

26 **Abstract** (<300 words)

27 Dramatic changes have occurred in the Arctic Ocean over the past few decades,
28 especially in terms of sea ice loss and ocean warming. Those environmental changes may modify
29 the planktonic ecosystem with changes from lower to upper trophic levels. This study aimed to
30 understand how the biogeographic distribution of a crucial endemic copepod species, *Calanus*
31 *glacialis*, may respond to both abiotic (ocean temperature) and biotic (phytoplankton prey)
32 drivers. A copepod individual-based model coupled to an ice-ocean-biogeochemical model was
33 utilized to simulate temperature- and food-dependent life cycle development of *C. glacialis*
34 annually from 1980 to 2014. Over the 35-year study period, the northern boundaries of modeled
35 diapausing *C. glacialis* expanded poleward and the annual success rates of *C. glacialis*
36 individuals attaining diapause in a circumpolar transition zone increased substantially. Those
37 patterns could be explained by a lengthening growth season (during which time food is ample)
38 and shortening critical development time (the period from the first feeding stage *N3* to the
39 diapausing stage *C4*). The biogeographic changes were further linked to large scale oceanic
40 processes, particularly diminishing sea ice cover, upper ocean warming, and increasing and
41 prolonging food availability, which could have potential consequences to the entire Arctic
42 shelf/slope marine ecosystems.

43 **Introduction**

44 Climate change is thought to drive shifts in marine ecosystems (e.g., Perry et al., 2005;
45 Grebmeier et al., 2006; Greene and Pershing, 2007) as planktonic communities respond and
46 adapt to the climatic variability (e.g., Beaugrand and Reid, 2003; Beaugrand et al. 2009). In the
47 Arctic Ocean, unprecedented sea ice loss and ocean warming have occurred over the past few
48 decades (Arctic Climate Impact Assessment, 2004; Carmack et al., 2015), with evidence
49 suggesting that the Arctic marine ecosystem is changing simultaneously (e.g., Carmack et al.,
50 2006; Loeng and Drinkwater, 2007; Wassmann, 2011; Barber et al. 2015; Meier et al., 2015).
51 Total integrated primary production has increased significantly, probably due to longer open
52 water periods and associated longer growing seasons (Arrigo et al., 2008; Arrigo and van Dijken,
53 2015). Earlier ice retreat and later ice advance (Stammerjohn et al., 2012) may also influence
54 phytoplankton phenology (timing). In some areas, significant trends toward earlier
55 phytoplankton blooms were detected in 1997-2009 (Kahru et al., 2011). Phytoplankton bloom
56 timing was strongly related to ice retreat timing (Ji et al., 2013), and shifts from a single bloom
57 polar mode to a double bloom temperate mode have been observed (Ardyna et al., 2014). These
58 changes to primary production phenology and magnitude should in turn impact the secondary
59 producers that rely on that production.

60 Four copepod species of the genus *Calanus* (*C. finmarchicus*, *C. glacialis*, *C.*
61 *hyperboreus*, and *C. marshallae*) are fundamental components of the Arctic/subarctic pelagic
62 ecosystem, rely on primary production, and are prey for large predators (Falk-Petersen et al.,
63 2009). Understanding the biogeographic distributions and range shifts of these copepods is a key
64 prerequisite for predicting ecosystem shifts and community reorganization under the rapid
65 changes of the Arctic system. *Calanus glacialis*, an endemic Arctic species, is widely distributed

66 throughout the Arctic shelf/slope seas and subarctic seas (Conover, 1988; Falk-Petersen et al.,
67 2009). The circumpolar distributions of *C. glacialis* imply that this species can adapt to a wide
68 range of environmental conditions and may utilize various life history strategies (Daase et al.,
69 2013; Banas et al., 2016). Given this plasticity and adaptation to the Arctic environment, the
70 response of this species to interannual fluctuations in environmental conditions is still largely
71 unknown. Because long-term time series observations in the extreme Arctic are almost
72 nonexistent, it is difficult to systematically examine the distributions of *C. glacialis* throughout
73 the years from a pan-Arctic perspective. Only recently have climatological mean abundances of
74 *C. glacialis* and other important copepod species been generated for the entire Arctic Ocean
75 based on data synthesis of historical zooplankton sampling; nevertheless, spatiotemporal scarcity
76 of the data made it impossible to determine interannual variability and long-term trends in
77 zooplankton distribution (Rutzen, 2017).

78 Various types of models have been developed and applied to investigate changing
79 Arctic/subarctic zooplankton dynamics and the potential drivers of those changes, from fully
80 coupled ice-ocean-biogeochemical models (Slagstad et al., 2011; Wassmann et al., 2015), to
81 data-driven statistical models (Kvile et al., 2014; Questel et al., 2016), to trait-based (Banas et al.,
82 2016) and individual-based models (IBMs; Ji et al., 2012; Feng et al., 2016; Elliott et al., 2016;
83 Coyle and Gibson, 2017). In the Arctic Ocean, IBMs are particularly useful for overcoming the
84 tremendous data gaps in zooplankton studies because of their capability to resolve both physical
85 and biological processes at the individual level. For example, Ji et al. (2012) examined the roles
86 of copepod life cycles and environmental seasonality in shaping the biogeographic patterns of
87 two endemic and two expatriate *Calanus* species. Banas et al. (2016) developed a unified
88 modeling framework that resolves relative developmental stage, structure and reserve biomass,

89 and survivorship, and successfully replicated the varying abundances of *C. glacialis/marshallae*
90 between warm and cold years in the Eastern Bering Sea and also the contrasting life cycle
91 strategies utilized by coexisting *C. finmarchicus*, *C. glacialis*, and *C. hyperboreus* in Disko Bay,
92 West Greenland.

93 The present study had two overarching questions: 1) how does *C. glacialis* biogeographic
94 distribution respond to multiple environmental drivers (i.e., sea ice, ocean temperature, and
95 phytoplankton prey) that vary on interannual to interdecadal time scales? and 2) what are the
96 driving mechanisms for potential range shifts of this critical species at both pan-Arctic and
97 regional scales? Here, the focus was on how these drivers and distributions have changed over
98 the last four decades, a period of unprecedented rapid environmental changes. This study
99 expanded on the prior work of Feng et al. (2016), which modeled *C. glacialis* individuals in two
100 contrasting years of the 2000s, and demonstrated a poleward expansion of this species'
101 distribution in a relatively warm and low sea ice year when temperature and food conditions
102 were favorable for its life cycle development. In the present work, IBM experiments were
103 conducted for a total of 35 years annually from 1980 to 2014, therefore allowing a better
104 characterization of the interannual variations and detection of decadal trends in *C. glacialis*
105 distribution and its drivers. A circumpolar transition zone in which the success of *C. glacialis* life
106 cycle development is sensitive to environmental conditions during the growth season was
107 identified from the model runs. Two life history traits (including critical development time and
108 growth season length) of the transition-zone individuals were derived and analyzed together with
109 temperature and food conditions to reveal the environmental drivers that ultimately define *C.*
110 *glacialis* geographic distributions and range shifts of its northern boundaries.

111 **Materials and methods**

112 **Coupled Individual-based and ice-ocean-biogeochemical models**

113 The approach was to offline couple an Arctic Copepod Individual-Based Model
114 (**ArcIBM**) with a pan-Arctic ice-ocean-biogeochemical model (i.e., **Biology/Ice/Ocean**
115 **Modeling and Assimilation System** or **BIOMAS** hereafter) to simulate temperature- and food-
116 dependent life cycle development for the endemic copepod species, *C. glacialis*. Here, the two
117 models and their coupling are briefly described. More details are found in Zhang et al. (2010,
118 2014, 2015), Ji et al. (2012), and Feng et al. (2016).

119 The BIOMAS has four sub-models, one each for ocean circulation, sea ice, pelagic
120 ecosystem, and sea ice algae. It assimilates satellite-derived sea ice concentration (Lindsay and
121 Zhang, 2006) and sea surface temperature (Manda et al., 2005). The model's generalized
122 orthogonal curvilinear mesh covers the Northern Hemisphere from 39°N to the geographical
123 North Pole, with the "north pole" of the mesh displaced over Alaska (Zhang et al., 2015). The
124 model employs a Z-coordinate in the vertical direction with a maximum of 30 layers of varying
125 thicknesses. The ocean mixed layer and euphotic zone are configured with 6 vertical layers of 5
126 m each in the upper 30 m and a total of 13 layers in the upper 100 m. In order to calculate
127 physical advection and life cycle progression of individual copepods in the ArcIBM, ocean
128 temperature, meridional (or northward) and zonal (or eastward) current velocities, and
129 phytoplankton biomass concentration are daily- and depth-averaged from the ocean surface to 60
130 m or to the bottom, whichever is shallower. Here, the phytoplankton (food or prey) in the water
131 column included both released sea ice algae and pelagic phytoplankton, and is a combination of
132 flagellates and diatoms (two basic phytoplankton components in the biogeochemical model of
133 BIOMAS; see Zhang et al., 2010).

134 The ArcIBM simulates both Lagrangian tracking (i.e., ocean-current-induced drifting)
135 and life cycle development of individual copepods. Single individual copepods are released
136 uniformly across the domain at the start of each year of the simulation; that copepod is then
137 advected and develops according to the temperature and food condition encountered along its
138 track. The Lagrangian tracking module solves the advection equation using a 4th order Runge-
139 Kutta (RK-4) scheme. Temperature- and food-dependent copepod aging and subsequent life
140 stage progression are represented by a combination of Bělehrádek (1935) and Ivlev (1955)
141 functions with coefficients fitted to the laboratory data of Campbell et al. (2001) based on the
142 intergeneric equiproportional rule of *Calanus* copepod development (Hart, 1990; see Ji et al.,
143 2012 for details). The Bělehrádek function describes that under food saturation the development
144 time within each life stage exponentially decreases with rising temperature (McLaren, 1963;
145 Corkett, 1986; Campbell et al., 2001). The Ivlev function serves as a nondimensional coefficient
146 to prolong the development time when food becomes limited. In the ArcIBM, the upper 60 m
147 depth-averaged BIOMAS variables (current velocity, ocean temperature, and phytoplankton
148 concentration) are temporally and spatially interpolated at each individual copepod's present
149 time and location to update its new location (advection), age (maturation), and life stage
150 (molting).

151 **Numerical Experiments**

152 The ArcIBM simulations were conducted annually for 35 calendar years from 1980 to
153 2014. All simulations were run from Day 1 to 360 of each year. In each simulation, a total of
154 17134 *C. glacialis* individuals starting from Stage-1 (i.e., egg) were uniformly released in space
155 north of 65°N at the onset of the ocean phytoplankton bloom, identified as the year-day when
156 cumulative biomass concentration exceeds 2.5% of the annual total biomass (see Supporting

157 Information Fig S1). The bloom onset timing was spatially variable but in general occurred
158 earlier in lower latitudes and less ice-covered regions than further to the north (Fig S1). In areas
159 with ice cover, this timing was largely synchronized with ice retreat timing (Fig S2). This
160 implementation represented the primary phenological strategy (or a timing match scenario) for *C.*
161 *glacialis* in which adult reproduction and subsequent development of the progeny occur
162 concurrently with the availability of released ice algae and/or pelagic phytoplankton food
163 (income breeding strategy; Varpe et al., 2007). The reliance on the food supply period is
164 supported by the observation that diapausing *C. glacialis* can quickly respond to light and food
165 emergence by significantly increasing their respiration rates and carbon demands (Morata and
166 Søreide, 2013). Note that released sea ice algae constitute most of the phytoplankton biomass at
167 the bloom onset in the ice-covered zone, implying that reproduction of *C. glacialis* underneath
168 the ice cover is dependent on released ice algal food (Plourde et al., 2005) that precedes the
169 pelagic phytoplankton bloom (Fig 1).

170 In the simulations, all *C. glacialis* individuals were advected by upper 60 m depth-
171 averaged ocean currents while developing through their life stages until Day-360 (Fig 1). Note
172 that the model does not simulate abundances but rather follows single individuals to understand
173 how environmental conditions interact with individual copepod development. A successful *C.*
174 *glacialis* diapauser was defined as an individual that developed beyond the mid-way point of the
175 first diapausing stage *C4* before the end of its growth season (determined by food availability).
176 This assumption allows *C. glacialis* to accumulate sufficient lipids for overwintering survival,
177 consistent with our previous modeling studies (Ji et al., 2012; Feng et al., 2016). During the post-
178 processing of model results, the year-day when an individual becomes a diapauser (or reaches
179 the age of mid-way through *C4*) was identified and its corresponding geographic location was

180 designated as a putative diapause entry site. To depict the annual northern boundary of *C.*
181 *glacialis* diapausers, the northernmost latitude of the diapause entry sites within each degree
182 longitudinal range was determined for each calendar year (see blue curves in Fig S3). To
183 quantify the boundary shifts, the latitudinal differences were calculated by subtracting the 5-year
184 mean northernmost latitudes of diapause entry in 1980-1984 from the mean northernmost
185 latitudes in 2010-2014. The 5-year means were applied to smooth fluctuations associated with
186 annually resolved northern boundaries.

187 Two *C. glacialis* life history traits were derived from model runs. The critical
188 development time (CDT) is the duration required for *C. glacialis* to develop from the first
189 feeding stage *N3* to mid-way *C4* during which time sufficient phytoplankton food is required,
190 while the growth season length (GSL) quantifies the total duration of food supply (Fig 1). In
191 order for a modeled individual to successfully develop to diapause, the growth season length it
192 experiences must exceed its critical development time.

193 For individuals released at identical geographic locations in each year between 1980 and
194 2014, their success in developing to diapause depended on the relative length of the growth
195 season versus the development time. For each release location, the number of years that *C.*
196 *glacialis* individuals successfully developed to diapause was counted. For some locations, *C.*
197 *glacialis* developed to diapause in all or most of the years, while at others *C. glacialis* never or
198 rarely developed to diapause. A transition zone was defined as the release locations where *C.*
199 *glacialis* individuals can develop to diapause in 20-80% of the 35 modeled years (i.e., 7-28
200 years). This zone can be regarded as a geographic envelope where individuals are most sensitive
201 to the interannual variations in developmental conditions so that interannual fluctuations and
202 inter-decadal changes of *C. glacialis* biogeography are likely to occur. Transition zone

203 individuals ($n = 2933$) accounted for about 17.1% of the total individuals in each run. Although
204 perturbing the threshold years would result in slightly expanded or compressed transition zones,
205 the center of distribution remained almost the same (Fig S4). In the transition zone, the number
206 of successful individuals (i.e., diapausers) in each calendar year was normalized by the total
207 number of individuals analyzed to obtain an annual success rate. A higher annual success rate
208 indicated more transition-zone regions were suitable for *C. glacialis* development in that year.
209 The annual mean (\pm one standard deviation) growth season length, critical development time,
210 temperature, and food of the transition-zone individuals also were calculated.

211 To further explore regional similarities and differences, the circumpolar shelf/slope seas
212 were partitioned into nine geographic sectors (Fig 2b): Beaufort (125°-160°W), Chukchi (160°-
213 180°W), Siberian (180°W-150°E), Laptev (150°-105°E), Kara (105°-55°E), Barents (55°-15°E),
214 Greenland-Iceland-Norwegian (GIN, 15°E-45°W), Baffin (45°-80°W), and Canadian Arctic
215 Archipelago (CAA, 80°-125°W) sectors. To a large degree, the longitude-based partitioning
216 followed the geographic convention of the Arctic seas (International Hydrographic Organization,
217 1953).

218 One-way analysis of variance (ANOVA) tests were performed to examine whether the 5-
219 year mean northern boundary shifts from 1980-1985 to 2010-2014 were significant. Linear
220 regression models of the annual time series were fitted against calendar years to obtain linear
221 trends. Non-parametric Spearman's rank correlation coefficients (r) between annual success rates
222 and annual mean life history traits were calculated. All statistical analyses were conducted using
223 Matlab Statistics Toolbox (Mathworks, Natick, MA). The statistical results were deemed
224 significant when p values were less than 0.01.

225 Results

226 The modeled spatial distributions of successful *C. glacialis* diapausers, as revealed by the
227 35 model runs for years of 1980 to 2014, were consistent with the established understanding of
228 this endemic species with high abundances in the Arctic shelf/slope seas and subarctic seas, but
229 much lower abundances (and less likely to sustain viable populations) in the central Arctic basins
230 (e.g., Conover, 1988; Ashjian et al., 2003; Hopcroft et al., 2005; Kosobokova and Hirche, 2009;
231 Rutzen, 2017). In general, the shelf/slope spawned *C. glacialis* individuals could succeed in
232 developing to diapause in all or most of the years (red dots in Fig 2a), whereas high Arctic basin
233 spawned individuals never or rarely succeeded (blue dots in Fig 2a). The transition zone, in
234 which individuals succeed in 7-28 of the modeled years, included the northern parts of the
235 shelf/slope seas along Beaufort, Chukchi, East Siberian, Laptev, and Kara Seas, as well as mid
236 and eastern Barents Sea, Fram Strait, East Greenland Shelf, Baffin Bay, and southern CAA (Fig
237 2b). Overall, the northern boundaries of the successful *C. glacialis* diapausers expanded
238 poleward from early 1980s to recent years with large regional variability (Fig 2c). The poleward
239 shifts between 1980-1984 and 2010-2014 were substantial, indicating that marked environmental
240 changes significantly shifted the biogeography of this critical species (Table 1). Large latitudinal
241 shifts of more than 2.5° were found in the CAA, Baffin, and Chukchi sectors, whereas no shift
242 occurred in the GIN sector (Table 1). One-way analysis of variance showed that the boundary
243 shifts were significant in all sectors except the GIN sector (Table 1).

244 The annual success rates of *C. glacialis* individuals in the transition zone increased
245 significantly over the 35 years with a linear trend of +1.9%/year ($R^2 = 0.87$, $p < 0.01$; Fig 3a and
246 Table S1). This suggested that modeled *C. glacialis* habitats expanded during the past 35 years,
247 as more and more *C. glacialis* individuals in the transition zone successfully developed to

248 diapause over the modeled period. Before 1990, only 20-30% of the transition-zone individuals
249 succeeded while success rates were always greater than 50% after 2000. Despite the substantial
250 interannual variability, the success rates of *C. glacialis* diapausers in nine circumpolar
251 geographic sectors all exhibited upward trends (Fig S5). All sectors, except Barents and GIN,
252 had statistically significant linear trends in the annual success rates (Table S1).

253 The changing biogeographic distribution of *C. glacialis* can be linked to
254 contemporaneous changes in the Arctic physical and biological environments (sea ice, upper
255 ocean temperature, and phytoplankton prey; Table 2). The annual success rates of transition-zone
256 individuals negatively correlated with modeled September-mean sea ice extents ($r = -0.94$, $p <$
257 0.01 ; Fig 3a) as well as March-mean sea ice extents ($r = -0.74$, $p < 0.01$; not shown), implying
258 that environmental conditions in years with less ice cover were more favorable for *C. glacialis*
259 development than those with more ice cover. The highest success rate (85.3%) occurred in 2012,
260 coincident with the year of the lowest sea ice extent among the 35-year study period. Transition-
261 zone annual mean temperature was negatively correlated with September-mean sea ice extent (r
262 $= -0.92$, $p < 0.01$), as was food availability ($r = -0.96$, $p < 0.01$). Annual mean temperature and
263 food for the transition-zone individuals also showed significant upward trends, although
264 temperature appeared to have much higher variability than food (Fig 3c). All 9 sectors had
265 significant upward trends in mean temperature, while all sectors except the Barents and GIN had
266 significant upward trends in mean food (Table S1 and Fig S7).

267 Overall, the poleward expansion of *C. glacialis* northern boundaries and the upward
268 trends in its success rate could be directly explained by the concurrent changes in both growth
269 season length and critical development time. Temperature and food availability together defined
270 the critical life history periods (growth season length and critical development time) that drove

271 whether *C. glacialis* could achieve the diapausing stage. During the 35-year modeled period, the
272 annual mean growth season lengths of all transition-zone individuals increased with a linear
273 trend of +0.61 day/year ($R^2 = 0.78, p < 0.01$) whereas mean critical development times decreased
274 with a linear trend of -0.59 day/year ($R^2 = 0.89, p < 0.01$) (Fig 3b and Table S1). Moreover, the
275 annual success rates were positively correlated with mean growth season lengths ($r = 0.97, p <$
276 0.01), but negatively correlated with mean critical development times ($r = -0.95, p < 0.01$).
277 Regionally, the 7 sectors that showed significant upward trends in annual success rates all had
278 significant linear trends in both mean growth season length and critical development time,
279 although the slopes varied among sectors (Fig S6 and Table S1). In the Barents and GIN sectors
280 that had only weak (not statistically significant) trends in annual success rates, significant trends
281 were detected in critical development time but not in growth season length (Table S1). The
282 annual success rates in all 9 sectors were positively correlated with mean growth season length,
283 but negatively correlated with mean critical development time (Table S2).

284

285 Discussion

286 Based on multi-decadal *C. glacialis* life cycle development simulations, marked poleward
287 range shifts of this critical copepod species in the Arctic Ocean from 1980 to 2014 was
288 demonstrated (Table 1 and Fig 2c). A circumpolar transition zone in which *C. glacialis*
289 individuals were susceptible to interannual environmental changes was identified (Fig 2b). A
290 significant upward trend in the number of individuals developing to diapause was detected in this
291 transition zone over the 35-year study period (Fig 3a). Also, during the copepod growth season,
292 both upper ocean temperatures and phytoplankton concentrations trended higher in the transition
293 zone (Fig 3c), which further led to lengthening growth seasons and shortening critical
294 development times for the copepods (Fig 3b) that in turn were correlated with sea ice extent
295 (Table 2).

296 Copepod boundary shifts in response to environmental changes

297 It is well known that the Arctic sea ice has been rapidly diminishing (Perovich and
298 Richter-Menge, 2009; Stroeve et al., 2012), especially in the marginal ice zone (Strong and Rigor,
299 2013). Many physical, biogeochemical, and biological components have been concurrently
300 changing (see review papers of Barber et al., 2015 and Meier et al., 2015). Modeled sea ice
301 extent, ocean temperature, and phytoplankton biomass were consistent with observational studies
302 documenting temporal changes in those attributes. Through analysis of ocean temperature
303 profiles and satellite-retrieved sea surface temperatures in the summer months of July-September,
304 Steele et al. (2008) found that the general long-term warming trends on the Arctic shelf seas
305 started in 1965 but were especially pronounced since 1995. The increasing food availability and
306 lengthening growth seasons corroborate the findings of Arrigo et al. (2008), Arrigo and van
307 Dijken (2015), and Kahru et al. (2017) based on satellite-retrieved chlorophyll and sea ice data,
308 which suggested that the significant increase in annual total net primary production over much of

309 the Arctic Ocean was mainly due to increases in both open water area and the length of
310 phytoplankton growing season.

311 Poleward expansions of the Arctic endemic copepod *C. glacialis* in response to changing
312 sea ice, upper ocean temperature and production regimes since 1980s were revealed by our
313 multi-decadal modeling to occur in all shelf/slope seas except the GIN seas (Table 1 and Fig 2c).
314 Climate-induced biogeographic shifts of phytoplankton and zooplankton have been documented
315 in the North Atlantic based on the long-term Continuous Plankton Recorder (CPR) surveys (e.g.,
316 Beaugrand et al., 2002; Beaugrand and Reid, 2003; Villarino et al., 2015; Barton et al., 2016)
317 and IBMs (e.g., Speirs et al., 2006; Wilson et al., 2016). However, because survey data in the
318 Arctic Ocean are rather sparse and seasonally and geographically biased with most field
319 observations done during summer-early fall and in the marginal seas and fjords, pan-arctic
320 studies of species distribution and their responses to the fast-changing Arctic climate and marine
321 environments are rare. This modeling study highlights the pressing needs of establishing long-
322 term observational programs in the critical regions, such as the identified transition zone for *C.*
323 *glacialis* (Fig 2b), where major ecosystem shifts are likely occurring. Such ecosystem changes
324 ultimately may have impacts for indigenous people who rely heavily on ecosystem services.

325 **Effects of environmental drivers: temperature and food**

326 The modeling results indicate that increasing temperature and food availability together
327 may cause northward expansion of *C. glacialis* diapausers (Fig 2c) and greater success rates in
328 life cycle development (Fig 3a). However, these two factors strongly correlate and interact with
329 each other (Table 2 and S2) and their relationships with *C. glacialis* development times are
330 highly nonlinear. It is difficult to disentangle the relative importance of temperature versus food
331 in driving *C. glacialis* distributional changes.

332 The direct physiological effect of temperature on *Calanus* copepod development has been
333 modeled in the ArcIBM and permits exploration of changes in this interaction. Despite large
334 interannual and regional variability, the mean water temperature experienced by transition-zone
335 individuals had a significant upward trend (Fig 3c). The increase in temperature reduces stage
336 durations and shortens critical development times, as indicated by the significant downward
337 trend of -0.59 days per year in that parameter (Fig 3b). On average, mean critical development
338 time decreased by about 3 weeks over the 35-year period. Observational evidence from
339 Arctic/subarctic seas that revealed responses of copepod cohort development indirectly
340 supported our model results. In the White Sea (Russia), analyses of 50-year zooplankton survey
341 data revealed that in warmer years, the biomass of *C. glacialis* populations increased earlier in
342 spring and consisted mostly of younger stages, while the biomass of fall populations declined
343 earlier due to the reductions of older stages (Persson et al., 2012), probably because warmer
344 temperatures accelerated growth and development with the resultant early descent into diapause.
345 In the Chukchi Sea, significant increases in the biomass and abundance of zooplankton
346 (particularly *C. glacialis*) were found in recent warm years as compared to the earlier cold years
347 (Ershova et al. 2015). The strong positive correlation between mean developmental stage of *C.*
348 *glacialis* and sea surface temperature from that study agreed with our modeling results, both
349 suggesting that warmer temperatures sped up *C. glacialis* cohort developmental process. It
350 should be noted that Chukchi Sea zooplankton surveys inherently may have included both *C.*
351 *glacialis* and *C. marshallae* (a congener that is difficult to distinguish taxonomically)
352 populations advected from the Bering Sea, whereas the model experiments only considered the *C.*
353 *glacialis* individuals spawned within the Chukchi Sea (i.e., local populations).

354 The effects of food on *C. glacialis* developmental success are twofold, depending both on
355 food quantity and the duration of food supply. In the ArcIBM, the coefficient of the Ivlev
356 function that prolongs stage durations under food-limited conditions was derived from a fit to the
357 experimental data of Campbell et al. (2001). Similar effects were observed in other laboratory
358 experiments (Cook et al., 2007; Daase et al., 2011; Jung-Madsen and Nielsen, 2015). The annual
359 mean food concentration of the transition-zone individuals in 1980-2014 varied between 0.23
360 and 0.72 mmol-N m⁻³. This range is an order of magnitude lower than the saturation
361 concentration (2.3 mmol-N m⁻³) that derived from the Ivlev function and Campbell et al. (2001)
362 experiment. This further suggests that, in the transition zone, food availability constrained *C.*
363 *glacialis* development over a substantial period of its growth season. The increase of mean food
364 concentration was modest, with a linear trend of +0.012 mmol-N m⁻³ per year (Fig 3c). The
365 annual duration of food supply, which is equivalent to the total growth season length, appeared
366 to be more important than the mean food concentration to the developmental success of those
367 transition-zone individuals. A significant trend of +0.61 days per year in the growth season
368 length was detected (Fig 3b), so that the average growth season was lengthened by about 3
369 weeks over a total of 35 years. In the southeastern Bering Sea, lower abundance and biomass of
370 *Calanus* spp. were found in warm and low-ice years with delayed spring blooms and higher
371 predations by larval and juvenile fish (Hunt et al., 2002; Eisner et al., 2014), suggesting that
372 timing and duration of food supply and also predation pressure, rather than physiological effect
373 of temperature, control copepod population dynamics in that region. Another modeling study
374 similarly concluded that the viability of *Calanus* copepods species near the high-latitude
375 boundaries is most sensitive to the duration of food availability (Banas et al., 2016), although the
376 structures and physiological mechanisms of that model are very different from ours.

377 By dividing the circumpolar transition zone into 9 geographic sectors, we showed that all
378 sectors except the Barents and GIN exhibited significant upward trends in *C. glacialis* annual
379 success rates, associated with upward trends in its growth season length and downward trends in
380 its critical development time (Table S1; Fig S5 and S6). In those 7 sectors, both mean
381 temperature and food showed significant upward trends that correlated with the copepod life
382 history traits. In the Barents and GIN sectors, the annual mean growth season length and food
383 concentration were generally stable throughout the years without significant trends (Fig S6 f-g
384 and S7 f-g). This suggests that temperature was the predominant driver that induced the
385 interannual fluctuations and weakly upward trends in *C. glacialis* developmental success in those
386 two sectors (Fig S5 f-g). The results agree with the findings of Kvile et al. (2014) from the
387 Norwegian and southwest Barents Seas, which found positive associations between seasonal
388 mean temperature and *C. finmarchicus* (a congener to *C. glacialis*) nauplii and copepodite
389 abundances in the spring but negative associations in the summer, and suggested that ocean
390 warming triggered an earlier abundance peak of *C. finmarchicus* copepodites.

391 **Copepods in changing Arctic marine ecosystems**

392 Rapid climate change in the Arctic undoubtedly drives species-level variability in
393 development and survivorship that will ultimately result in biogeographic range shifts. Marine
394 plankton may be regarded as sentinels for ecosystem changes given their paramount importance
395 in the food web (Hays et al. 2005). Numerous studies have provided evidence of large-scale
396 biogeographic changes in key copepod species in the North Atlantic Ocean, especially the
397 dominant *C. finmarchicus* (e.g. Beaugrand et al. 2002; Beaugrand et al. 2009; Reygondeau and
398 Beaugrand, 2011). Climate change may alter food web interactions between copepods and other
399 critical ecological components of the Arctic system from both bottom-up and top-down

400 perspectives and ultimately shift the ecosystem as a whole. Furthermore, the Arctic Ocean is
401 tightly linked with the North Pacific and North Atlantic Oceans and its ecosystems are thought to
402 be net biomass beneficiaries through large-scale ocean circulation (i.e., the total amount of
403 biomass transported into the Arctic Ocean far exceeds that exported; Wassmann et al. 2015). A
404 direct linkage between hydrography and zooplankton population and phenological shifts has
405 been identified in the Chukchi Sea, suggesting that higher abundance and biomass of copepods
406 (*C. glacialis/marshallae*, *Metridia pacifica* and *Neocalanus* spp.) were driven by higher
407 northward transport of Pacific water through the Bering Strait (Ershova et al. 2015; Woodgate et
408 al. 2015). Regarding changes in zooplankton prey quantity and quality, climate change may drive
409 shifts in the phytoplankton abundance and species composition, which likely influence fecundity,
410 feeding, development, and survival of zooplankton, consequently shaping the population
411 dynamics (Cook et al. 2007; Leu et al. 2010; Daase et al. 2011). Additionally, in the shallow
412 inflow shelf seas (such as northern Bering/Chukchi Seas) with characteristically high benthic
413 biomass and production, enhanced grazing pressure from zooplankton in warmer waters with
414 less sea ice may weaken pelagic-benthic coupling and induce a regime shift from benthic-
415 dominated to pelagic-dominated ecosystems (Grebmeier et al. 2006; Grebmeier, 2012). Finally,
416 lightscape changes likely lead to an intensified top-down control through vision-based fish
417 foraging as a quadrupling of its visual search range following the loss of sea ice over last 3-4
418 decades would increase its clearance rate by 16 times (Langbehn and Varpe, 2017).

419 **Model caveats and future research directions**

420 Individual-based models have considerable skill in studies of zooplankton biogeography
421 and its responses to environmental drivers despite huge gaps in observational data. This study
422 gained new insights into *C. glacialis* biogeographic distribution shifts and relevant

423 environmental drivers and life history traits over multiple decades. However, the present
424 modeling approach has the following limitations that could be addressed in future research.

425 First, *C. glacialis* prey selection, particularly use of microzooplankton as prey, as well as
426 diel vertical migration (DVM), was not included. Grazing experiments suggest that *C. glacialis*
427 is an omnivore rather than an herbivore, and its prey preference for phytoplankton versus
428 microzooplankton depends on life stages, seasons, and also prey species and sizes (Campbell et
429 al., 2009, 2016). Adding prey preference in the ArcIBM to explore how prey selection might
430 affect copepod distribution and population variability is a future research topic. In addition, *in*
431 *situ* observations suggested that Arctic copepods display DVM patterns during summer/autumn
432 (Falk-Petersen et al., 2008; Rabindranath et al., 2011) and even during winter polar night (Berge
433 et al., 2009, 2014). A proper parametrization of DVM requires a more complete understanding of
434 the seasonally varying zooplankton behaviors and their relationships with environmental cues
435 (e.g., light, temperature, and salinity), as well as predator and prey distributions. Overall, the
436 temperature and food fields from the ice-ocean-biogeochemical model were capable of capturing
437 the seasonality, interannual variations, and decadal trends of the Arctic marine environment
438 (Zhang et al., 2010, 2015; Jin et al., 2016). Therefore, the results of the present study that relied
439 on the depth-averaged environmental conditions from the typical depth range of active *C.*

440 *glacialis* cohorts should provide reasonable estimates of *C. glacialis* diapauser distributions.

441 Additionally, food web interactions were not considered when modeling life cycle
442 development and biogeographic distribution for *C. glacialis* (e.g., predation, interspecific
443 competition, cannibalism, and hybridization). The modeling experiments were only intended to
444 explore whether *C. glacialis* individuals could potentially reach successful diapausing stage
445 based on a combination of temperature and food conditions along their advective paths. The

446 modeled *C. glacialis* diapausers and corresponding pathways may be interpreted as fundamental
447 ecological niches (Hutchinson, 1957) in which this species can potentially survive and tolerate
448 the harsh Arctic environment. Resolving the realized niches in which *Calanus* populations
449 actually exist and thrive would require additional equations and parameters to represent species
450 interactions, such as egg reproduction rate and mortality rate (Helaouët and Beaugrand, 2009;
451 Banas et al. 2016), and so was beyond the scope of present work. A prior study hypothesized that
452 predatory mortality is a controlling factor in *C. glacialis* distribution and prevalence near its
453 southern boundary (Kaartvedt, 2008). This was based on observational evidence from four
454 Norwegian fjords with different predator regimes, suggesting that *C. glacialis*, rather than *C.*
455 *finmarchicus*, prevails in the relatively warm Lurefjorden, due to a lack of planktivorous fish and
456 a low overwinter mortality in this fjord (Bagøien et al. 2001; Kaartvedt, 2008).

457 For simplicity, the whole suite of life history strategies and adaptation was not included,
458 but rather a phenological strategy was implemented to optimize *C. glacialis* adult reproduction
459 and progeny development with upper ocean food availability, and assumed that *C. glacialis*
460 enters diapause when attaining midway through the first diapausing stage *C4*. In recent years
461 with reduced sea ice cover and warming temperature, the earlier modeled dates for *C. glacialis*
462 individuals to reach the diapausing stage (embodied in the shorter critical development times)
463 may imply an earlier diapause entry. Earlier diapause could potentially reduce predation risk
464 (Varpe et al., 2007; Banas et al., 2016), but also may jeopardize overwintering survivorship by
465 depleting lipid reserves before the next spring/summer bloom if coupled with warm winter
466 temperatures (Maps et al., 2012; Coyle and Gibson 2017). Alternatively, a fitness-maximization
467 strategy (Ji, 2011) may allow *C4* individuals to continue developing to *C5*, and even adulthood,
468 if food is still adequate later in the growth season so that a 1-year life cycle for *C. glacialis* may

469 become more prevalent in a warmer Arctic. Additionally, the modeling experiments only
470 investigated *C. glacialis* life cycle development during the first growth season for newly
471 spawned egg individuals, but did not take into account the potential effects of diapause
472 (particularly timing, depth, and duration) on its survival through inactive diapause period and
473 continued development during successive growth season. Calanoid copepods in polar and
474 subpolar regions demonstrate remarkable plasticity in diapause, with little knowledge on the cues
475 that may trigger diapause entry and exit (Baumgartner and Tarrant, 2017), making it difficult to
476 parameterize diapause-related processes in present model. One possibility is to adopt the lipid-
477 accumulation-window hypothesis by dynamically calculating lipid accumulation and metabolism
478 and further determining diapause timing and duration based on lipid content (Maps et al. 2010
479 and 2012).

480 Lastly, with limited knowledge on individual-level species adaptation to the new normal
481 Arctic (e.g., warming temperature, shrinking and thinning sea ice, earlier ice retreat and later ice
482 advance), it is difficult to project future population distribution and persistence of the Arctic
483 copepods. From metabolic theory, Alcaraz et al. (2014) determined that 6 °C is an upper
484 temperature threshold for *C. glacialis* and further speculated that exceeding this bio-energetic
485 limit or tipping point might lead to an ecosystem-level disruption. Søreide et al. (2010)
486 hypothesized a timing mismatch scenario that, in a future Arctic shelf regime, a shorter growth
487 season for ice algae (due to much earlier ice retreat) would result in a shorter time difference
488 between the ice algal and phytoplankton bloom peaks and subsequently lead to a timing
489 mismatch for the development of *C. glacialis* offspring. More studies are needed to better
490 understand the adaptation of these copepods to the changes in primary production regimes and
491 ambient environment in their entire life cycles (both during the growth season and diapause

492 period). This would require long-term and ideally year-round field observations on the
493 abundance, stage composition, and biomass of the zooplankton communities and application of
494 emerging tools such as acoustics and genetics, to uncover changing/evolving life strategies of
495 critical species, including *C. glacialis*. More laboratory studies on the body energetics during
496 both active and dormant periods are needed to better quantify energy gain and loss, and diapause
497 duration in relation to lipid content and surrounding environment, so that copepod population
498 plasticity and persistency can be better understood, modeled, and predicted.
499

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- 731

732 Table.1 Latitudinal shifts of *C. glacialis* diapauser northern boundaries in all and each of the 9
 733 sectors, represented by the changes of mean northernmost latitudes in a recent 5-year period of
 734 2010-2014 compared to an earlier period of 1980-1984. Positive values indicate northward (or
 735 poleward) boundary shifts, and vice versa. Bold numbers denote statistically significant
 736 latitudinal shifts using a one-way ANOVA test ($p < 0.01$).

Sector	All	Beaufort	Chukchi	Siberian	Laptev	Kara	Barents	GIN	Baffin	CAA
Shift (°)	1.68	0.96	2.53	2.12	1.50	2.01	1.15	-0.02	3.55	3.13

737

738 Table.2 Spearman's rank correlation coefficients between each two of the following metrics:
 739 modeled September mean sea ice extent (Ice), temperature (T), food (F), growth season length
 740 (GSL), critical development time (CDT), and annual success rate (ASR) in the circumpolar
 741 transition zone. Bold numbers denote statistically significant correlations ($p < 0.01$).

	Ice	T	F	GSL	CDT	ASR
Ice	1	-0.92	-0.96	-0.90	0.94	-0.94
T		1	0.93	0.85	-0.95	0.92
F			1	0.93	-0.96	0.97
GSL				1	-0.90	0.97
CDT					1	-0.95
ASR						1

742

743 Figure Captions

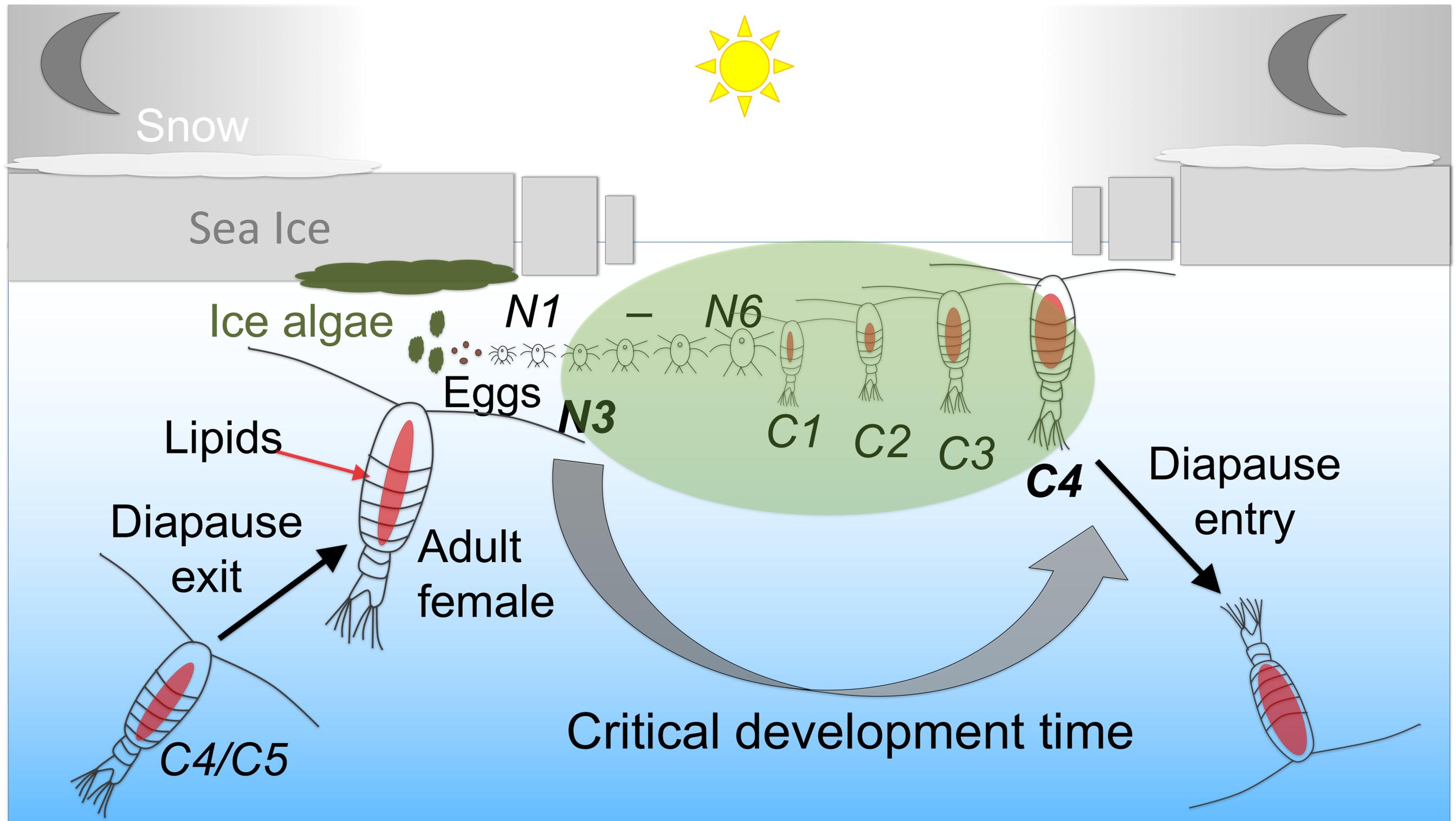
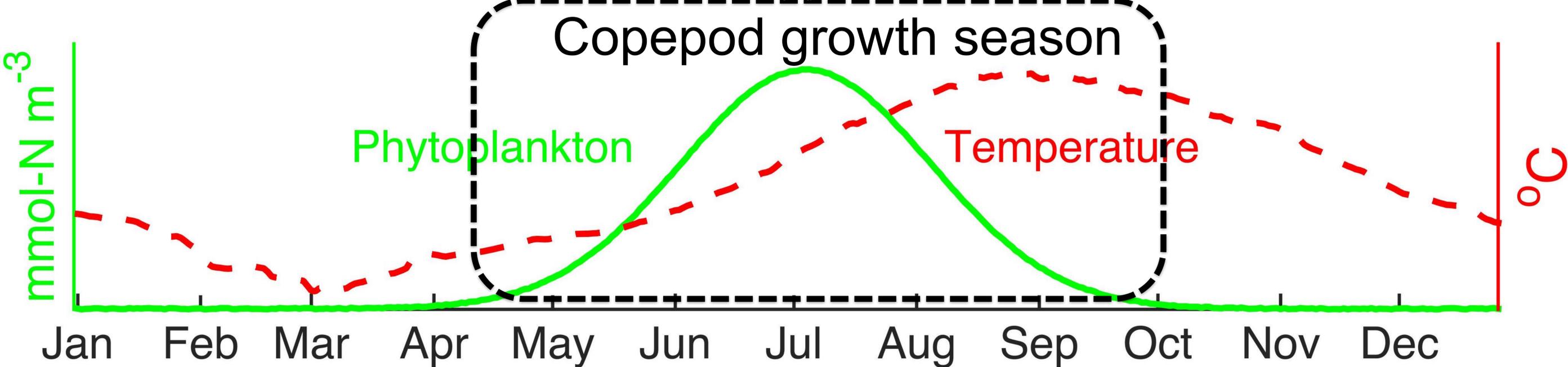
744 Fig.1 Annual life cycle of the copepod *C. glacialis* in the Arctic/subarctic environment. Idealized
745 single-peaked phytoplankton concentration and temperature annual time series are shown in
746 green and red curves to exemplify environmental conditions that control *C. glacialis* life cycle
747 development. In the springtime, *C4/C5* individuals become active and ascend from the deep
748 water. Individuals that overwintered in stage *C5* mature to adult, while those that overwintered in
749 stage *C4* likely require another year to mature. Growth season length is likely the main
750 determinant for which populations have 1- or 2-year life cycle. Populations in relatively lower
751 latitudes tend to have a 1-year life cycle, while a 2-year life cycle is more likely in higher
752 latitudes. Adult females produce eggs by utilizing released sea ice algae (i.e., income breeding).
753 During spring/summer periods, the offspring feed on phytoplankton prey (food) in the upper
754 euphotic zone (illustrated by the green shade) and develop through egg, naupliar (*N1* to *N6*), and
755 copepodid (*C1* to *C4*) stages, and accumulate body lipids (denoted by red-shaded ellipsoids).
756 After maturing to stage *C4* and gaining sufficient lipids, *C. glacialis* descends to the deep water
757 and enters dormancy (diapause) to survive the long starvation period with reduced metabolic
758 rates. The copepod growth season is the time period in which phytoplankton prey is sufficient for
759 *C. glacialis* reproduction, development, and growth. The critical development time is defined as
760 the period required for *C. glacialis* to develop from the first feeding stage *N3* to mid-way into the
761 first diapausing stage *C4*. Some concepts were adapted from Kosobokova (1999), Søreide et al.
762 (2010), and Varpe (2012).

763

764 Fig. 2 Number of years that *C. glacialis* individuals develop to diapause before the end of the
765 growth season: (a) in the Pan-Arctic and (b) in the transition zone, and (c) 5-year mean northern
766 boundaries of diapausers in the years of 1980-1984, 1990-1994, 2000-2004 and 2010-2014. In
767 Panel 2a, the 1000 m isobaths (white lines) are illustrated to separate shelf/slope seas from
768 central basins. All *C. glacialis* individuals are positioned at their initial release locations. In
769 Panel 2b, the transition zone is defined as the release location where *C. glacialis* individuals can
770 successfully develop to diapause in 20-80% of the 35 modeled years (7-28 years). The names
771 and longitudinal ranges of all 9 geographic sectors are shown. In Panel 2c, the northern
772 boundaries of each 5-year period are the mean annual northernmost latitudes of all simulated
773 diapausers in that period.

774

775 Fig. 3 Annual success rates (ASR; 3a), mean growth season length (GSL; 3b), critical
776 development time (CDT; 3b), temperature (T; 3c), and food (F; 3c) of transition-zone *C.*
777 *glacialis* individuals for the modeled years, September mean sea ice extent (3a), and fitted linear
778 trends for all parameters (black dotted lines). Error bars show standard deviations.



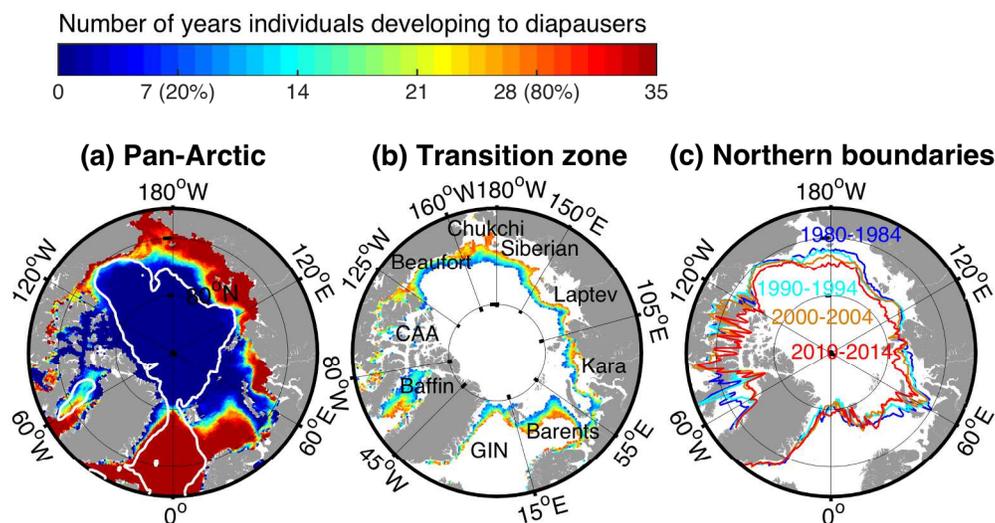


Fig 2 Number of years that *C. glacialis* individuals develop to diapause before the end of the growth season: (a) in the Pan-Arctic and (b) in the transition zone, and (c) 5-year mean northern boundaries of diapausers in the years of 1980-1984, 1990-1994, 2000-2004 and 2010-2014. In Panel 2a, the 1000 m isobaths (white lines) are illustrated to separate shelf/slope seas from central basins. All *C. glacialis* individuals are positioned at their initial release locations. In Panel 2b, the transition zone is defined as the release location where *C. glacialis* individuals can successfully develop to diapause in 20-80% of the 35 modeled years (7-28 years). The names and longitudinal ranges of all 9 geographic sectors are shown. In Panel 2c, the northern boundaries of each 5-year period are the mean annual northernmost latitudes of all simulated diapausers in that period.

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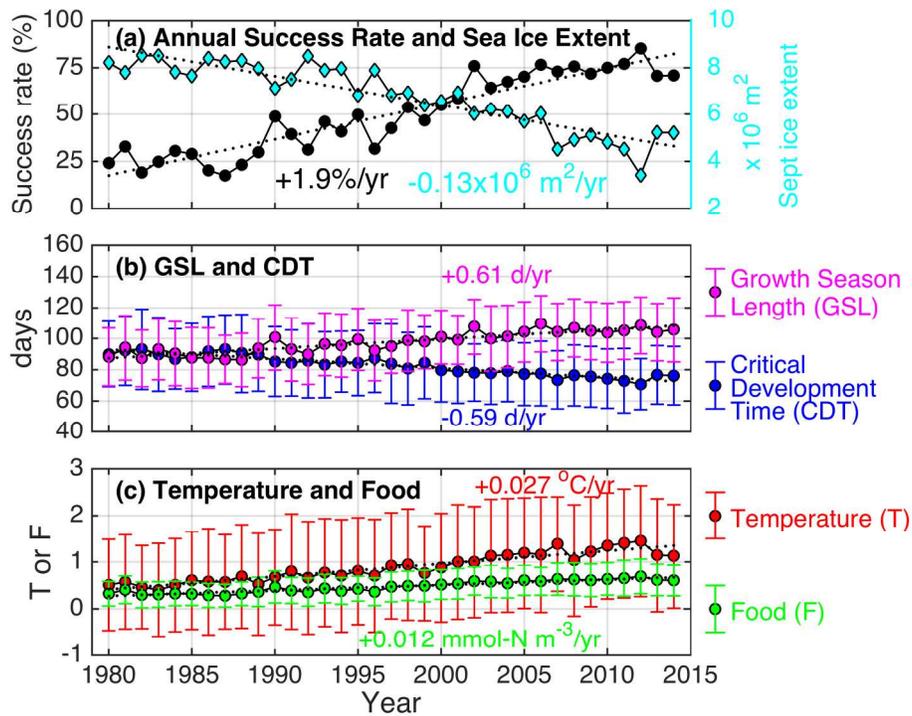


Fig 3 Annual success rates (ASR; 3a), mean growth season length (GSL; 3b), critical development time (CDT; 3b), temperature (T; 3c), and food (F; 3c) of transition-zone *C. glacialis* individuals for the modeled years, September mean sea ice extent (3a), and fitted linear trends for all parameters (black dotted lines). Error bars show standard deviations.

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