

Winners and Losers in a Warming Arctic: Potential Habitat Gain and Loss for Epibenthic Invertebrates of the Chukchi and Bering Seas, 2008-2100.

Elizabeth Logerwell^{a,*}, Muyin Wang^b, Lis Jorgensen^c, Kimberly Rand^d

^a Alaska Fisheries Science Center
National Marine Fisheries Service
National Oceanic and Atmospheric Administration
7600 Sand Point Way, NE, Seattle, WA, 98115, USA
Libby.Logerwell@noaa.gov

^b Pacific Marine Environmental Laboratory
Oceanic and Atmospheric Research
National Oceanic and Atmospheric Administration
7600 Sand Point Way, NE, Seattle, WA, 98115, USA
Muyin.Wang@noaa.gov

^c Institute of Marine Research
Hjalmar Johansens gate 14, 9007 Tromsø, Norway
Lis.Lindal.Joergensen@hi.no

^d Lynker Technologies, LLC,
202 Church Street SE, Number 536, Leesburg, Virginia 20175, USA
Kimberly.Rand@noaa.gov

*corresponding author

1 Abstract

2 Our goal was to examine how the epibenthic invertebrate community in the Pacific Arctic
3 Region might be affected by continued increases in ocean temperatures. We used epibenthic
4 invertebrate catch and bottom temperature data collected on groundfish assessment and ecosystem
5 surveys in the Bering and Chukchi seas from 2009-2018 to determine the “preferred” temperature of all
6 taxa. We grouped taxa into five clusters according to their similarity in median temperature and
7 temperature range. We then used an ensemble of eight climate models under Representative
8 Concentration Pathway 8.5 (RCP8.5) scenarios to project bottom temperature from present (2008) to
9 mid-century (2050) and end of the century (2100). Based on these projections, we show how the
10 amount and distribution of cluster-specific thermal habitat might change with ocean warming. We
11 found that by mid-century there was a 50% decrease in thermal habitat for all clusters except for the
12 most eurythermic cluster, and that thermal habitat contracted to the north. By the end of the century
13 there was very little thermal habitat for all clusters, except the most eurythermic cluster, and habitat
14 was further contracted to the north. The cold-water and stenothermic cluster, hypothesized to be the
15 most vulnerable to ocean warming, had virtually no projected thermal habitat by the end of the century.
16 These “losers” were primarily gastropods and the bivalve mussel *Musculus* sp. These taxa are some of
17 the primary prey to the endangered Pacific walrus (*Odobenus rosmarus*), which is harvested as a food
18 resource in native Alaskan communities. Bivalves are prey for commercial flatfish such as yellowfin sole
19 (*Limanda aspera*) and Alaska plaice (*Pleuronectes quadrituberculatus*). By 2100 the most eurythermic
20 cluster, hypothesized to be the least vulnerable to warming, had projected suitable thermal habitat
21 throughout most of the Bering and Chukchi seas, except nearshore coastal regions. The most abundant
22 species of these “winners” was the basketstar *Gorgonocephalus cf. arcticus*. The loss of thermal habitat
23 for all but the “winners” could impact the species diversity of the Bering and Chukchi seas because the
24 “winner” cluster accounted for only 26 taxa or 8% of all taxa observed. Although temperature is a key

25 determinant of habitat, a full habitat and ecosystem model is needed to provide more detailed
26 predictions. In addition, more laboratory studies of thermal acclimation potential of Arctic benthic
27 invertebrates are needed. Our results provide the first indications that the epibenthic invertebrate
28 community in the Bering and Chukchi seas, which supports marine mammals, seabirds and human
29 communities, may be seriously impacted by future ocean warming.

30

31 Keywords: Arctic environment, marine invertebrates, epibenthos, thermal habitat, climate change,
32 climate prediction,

33

34 1.0 Introduction

35 Loss of sea ice and rise of ocean temperature are impacting Arctic ecosystems in the Pacific and
36 Atlantic regions (Huntington et al., 2020; Polyakov et al., 2020; Renaud et al., 2015). Ocean warming has
37 been shown to result in northward shifts in distribution (i.e., “borealization”), declines in abundance and
38 shifts in community composition of ecosystem components such as plankton (Dalpadado et al., 2020;
39 Eisner et al., 2014), fish (Aune et al., 2018; Mueter and Litzow, 2008; Wisz et al., 2015), infaunal
40 invertebrates (Grebmeier, 2012; Solan et al., 2020), seabirds (Gall et al., 2016) and marine mammals
41 (Davis et al., 2020; Laidre et al., 2015). In contrast, the potential impacts of ocean temperature increase
42 on epibenthic invertebrate community distribution and abundance have not been extensively examined.
43 Northward shifts in the distribution of a small number of demersal species have been observed and
44 attributed to ocean warming: crab and shrimp in the Bering Sea (Alabia et al., 2018; Mueter and Litzow,
45 2008; Parada et al., 2010); shrimp in the Barents Sea and Western Eurasian Basin (Polyakov et al., 2020);
46 crab and a clam in the Chukchi Sea (Sirenko and Gagaev, 2007); and an Atlantic mussel in Svalbard
47 (Berge et al., 2005).

48 The potential impacts of future ocean warming is a critical knowledge gap because the
49 epibenthic invertebrate community, along with the infauna, supports a number of key upper trophic
50 level predators including commercial groundfish, marine mammals, and seabirds (Bluhm and Gradinger,
51 2008; Packer et al., 1994; Whitehouse et al., 2017). Arctic native communities depend heavily on many
52 of these predators (including cetaceans, pinnipeds, and sea ducks) for nutrition and for cultural and
53 spiritual fulfillment (Hovelsrud et al., 2008; Huntington et al., 2020).

54 The ability of organisms to exist across the local range of temperatures is a significant
55 component of fitness and temperature is regarded to be a key determinant of species distribution
56 (Calosi et al., 2010; Chown et al., 2009). Thus although the habitat of Arctic epibenthic invertebrates is
57 characterized by a variety of environmental variables in addition to temperature, such as: sediment

58 type; depth; freshwater runoff; sea ice extent and ice algal production; water column primary
59 production and export to the benthos; nutrients; oxygen; and ocean transport (Degen et al., 2016, 2015;
60 Grebmeier et al., 2015; Hansen et al., 2020; Kedra et al., 2015), defining thermal habitat is a high priority
61 for understanding the impacts of climate change on the epibenthic community. Other processes impact
62 species distribution such as historical factors (species origin, dispersal barriers, etc.), statistical
63 characteristics of the data (distribution of sampling efforts, catching efficiency), and data reliability (e.g.,
64 possible misidentifications and taxonomic problems). Although these factors play a role in shaping
65 species distribution, we assumed that temperature was a primary factor, particularly when examining
66 the possible effects of future ocean warming. Several studies of epibenthic invertebrates in a variety of
67 ecosystems, the Bering Sea (Mueter and Litzow, 2008), the Barents Sea (Jørgensen et al., 2019),
68 Antarctica (Griffiths et al., 2017) and Arctic oceans globally (Jorgensen et al., 2022; Renaud et al., 2015),
69 have focused on thermal habitat in an effort to predict the impacts of ocean warming.

70 Despite the critical need to understand the impacts of temperature on epibenthic invertebrates,
71 very few temperature-dependent rate measurements of benthic macrofauna have been made. The
72 physiological capacity of benthic organisms to acclimate or adapt to warming or otherwise changing
73 conditions is also understudied (Pörtner, 2010). A macrophysiological approach can be useful when
74 physiological data from laboratory studies are not available. Macrophysiology is the study of
75 interpopulation, interspecific and high taxonomic variation in physiological traits over large geographical
76 and temporal timescales. The overall goal of the approach is to understand the reasons for variation in
77 physiological traits and the subsequent ecological implications, particularly in the face of substantial
78 environmental change (Chown et al., 2004). We took a macrophysiological approach by analyzing (at
79 the population level) the thermal habitat of the entire sampled epibenthic community over a large
80 geographical and temporal scale.

81 Our objective was to study the potential impacts of ocean warming by using the range of
82 temperatures at which all sampled epibenthic invertebrate taxa over the US Pacific Arctic have been
83 observed over the past decade. We took advantage of a decade's (2009-2018) worth of epibenthic
84 invertebrate catch and temperature data from groundfish assessment surveys (Lauth et al., 2019) and
85 ecosystem surveys of the Bering and Chukchi seas (including the Arctic Ecosystem Integrated Survey and
86 the Arctic Integrated Ecosystem Research Program: Baker et al., 2020; Mueter et al., 2017). Instead of
87 defining taxa *a priori* to be Arctic or boreal, as other investigators have done (e.g., Renaud et al., 2015),
88 we used cluster analysis to group taxa by the median and the range of temperatures at which they have
89 been observed during the reference period (2009-2018), similar to studies by Mueter and Litzow (2008),
90 Jørgensen et al. (2019) and Griffiths et al. (2017). We used an ensemble of eight coupled climate models
91 that participated in the Coupled Model Intercomparison Project Phase 5 (CMIP5) to predict the mean
92 increase in bottom temperature from present to mid-century as well as to the end of the century and
93 calculated the amount and distribution of seafloor thermal habitat (i.e., the area within the temperature
94 range of each cluster of taxa). We posit that cold-water and stenothermic taxa would be highly
95 susceptible to ocean warming (i.e., the "losers"), whereas warm-water and eurythermic taxa would be
96 relatively tolerant to warming (i.e., the "winners"). We then discuss the impacts of projected changes in
97 thermal habitat on epibenthic community diversity and Arctic foodwebs.

98

99 2.0 Material and methods

100 The study area for this work encompassed the Bering and Chukchi seas which are seasonally ice-
101 covered shelves (<200 m depth) with currents typically flowing northward due to the difference in sea
102 level between the Pacific and the Arctic (Aagaard et al., 1981). South and north of the shelf breaks are
103 the Aleutian Basin and Central Arctic Ocean, respectively, and the two seas are separated by Bering
104 Strait which is 88 km wide (Fig. 1a). The water masses of the Bering Sea include the nutrient-rich Anadyr

105 Water, Bering Shelf Water, and the comparatively fresh and nutrient-poor Alaska Coastal Water
106 (Coachman, 1986; Danielson et al., 2016). These water masses bring freshwater, nutrients, and organic
107 matter into the Chukchi Sea through the Bering Strait (Danielson et al., 2016; Walsh et al., 1989). The
108 Bering Sea is home to some of the most productive and lucrative demersal fisheries in the world (FAO,
109 2021). Alaska fisheries as a whole accounted for 57% of the weight and 35% of the ex-vessel value of
110 total U.S. domestic landings in 2020 (Hiatt et al., 2021). In comparison, the Chukchi Sea currently lacks
111 large stocks of commercial groundfish and it is closed to commercial fishing in the US Exclusive
112 Economic Zone (North Pacific Fishery Management Council, 2009). There are several human
113 communities that rely on the northern Bering and Chukchi seas for food security through subsistence
114 harvest of marine mammals, fish and seabirds (Huntington, 2000). In addition, the Arctic ecosystem
115 provides these communities with a means for social and cultural expression (Huntington, 2000).

116 The epibenthic communities of the Bering and Chukchi seas were sampled during groundfish
117 assessment and ecosystem surveys conducted by National Oceanic and Atmospheric Administration
118 (NOAA) National Marine Fisheries Service, Alaska Fisheries Science Center (AFSC) (Baker et al., 2020;
119 Lauth, 2011; Lauth et al., 2019; Mueter et al., 2017; Rand et al., 2018). While the Southeast Bering Sea
120 has been surveyed annually for epibenthos since 1975, the other areas were surveyed less often and
121 only since the 2000s. To minimize the effect of long-term trends, catch data were used from surveys
122 from 2009-2018 in the Southeast Bering Sea; 2010 and 2017 in the North Bering Sea; 2012 and 2017 in
123 the Chukchi Sea shelf; and 2013 in the Northeast Chukchi Sea around Barrow Canyon (Fig. 1b). The 83-
124 112 Eastern bottom trawl was used for sampling in all years (Stauffer, 2004), with the exception of the
125 2017 Chukchi Sea survey which employed a 3-m plumb staff beam trawl (Abookire and Rose, 2005). For
126 both nets, net mensuration equipment coupled with a GPS feed was used to calculate area swept and
127 catch-per-unit effort (CPUE kg km^{-2}). Net width was not measured for the beam trawl because the beam
128 keeps the net width constant. Catch was enumerated, weighed, and identified to the lowest taxonomic

129 level feasible on board or from voucher specimens and photographs after the surveys. Catch data of fish
130 were removed before further analysis.

131 Bottom water temperature data were collected at each trawl station using a Sea-Bird
132 bathythermograph continuous data recorder attached to the headrope of the net (Sea-Bird Scientific,
133 seabird.com). In addition, temperature and salinity with depth were measured with CTDs during the
134 2012 and 2017 Chukchi Sea surveys.

135 The median temperature at all stations where each invertebrate taxa occurred in the data set
136 was calculated. The temperature range of each taxa was calculated as the 10th and 90th percentiles of
137 temperatures at all stations where it occurred. K-means clustering was used to group taxa by median
138 temperature and range. K-means clustering is a method of vector quantization that partitions n
139 observations into k clusters in which each observation belongs to the cluster with the nearest mean
140 while minimizing the within-cluster variances (i.e., the squared Euclidean distances; Bock, 2008). The
141 number of clusters (k) was chosen as a balance between the number of groups and the variance within
142 groups. Bigger k results in a lower variance to the extreme case of $k=n$ which results in variance of 0. The
143 final k was selected by plotting the variance (sum of squares) within groups by the number of groups
144 and observing the 'elbow', or where the slope of the decrease in variance changes from steep to
145 shallow.

146 The diversity represented by each cluster was assessed by calculating the number of taxa and
147 the percent of all taxa (i.e., Alpha diversity). The relative abundance in each cluster was calculated as the
148 mean of the percent CPUE (kg km^{-2}) at all stations, where percent CPUE at each station was calculated as
149 CPUE for each species at that station divided by total CPUE at that station over all years.

150 To select climate models for bottom temperature projections, model summer ocean
151 temperature data from Representative Concentration Pathway 8.5 (RCP8.5) scenarios were
152 interpolated on to the survey stations (by latitude, longitude and bottom depth). RCP8.5 combines

153 assumptions about high population and relatively slow income growth with modest rates of
154 technological change, leading in the long term to high energy demand and high greenhouse gas
155 emissions in the absence of climate change policies (IPCC, 2014). This high emissions scenario is
156 frequently referred to as “business as usual”, suggesting that it is a likely outcome if society does not
157 make concerted efforts to cut greenhouse gas emissions. Visual comparison of model projections with
158 CTD data collected during 2017 and 2019 on the Chukchi Sea surveys, indicated that 8 of the 22 models
159 downloaded had relatively good agreement with the observed bottom temperature during those year.
160 The data points from these 8 models were combined and separated into a northern ($\geq 66^\circ \text{N}$), and a
161 southern ($< 66^\circ \text{N}$) domain because the whole domain spans a large latitudinal range ($54^\circ \text{N} - 74^\circ \text{N}$)
162 which may contain large meridional gradients. Model projections for July and August were averaged
163 because those months were when the surveys were conducted. Decadal average bottom temperatures
164 were calculated for 2008-2017 (“present”), 2045-2054 (“mid-century”), and 2091-2100 (“end-of-
165 century”).

166 Maps of the bottom temperature projections were generated by averaging model output within
167 100 km^2 grid cells. The 8 projection models had varying spatial resolutions (from 0.18° Longitude to
168 1.71° Longitude), and the 100 km^2 grid cell captured at least one data point for each model.

169 The amount of thermal habitat available for each cluster of species was calculated as the
170 proportion of the total study area projected to be within the temperature range for that cluster.
171 Thermal habitat was calculated for each cluster for present, mid-century and end-of-century projections
172 of bottom temperature. Maps of the distribution of thermal habitat for all clusters and decadal
173 projections were also produced. ArcGIS Desktop 10.6, version: 10.6.0.8321 (www.esri.com) was used to
174 create the maps. Because thermal habitat was based on species occurrence, and not weighted by
175 biomass, we did not project habitat displacements using center of gravity analyses such as in Fossheim
176 et al. (2015).

177

178 3.0 Results

179 Variance within k-means cluster groups declined rapidly as group number increased from 1 to 5
180 in all regions (Fig. 2). For group numbers larger than 5, variance decreased less rapidly. Therefore group
181 size (k) was chosen to be 5 for further analysis.

182 The 5 k-means clusters were given qualitative descriptors arbitrarily based on average median
183 and range of temperature for taxa in the cluster. Clusters for which median temperatures were 0.6 °C or
184 less were designated as representing “cold-water” taxa. Clusters for which median temperatures were
185 2.5 °C or greater were designated as “warm-water”. “Stenothermic” clusters were those with a range of
186 2.8 °C or less and “eurythermic” clusters were those with a range of 5.5 °C to 6 °C; “highly eurythermic”
187 was a range of 9.0 °C (Table 1).

188 Cluster A, the “cold, stenothermic” cluster and Cluster E, the “warm, high eurythermic” cluster
189 contained the lowest proportion of taxa (12% and 8%, respectively; Table 1). Cluster D, “warm,
190 eurythermic”, contained the greatest proportion of taxa (38%). Cluster B, “cold, eurythermic” and
191 Cluster C “warm, stenothermic” contained intermediate proportions of taxa (21% and 19%,
192 respectively). Clusters B and D had the greatest proportional catch density (49% and 38%). The other
193 clusters had catch densities less than 10% of total catch (Table 1).

194 The most abundant taxa (in terms of biomass density) in Cluster A, “cold, stenothermic”, were
195 Gastropoda and *Musculus* sp. at 3.8% and 3% of total catch density, respectively. Other taxa, occurring
196 at less than 1% of catch density but greater than 0.1%, included echinoderms, sipunculids, and
197 arthropods (Table 2). The most abundant taxa in Cluster B, “cold, eurythermic”, were *Ophiura sarsii* and
198 *Ophiura* sp. at 39% of total catch density. Other taxa in this cluster included echinoderms, mollusks,
199 chordates, gastropods, cnidarians, arthropods, and annelids. The most abundant taxon in Cluster C,
200 “warm, stenothermic”, was *Nuculana radiata*. The other taxa caught at densities greater than 0.1% were

201 a gastropod and a bryozoan. The most abundant taxon in Cluster D “warm, eurythermic”, was
202 *Chionoecetes opilio*, at 9% of total catch density. Other taxa in this cluster included echinoderms,
203 cnidarians, bryozoans, sponges, arthropods, gastropods, mollusks, cnidarians, chordates, and annelids.
204 The most abundant taxon in Cluster E “warm, highly eurythermic” was *Gorgonocephalus* cf. *arcticus*.
205 Other taxa in this cluster included arthropods, cnidarians, and echinoderms.

206 Observed temperatures from the CTD data collected in 2017 and 2019 fell within the range of
207 model projections for both domains and were very close to the ensemble mean of the model in the
208 northern domain (Fig. 3). However, in general, these eight models overestimated the mean bottom
209 temperature in the southern domain. The spread in the projected temperature was larger in the
210 northern domain compared with southern domain. This is more obvious in the latter half of the 21st
211 century. Looking forward to the future decadal changes, model projections indicated an increase in
212 average bottom temperature in the northern domain from 0.98 °C at present to 2.25 °C by mid-century
213 (an increase of 1.27 °C) and to 5.60 °C by the end of century (an increase of 4.62 °C). Model projections
214 of the southern domain indicate an increase from 3.83 °C at present to 5.15 °C by mid-century (an
215 increase of 1.32 °C); and to 8.10 °C by the end of the century (an increase of 4.27 °C) (Table 3).

216 The spatial distribution of model projections of bottom temperature shows the coldest water in
217 the north and the warmest to the south and nearshore, as expected (Fig. 4). The range of the coldest
218 water shrinks to the north from present (Fig. 4a) to mid-century (Fig. 4b) to end-of-century (Fig. 4c); and
219 the temperature of waters to the south increases. Bottom waters less than 0 °C virtually disappear by
220 the end of the century (Fig. 4c).

221 The present-day model projection of bottom temperature shows that there was the least
222 thermal habitat for Cluster A “cold, stenothermic” (31% of the total survey area) and the most for
223 Cluster E “warm, highly eurythermic” (96%) (Table 4). The other two eurythermic clusters, Clusters B and

224 D, also had a relatively large proportion of thermal habitat available to them, 88% for both. There was
225 an intermediate proportion of thermal habitat available for Cluster C, “warm, stenothermic” (61%).

226 The amount of thermal habitat decreased for all clusters from present to mid-century, except
227 for Cluster E for which there as an increase of 2%. The amount of thermal habitat available at mid-
228 century ranged from a low of 13% for Cluster A and a high of 98% for Cluster E. The decrease in thermal
229 habitat from mid-century to end-of-century was even greater than from present to mid-century.
230 Thermal habitat for Cluster A virtually vanished by the end of the century, at 2%. There was 10% or less
231 thermal habitat available for Clusters B and C, and 13% available for Cluster D. 72% of thermal habitat
232 was available for Cluster E at the end of the century.

233 The spatial distribution of thermal habitat, based on present-day model projections under RCP
234 8.5 scenarios, was similar for all clusters, except Cluster A, “cold, stenothermic”, for which thermal
235 habitat was confined to the north and west; and Cluster C, “warm, stenothermic”, whose thermal
236 habitat did not extend as far north as the others (Fig. 5). Projected available thermal habitat contracts to
237 the north for all clusters from present to mid-century, except for Cluster E, the most eurythermic (Fig.
238 6). By the end of the century the contraction to the north is so great that there is projected to be
239 suitable thermal habitat for Clusters A-D only north of 65° N, in the northern Chukchi Sea. Thermal
240 habitat for Cluster A is only found at the slope between the Chukchi Sea and Central Arctic Ocean (Fig.
241 7). The distribution of thermal habitat for Cluster E at the end of the century contracts very slightly to
242 the north (approx. 10 km) and more noticeably to the west (approx. 30 km).

243

244 4.0 Discussion

245 An ensemble of eight coupled climate models projected a mean increase in summer bottom
246 temperature in the Bering and Chukchi seas of around 1.3 °C by mid-century and an even greater
247 increase of around 4.5 °C by the end of the century. Warmer waters were projected to expand

248 northward, as expected; and the nearshore area, the location of the typically warm and low salinity
249 Alaska Coastal Current (ACC; Coachman et al., 1975), was projected to be the warmest by the end of the
250 century, as high as 12.3 °C. Although the climate models showed good agreement with observations in
251 the northern domain, in the southern domain the models overestimated the bottom temperatures.
252 This illustrates that models behave differently in different regions. This does add some uncertainty into
253 our projections, which can be addressed in our future studies. There are several possibilities that explain
254 why models overestimated the bottom temperature in the southern domain. One of them is the coarse
255 resolution (both horizontal and vertical) of the models. Whether physical processes such as the
256 freshwater input being properly resolved could be another one. This is out of the scope of our current
257 study. In this study, only eight models were used for two reasons: 1) these models are part of the group
258 that simulated the sea-ice cover in good agreement with observations in their historical runs (Wang &
259 Overland, 2015) – as we know sea ice plays an important role in regulating the ocean temperature in
260 these regions; and 2) these models have decent vertical resolution in the ocean model in our study
261 region. The bottom temperature presented from these models is the interpolation of model grid
262 averaged to the survey layer. Thus, some of the bias could be from the interpolation process. Despite
263 the possibility of bias, our projections of bottom temperature are consistent with projected future
264 reductions of sea ice cover, and earlier seasonal spring sea ice retreat in the region (Wang et al., 2018).
265 They are also consistent with analyses of past trends. For example, the heat content of the Chukchi Sea
266 shelf has warmed significant in the summer and fall since 1922, and that rate has accelerated since 1990
267 (Danielson et al., 2020). In addition, sea-ice extent, concentration and duration have declined over the
268 past two decades in the Chukchi Sea, and since 2014 in the Bering Sea (Baker et al., 2020).

269 Cold-water and stenothermic taxa, which we suggest would be the most vulnerable to ocean
270 warming, were projected to experience the greatest decline in the proportion of thermal habitat
271 available. Thermal habitat for these taxa, “the losers”, decreased by more than 50% by mid-century;

272 and by the end of the century only 2% of the total Bering-Chukchi Sea region was projected to be within
273 their temperature range. The scant thermal habitat that was projected to be available was distributed at
274 the far north on the shelf break and slope between the northern Chukchi Sea and the deep Central
275 Arctic Ocean basin. Temperature projections of the Arctic slope and basin were not examined for this
276 study, but we suggest that even if bottom temperatures were projected to be suitable, the depth of the
277 slope and the basin would not match the habitat requirements of these shelf-occupying taxa. In other
278 words, retreat of shelf benthos can only continue until they reach the northern shelf break and slope,
279 with local extinctions a likely consequence. Similar to our predictions, northward range contractions of
280 the commercially important snow crab (*Chionoecetes opilio*), driven by ocean warming and the shrinking
281 of the Bering Sea cold pool, have been documented (Parada et al. 2010). This may seem to contradict
282 previous field and laboratory studies documenting positive impacts of warmer temperatures on snow
283 crab growth and reproduction (Dawes et al., 2012; Konar et al., 2014; Kolts et al., 2015; Yamamoto et al.,
284 2015; Fedewa et al., 2020). However, most of these studies were constrained to temperatures at which
285 crab are currently found, around -1 to 6 °C and found optimum temperatures to be around 5 °C. These
286 studies can not predict how crab will respond to temperatures that we forecasted will cover much of the
287 Bering Sea and southern Chukchi Sea by the end of the century (up to 8.5 °C). In fact, a laboratory study
288 that did test crab growth and bioenergetics at temperatures as high as 18 °C, showed that at
289 temperatures above 7 °C metabolic costs exceeded caloric intake with negative impacts on growth
290 (Foyle et al. 1989).

291 Warm-water and highly eurythermic taxa, hypothesized to be the least vulnerable to ocean
292 warming, were projected to experience the least decline in the proportion of thermal habitat available.
293 Thermal habitat for these taxa, the “winners”, increased slightly from present to mid-century and then
294 decreased from 98% to 72% of the study area by the end of the century. There was virtually no

295 latitudinal shift in the available thermal habitat for these taxa, the reduction in available habitat was the
296 result of a slight westward contraction away from the area of the ACC.

297 Although temperature is regarded to be a key determinant of species distribution (Calosi et al.,
298 2010; Chown et al., 2009), other environmental factors have been shown to influence benthic marine
299 species distribution. For example, at the level of an individual species, temperature and depth both
300 affected Tanner crab distribution in the eastern Bering Sea (Murphy, 2020). At the community level,
301 depth, bottom temperature and oceanographic fronts delineated pelagic and benthic communities in
302 the eastern Bering Sea (Baker and Hollowed, 2014). Water depth and substrate characteristics
303 influenced epifaunal community structure in the Chukchi Borderland region (Zhulay et al., 2019),
304 whereas substrate type and latitude influenced epifaunal community composition and distribution in
305 the Russian and US sectors of the Chukchi Sea (Bluhm et al., 2009). In addition, model simulations
306 showed that changes in sediment organic matter supply from pelagic phytoplankton sources can lead to
307 shifts in benthic biomass and community structure (Lovvorn et al., 2016). Thus, a full habitat model
308 incorporating other parameters such as depth, sediment type and export phytoplankton production
309 coupled with an ecosystem model that captures trophic and competitive interactions would provide a
310 more detailed picture of the possible future of Arctic benthic communities.

311 A comparison of thermal thresholds of selected Arctic epibenthic invertebrate taxa and
312 predicted changes in bottom temperature across the Pacific and Atlantic Arctic showed some similar
313 results as our study (Renaud et al., 2015). Of the 65 species Renaud et al. (2015) analyzed (the majority
314 of which were annelids), only seven of the Arctic species had clear upper temperature thresholds, and
315 these ranged between 2 °C and 6 °C. These seven species are analogous to Clusters A through D which
316 had upper temperature thresholds ranging from 2 °C to 5.1 °C. Similar to our conclusion that these
317 clusters may experience a northward contraction of suitable thermal habitat, Renaud et al. (2015)
318 concluded that the northward progression of low-temperature isotherms suggest shrinking distribution

319 ranges for these taxa in the future. Fourteen of the boreal species that Renaud et al. (2015) studied
320 showed clear lower temperature thresholds, ranging from 4 °C to 10 °C. By this definition, our study did
321 not include any boreal species, the lower temperature thresholds of the taxa we examined ranged from
322 -1.5 °C to 1.8 °C. Renaud et al. (2015) concluded that the boreal species with the lowest thresholds are
323 expected to be the first to expand into the Arctic. In contrast, our results did not predict northward
324 expansions of thermal habitat, only contractions of habitat to the north. This could be due to the fact
325 that most of the taxa in our study were cold-water “Arctic” taxa, as defined by Renaud et al. (2015).

326 In contrast to Renaud et al.’s (2015) study of benthic invertebrates and other studies on the
327 distribution of fishes (e.g., Alabia et al., 2018; Polyakov et al., 2020), our projections of thermal habitat
328 did not predict range expansions to the north, only contractions of habitat to the north and offshore.
329 Alabia et al. (2018) documented changes in the distributions and trophic levels of Bering Sea epibenthic
330 communities from 1982-2016 with ocean warming. They observed a northward expansion of subarctic
331 fish and crustacean species and an increase in community trophic level (more large groundfish) over
332 time. In contrast to our analysis, which was of the entire epibenthic invertebrate community (at least as
333 reflected in our catch data), their analysis was limited to catch data on 36 fish and 10 crustacean (crab
334 and shrimp) species. Retrospective studies also show northward expansion of subarctic groundfish
335 which would have competitive and predatory implications for Arctic benthic epifauna (Stevenson &
336 Lauth, 2019; Eisner et al., 2020; Spies et al., 2020; Baker, 2021).

337 There is also evidence for northward range expansions of demersal fish and shrimp species in
338 the Barents Sea and Western Eurasian Basin (Polyakov et al., 2020). These previous studies documenting
339 distributional shifts northward with ocean warming focused on fishes and a few crustaceans, not the
340 epibenthic invertebrate community we examined. We did not examine whether North Pacific epibenthic
341 invertebrate taxa, found south of the Bering Sea might find expand to the north and find suitable habitat
342 in a warming Bering Sea. However, the relatively shallow depths of the Bering Sea shelf, compared to

343 the depth of the slope and basin, might make the “new” habitat unsuitable for southern taxa. Analogous
344 to the situation to the north, we suggest that the possibility of new species invading from the south with
345 warming ocean temperatures might be constrained by the southern shelf break and slope.

346 We also did not examine whether epibenthic invertebrates in the Gulf of Alaska could expand
347 into the Bering Sea with ocean warming. Dispersal of benthic invertebrates primarily occurs during the
348 pelagic egg or larval stage through an interplay of two types of processes: physical (current flow and
349 retention) and biological (vertical migration and directed horizontal swimming). Pelagic larval duration
350 also impacts dispersal distances. Finally, prey availability, growth and predation have consequences for
351 larval survival to settlement (Cowen & Sponaugle 2009). Past research suggested that long-distance
352 larval dispersal between sub-populations was pervasive. However, more recent research indicates that
353 dispersal distances are smaller and subpopulations are more isolated than previously thought (Cowen et
354 al., 2007; Cowen and Sponaugle, 2009). There is a strong oceanographic connection between the Gulf of
355 Alaska (GOA) and the Bering Sea (BS) by way of the narrow, high-speed Alaska Coastal Current which
356 extends for more than 1000 km along the coast of the GOA and through Unimak Pass to the BS (Stabeno
357 et al., 1995). Simulation modeling studies of GOA fish show that eggs and larvae released in the western
358 GOA can be advected into the BS (Parada et al., 2016; Gibson et al., 2019; Stockhausen et al., 2019).
359 Further study is required to determine whether benthic invertebrate populations of the GOA are
360 relatively isolated as reviews of recent research suggest; or whether invertebrate eggs and larvae can
361 disperse from the GOA to the BS as some fishes may and thus expand their population range with ocean
362 warming. Our projections of changes in the distribution and extent of thermal habitat do not address
363 the potential for changes in benthic invertebrate biomass over time. Decreases over the past three
364 decades in biomass of benthic infauna (mostly bivalves, amphipods, polychaetes, and sipunculids) in the
365 northern Bering Sea and increases in the southeast and northeast of the Chukchi Sea have been
366 documented (Grebmeier, 2012; Grebmeier et al., 2018, 2006). The decreases in the Bering Sea were

367 attributed to the loss of sea ice and a weakening of the benthic-pelagic coupling that provides pelagic
368 carbon to the benthos. The increases in the Chukchi Sea were attributed to higher export of pelagic
369 production to the benthos resulting from a longer open water season. Increases in epibenthic biomass
370 (mostly ophiuroids, snow crab *Chionoecetes opilio*, holothurians, and urchins) in the southeast Chukchi
371 Sea, Norton Sound, and the southeast Bering Sea have been documented (Bluhm et al., 2009). Although
372 snow crab abundance increased from the late 1970s to the 2000s in the Chukchi Sea (Bluhm et al.,
373 2009), recent surveys show that snow crab stocks in the Bering Sea are in decline. Biomass of crab was
374 the lowest on record in 2021, continuing a declining trend that began in 2015 (Zacher et al., in prep.). To
375 address changes in biomass, an ecosystem model that incorporates projections of primary production,
376 pelagic consumption, supply of pelagic carbon to the benthos, benthic infaunal and epifaunal biomass
377 and bottom temperature would be useful.

378 The presently predicted changes in amount of thermal habitat available to epibenthic
379 invertebrates could have reverberating impacts on whole Arctic food webs. The most abundant taxa (in
380 terms of biomass) in the cold-water and stenothermic cluster, i.e., the “losers”, were gastropods and
381 the bivalve *Musculus* sp. These taxa are prey to the endangered Pacific walrus (*Odobenus rosmarus*),
382 which is harvested as a food resource in native Alaskan communities (Hovelsrud et al., 2008; Sheffield et
383 al., 2001; Sheffield and Grebmeier, 2009). Bivalves, possibly including *Musculus* sp., are the primary
384 prey to commercially important flatfish, such as yellowfin sole (*Limanda aspera*), Alaska plaice
385 (*Pleuronectes quadrituberculatus*), rock soles (*Lepidopsetta* spp.) and flounders (*Atheresthes* spp.,
386 *Hippoglossoides robustus*, and *Platichthys stellatus*). Small Pacific halibut (*Hippoglossus stenolepis*) also
387 prey on bivalves (data from AFSC food habits collections as described in Livingston et al. (2017) (Aydin
388 pers.com). The most abundant species in the warm-water and highly eurythermic cluster, i.e., the
389 “winners”, was the basket star *Gorgonocephalus* cf. *arcticus*. Basket stars feed on zooplanktonic prey,
390 such as euphausiids using their sticky tube feet and a sophisticated system of spines and hooks

391 (Rosenberg et al., 2005). It is not known who their predators are. Our conclusions about these specific
392 potential food web impacts are qualified by the coarse taxonomic resolution of our data on gastropods
393 and bivalves. It is possible that these groups include species with different thermal preferences and that
394 we have missed the fine-scale differentiation between individual gastropod and bivalve species
395 responses.

396 The predicted changes in thermal habitat could also impact the taxonomic diversity of the
397 region. Thermal habitat for all taxa (except those with the broadest temperature range) contracted to
398 the north, such that by the end of the century the projection was that south of 65 °N (Point Hope) there
399 would only be suitable thermal habitat for the “winners”. This could have an impact on taxonomic
400 diversity of the Bering-Chukchi Sea region because this cluster accounted for only 26 taxa or 8% of all
401 taxa observed. Our diversity calculations are based on data with varying levels of taxonomic resolution,
402 so this estimate may be biased low because of the inclusion of catch data at resolutions higher than
403 species.

404 A key assumption of our approach was that the observed temperature ranges in the Bering to
405 Chukchi Sea region were representative of species local physiological tolerances. Laboratory studies of
406 thermal acclimation potential of Arctic epibenthic invertebrate megafauna are scarce. Laboratory
407 experiments have been conducted to determine the temperature limit of 4 species from Kongsfjorden in
408 Svalbard: a sea urchin (*Strongylocentrotus droebachiensis*), a gastropod mollusk (*Margarites helycinus*), a
409 bivalve mollusk (*Serripes groenlandicus*), and an amphipod of the genus *Onisimus* (Richard et al., 2012).
410 The results were that the sea urchin and the gastropod could acclimate to the highest experimental
411 temperature, 10.3 °C. These two species were in the “warm, broad range” cluster in our analysis,
412 although their temperature range (as defined by the 10th and 90th percentiles) was up to only 5.1 °C.
413 Richard et al. (2012) conclude that their results that Arctic species could acclimate to high temperatures
414 “appear anomalous”, most likely because the Gulf Stream increases sea temperatures in Svalbard in

415 summer to an average of 4 °C to 6.5 °C, more similar to temperate regions than to other polar regions.
416 Indeed, these temperatures are higher than most of our study area. The climate variability hypothesis
417 predicts that high seasonal variation in ocean temperature, such as observed in temperate regions, will
418 result in greater ability to acclimate to increased temperature compared to environments with less
419 seasonal temperature variability such as the tropics and polar regions (Stevens, 1989). Supporting this
420 hypothesis, a number of thermal tolerance experiments have been conducted with Antarctic species in
421 which most have demonstrated a narrow thermal tolerance range (Morley et al., 2011; Peck et al., 2010,
422 2009a, 2009b). Laboratory acclimation experiments of Arctic taxa occurring in less variable and colder
423 temperatures than previously studied are needed (Richard et al., 2012). It is also important to note that
424 temperature increases within physiological tolerance extremes, but outside the 'normal operating
425 temperature range' of an organism can result in lower growth and reproduction (Pörtner and Knust,
426 2007; Wang and Overgaard, 2007).

427 A related assumption is that species have undergone adaptation to ocean temperatures at the
428 regional scale. Local adaptation results in resident genotypes that have a higher fitness in their native
429 habitat than do other genotypes from more distant populations. Local adaptation was once thought to
430 be rare in marine invertebrates with planktonic larvae and potentially high rates of dispersal. But there
431 is now considerable evidence that variation in temperatures across a variety of scales from vertical
432 gradients in the intertidal to latitudinal gradients across the globe has led to divergence in physiological
433 traits among populations of marine invertebrate taxa with a range of life histories, including planktonic
434 dispersal (Sanford and Kelly, 2011). Thus, although some of the taxa that we predict will lose Arctic
435 habitat with ocean warming have relatively widespread distributions into temperate latitudes, we
436 assume that they have adapted to the cooler ocean temperatures of the Bering to Chukchi seas and will
437 experience reduced fitness as temperatures warm there. Examples of these taxa are brittlestars
438 (*Ophiura sarsii*) (Pawson et al., 2009; Stöhr et al., 2019), mussels (*Musculus* spp.) (Zenetos et al., 2005)

439 and nut clams (*Nuculana pernula*) (Kamenev, 2013). Although we assume that local adaptation to
440 temperature has occurred over the past millenia, we also assume that there will be no significant
441 evolutionary adaptation to ocean warming in the future because climate change will outpace the ability
442 of species to adapt. Climate change in the Arctic has been and will likely continue to be rapid: sea
443 temperatures have risen 1-3 degrees in 40 years (Timmermans and Labe, 2020), and our projections are
444 that sea temperatures are predicted to rise 4 degrees over the next 80 years. This increase is more rapid
445 than has been observed over the past million years or on record over the last glacial cycle (PAGES 2K
446 Consortium et al., 2019) and is faster than normal evolutionary timescales (Peck et al., 2009b). We
447 therefore suggest that it is unlikely that Arctic benthic macrofauna will be able to evolutionarily adapt to
448 such a rapid increase in ocean temperature.

449

450 5.0 Conclusions

451 Model projections of ocean bottom temperature suggest that by the end of the century thermal
452 habitat will be reduced for many Arctic epibenthic invertebrate taxa. We acknowledge that models
453 informed by temperature alone and assumptions of future distributions based on past distributions have
454 limitations. Although temperature is a primary determinant of habitat, a full habitat model incorporating
455 other relevant environmental parameters such as sediment type and export production coupled with an
456 ecosystem model that captures trophic and competitive interactions and additional information on
457 species-specific plasticity and thermal tolerance thresholds would provide a more detailed picture of the
458 possible future of Arctic benthic communities. In addition, more laboratory studies of thermal
459 acclimation potentials of Arctic benthic invertebrates are needed. The potential for taxa from the North
460 Pacific and Gulf of Alaska to expand their range into a warming Bering Sea also deserves further study.
461 Finally, continued monitoring of the distribution, abundance and species composition is needed to track

462 changes and refine predictions about the future of this diverse and productive community that supports
463 a number of upper trophic taxa and Arctic human communities.

464

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Table 1. Median temperature and range for each cluster and percent of species in each cluster. “Cold” clusters are those which median temperatures 0.6° C or less and “warm” clusters are those with median temperatures 2.5° C or greater (arbitrarily defined). “Stenothermic” clusters are those with a range (10th to 90th percentile) of 3.5° C or less; “eurythermic” clusters are those with a range of 5.5° to 6° C and the “highly eurythermic” cluster has a range of 9.0° C (arbitrarily defined). Number and percent of taxa and percent catch biomass density are also shown.

Cluster	Median temperature	Temperature range (°C)	Magnitude of range	Qualitative descriptors	# of taxa	% kg km ⁻²
A	-0.3	-1.5° – 2.0°	3.5°	cold, stenothermic	40 (12%)	9%
B	0.6	-1.4° – 4.6°	6.0°	cold, eurythermic	65 (21%)	49%
C	3.4	1.8° – 4.6°	2.8°	warm, stenothermic	60 (19%)	2%
D	2.5	-0.5° – 5.1°	5.5°	warm, eurythermic	119 (38%)	38%
E	2.8	-0.7° – 8.3°	9.0°	warm, highly eurythermic	26 (8%)	3%

Table 2. Percent catch by species (or lowest taxon) in each cluster. Taxa with percent catch greater than or equal to 0.1% are shown, the rest of the catch is summed and shown as 'Other'.

Cluster A "cold, stenothermic" taxa	
Taxon	% kg km ⁻²
Gastropoda	3.8%
<i>Musculus</i> sp.	3.0%
<i>Urasterias lincki</i>	0.4%
<i>Solaster dawsoni</i>	0.3%
<i>Golfingia (Golfingia) margaritacea</i>	0.3%
<i>Myriotrochus rinkii</i>	0.2%
Naticidae	0.2%
<i>Buccinum glaciale</i>	0.1%
<i>Margarites</i>	0.1%
Pandalidae	0.1%
Other	0.2%
Grand Total	9%

Cluster B "cold, eurythermic" taxa	
Taxon	% kg km ⁻²
<i>Ophiura sarsii</i>	36%
<i>Ophiura</i> sp.	3%
Clypeasteroidea	2%
<i>Nuculana pernula</i>	1%
<i>Ocnus glacialis</i>	1%
<i>Psolus fabricii</i>	1%
<i>Halocynthia aurantium</i>	1%
<i>Musculus discors</i>	1%
<i>Buccinum polare</i>	0.5%
<i>Leptasterias (Hexasterias) polaris</i>	0.5%
<i>Gersemia rubiformis</i>	0.3%
<i>Eualus</i> sp.	0.3%
<i>Eualus gaimardii</i>	0.3%
<i>Pagurus rathbuni</i>	0.2%
<i>Leptasterias groenlandica</i>	0.2%
Polychaeta	0.2%
<i>Crossaster papposus</i>	0.2%
<i>Euspira pallida</i>	0.2%
<i>Astarte</i> sp.	0.2%
<i>Buccinum</i> sp.	0.1%
<i>Benthoctopus</i> sp.	0.1%
<i>Eualus macilentus</i>	0.1%
<i>Macoma calcarea</i>	0.1%

<i>Leptasterias arctica</i>	0.1%
Other	0.4%
Grand Total	49%

Cluster C "warm, stenothermic" taxa

Taxon	% kg km ⁻²
<i>Nuculana radiata</i>	1%
<i>Pyrulofusus</i> sp.	0.4%
<i>Alcyonidium gelatinosum</i>	0.1%
Other	0.04%
Grand Total	2%

Cluster D "warm, eurythermic" taxa

Taxon	% kg km ⁻²
<i>Chionoecetes opilio</i>	9%
Bivalvia	4%
<i>Ctenodiscus crispatus</i>	4%
<i>Asterias amurensis</i>	3%
Actinaria	2%
<i>Echinarachnius parma</i>	2%
<i>Alcyonidium disciforme</i>	1%
<i>Gorgonocephalus</i> sp.	1%
<i>Strongylocentrotus</i> sp.	1%
Porifera	1%
<i>Pagurus trigonocheirus</i>	1%
<i>Hyas coarctatus</i>	1%
<i>Solaster</i> sp.	1%
<i>Neptunea heros</i>	1%
<i>Ennucula tenuis</i>	0.4%
<i>Evasterias echinosoma</i>	0.4%
<i>Cyanea capillata</i>	0.4%
<i>Neptunea</i> sp.	0.4%
<i>Neocrangon communis</i>	0.4%
<i>Gersemia</i> sp.	0.3%
<i>Eucratea loricata</i>	0.3%
<i>Stomphia</i> sp.	0.3%
<i>Cryptonatica affinis</i>	0.3%
<i>Buccinum scalariforme</i>	0.2%
<i>Strongylocentrotus droebachiensis</i>	0.2%
Bryozoa	0.2%
<i>Gorgonocephalus eucnemis</i>	0.2%
<i>Labidochirus splendescens</i>	0.2%

<i>Chrysaora melanaster</i>	0.2%
<i>Pyrulofusus deformis</i>	0.2%
<i>Boltenia ovifera</i>	0.1%
<i>Styela rustica</i>	0.1%
<i>Neptunea communis</i>	0.1%
Scyphozoa	0.1%
<i>Eualus fabricii</i>	0.1%
Ascidacea	0.1%
<i>Lethasterias nanimensis</i>	0.1%
<i>Eualus belcheri</i>	0.1%
<i>Pagurus capillatus</i>	0.1%
<i>Cistenides</i> sp.	0.1%
<i>Hyas lyratus</i>	0.1%
<i>Anonyx</i> sp.	0.1%
<i>Beringius</i> sp.	0.1%
<i>Neptunea ventricosa</i>	0.1%
<i>Tachyrhynchus erosus</i>	0.1%
<i>Crangon dalli</i>	0.1%
Other	0.6%
Grand Total	37.5%

Cluster E "warm, highly eurythermic" taxa	
Taxon	% kg km ⁻²
<i>Gorgonocephalus</i> cf. <i>arcticus</i>	2%
<i>Argis lar</i>	0.3%
<i>Balanus</i> sp.	0.3%
<i>Sclerocrangon boreas</i>	0.2%
<i>Urticina crassicornis</i>	0.1%
<i>Argis dentata</i>	0.1%
<i>Stegophiura nodosa</i>	0.1%
Other	0.1%
Grand Total	3%

Table 3. Mean survey bottom temperature, decadal averages from the ensemble mean of the bottom temperature projection models, and temperature increases from present to mid-century and end-of-century (°C)

Domain	Survey	2008-2017	2045-2054	2091-2100	Present to mid-century	Present to end-of-century
North	1.77	0.98	2.25	5.60	1.27	4.62
South	2.86	3.83	5.15	8.10	1.32	4.27

Table 4. Proportion of area within temperature range of each cluster based on model projections of bottom temperature at present (2008-2017), mid-century (2045-2054), and end of century (2091-2100).

Cluster	Temperature range	Qualitative descriptors	Proportion of area within temperature range			# of Species
			Present	Mid-century	End-century	
A	-1.5° – 2.0°	cold, stenothermic	31%	13%	2%	40 (12%)
B	-1.4° – 4.6°	cold, eurythermic	88%	51%	10%	65 (21%)
C	1.8° – 4.6°	warm, stenothermic	61%	38%	8%	60 (19%)
D	-0.5° – 5.1°	warm, eurythermic	88%	64%	13%	119 (38%)
E	-0.7° – 8.3°	warm, highly eurythermic	96%	98%	72%	26 (8%)

Figure legends

Figure 1. a)The Bering Sea and Chukchi Sea study area showing shelf breaks, Aleutian Basin, Central Arctic Ocean, Bering Strait, currents and/or typical water mass pathways and coastal human communities, b) Stations and years survey data used in the analysis.

Figure 2. Relationship between number of groups in k-means clustering and within-cluster variance (sum of squares).

Figure 3. Time series of July and August bottom temperature interpolated to the survey grid and then averaged over the northern (66-75 °N) and southern (54-66 °N) domain. Thin colored lines are based on each individual model, and thick black line indicates the ensemble mean of the eight models. Grey dots are the based on survey data (light grey dots are survey mean bottom temperature interpolated on the grid of each model; dark grey dot is the mean).

Figure 4. Maps of bottom temperature forecasts (average of 8 models): a) present (2008-2017), b) mid-century (2045-2054), c) end of century (2091-2100). Temperature scale shown on Figure 4c is the same for all maps.

Figure 5. Maps of temperature-defined habitat for each cluster based on present-day model forecasts. Temperature scale is the same for all maps.

Figure 6. Maps of temperature-defined habitat for each cluster based on mid-century model forecasts. Temperature scale is the same for all maps.

Figure 7. Maps of temperature-defined habitat for each cluster based on end-of-century model forecasts. Temperature scale is the same for all maps.