothuroidea) of the Eurasian seas and adjacent deep regions of the  
968 Arctic. Unpublished manuscript

969 Vassilenko SV, VV Petryashov (eds.) (2009) Illustrated Keys to Free-Living Invertebrates of Eurasian Arctic  
970 Seas and Adjacent Deep Waters, Vol. 1. Rotifera, Pycnogonida, Cirripedia, Leptostraca, Mysidacea,  
971 Hyperiidea, Caprellidea, Euphausiacea, Dendrobranchiata, Pleocyemata, Anomura, and Brachyura.  
972 Alaska Sea Grant, University of Alaska Fairbanks

973

974 ESM 3: Dendrogram from cluster-analysis combined with SIMPROF test of 136 stations based on  
975 biomass of epibenthic communities in the Beaufort Sea color-coded by water mass.



976

977