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1 Title: Projected impact of 21st century climate change on diapause in *Calanus finmarchicus*

2 Running title: Warming impacts on *C. finmarchicus* diapause

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11

12 **Abstract**

13 High latitude zooplankton typically spend over six months diapausing in deep waters each
14 year, where metabolic demands are met by lipid reserves. The potential time an animal can
15 diapause for is related to overwintering respiration rates, lipid levels and body size. Climate
16 change is therefore expected to reduce diapause duration, which will affect population
17 dynamics and regional biological carbon pumps. However, geographic variations in the
18 impact of climate change and potential behavioural adaptations to changing temperatures are
19 poorly understood. Here, we project changes in potential diapause duration over the 21st
20 century in the key North Atlantic copepod *Calanus finmarchicus* under IPCC RCP 8.5 using
21 a new bioenergetic model. Potential diapause duration was related to surface and deep-water
22 temperature and body size. Climate change has two key effects: increased deep-water
23 temperature will increase metabolism and shorten diapause, whereas surface warming will
24 reduce body size and relative lipid reserves and thus shorten diapause. The projections show
25 pronounced geographic variation in the impact of climate change. Northwestern Atlantic
26 populations see reductions in potential diapause duration of over 30%, whereas the
27 overwintering centre in the Norwegian Sea will only see marginal changes. In deep basins
28 such as the Labrador Sea animals can potentially diapause in deeper waters, which experience
29 significantly less warming, but the ability to control diapause depth may be limited. Animals
30 exiting diapause significantly earlier in the Northwest Atlantic is likely to have a significant
31 impact on ecosystems and disrupt the biological lipid pump.

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36 **Introduction**

37 The continued and largely unabated emissions of anthropogenic greenhouse gases
38 (Friedlingstein et al., 2014) and the fundamental inertia of global energy systems (Davis and
39 Socolow, 2014) mean that large increases in oceanic temperatures are probably unavoidable.
40 These changes are already affecting marine ecosystems (Doney et al., 2012), and future
41 pressures on fisheries will have significant economic consequences (Barange et al., 2014).
42 Changes in zooplankton populations are particularly important because of their impacts on
43 higher trophic levels (Blanchard et al., 2012; Chust et al., 2014) and zooplankton's role as
44 prey for many commercially important fish (Beaugrand and Kirby, 2010). It is therefore a
45 priority of zooplankton research to anticipate the responses of individual species and
46 communities to rising temperatures.

47 Calanoid copepod species frequently dominate North Atlantic mesozooplankton communities
48 (Head et al., 2003). The most well studied, and arguably most important, is *Calanus*
49 *finmarchicus* (Melle et al., 2014), whose geographic range extends from the Gulf of Maine to
50 the North Sea (Planque and Fromentin, 1996). Oceanic warming has caused a significant
51 northward shift in its geographic distribution in recent decades (Barnard et al., 2004; Chust et
52 al., 2013).

53 Oceanic warming will not be uniform in the North Atlantic (Collins et al., 2013). Some
54 regions will warm significantly less than others (Drijfhout et al., 2012), while deep water
55 warming will lag that at the surface (Li et al., 2013). In addition, weakening of the Atlantic
56 Meridional Overturning Circulation (AMOC) could result in cooling in some regions (Banks
57 and Gregory, 2006). These complexities result in difficult to predict regional changes, but it
58 is clear that they will result in the general northward shift of species (Reygondeau and
59 Beaugrand, 2011).

60 Research on the impact of climate change on *C. finmarchicus*'s biogeography has focused
61 almost exclusively on changes in surface temperatures (e.g. Reygondeau and Beaugrand
62 (2011); Hinder et al. (2013); Chust et al. (2013)). However, in response to low food in
63 autumn and winter, *C. finmarchicus* populations spend over half of the year diapausing in
64 deep waters (Svetlichny et al., 1998; Johnson and Checkley, 2004; Falk-Petersen et al.,
65 2009). During diapause, animals reduce their metabolism (Maps et al., 2014) and do not feed
66 (Hirche, 1996). *C. finmarchicus* is probably the only calanoid copepod species where
67 quantitative empirical knowledge is advanced enough to allow modelling of diapause
68 duration. Furthermore, diapause of *C. finmarchicus* acts as an important carbon sink in the
69 North Atlantic (Jónasdóttir et al. 2015). *C. finmarchicus* is therefore an excellent target
70 species if we want to understand the impacts of climate change on diapause

71 Existing models of diapause (Ingvarsdóttir et al., 1999; Saumweber & Durbin, 2006; Maps et
72 al., 2014) have focused on the key role of lipids (Irigoien, 2004). Before diapausing as
73 copepodite stage C5, animals acquire large lipid reserves to meet the metabolic requirements
74 of overwintering (Ingvarsdóttir et al., 1999) and the energy costs of molting and gonad
75 formation (Rey-Rassat et al., 2002). Potential diapause duration is therefore a result of the
76 combined effects of pre-diapause lipid levels, the costs of metabolism, and the energy
77 requirements of molting and gonad formation (Ingvarsdóttir et al., 1999; Saumweber and
78 Durbin, 2006).

79 Effective modelling of potential diapause duration therefore requires understanding the key
80 determinants of lipid levels and overwintering metabolism. Evidence shows that body size
81 (Miller et al., 2000) and food quantity and quality (Gatten et al., 1980; Hygum et al., 2000)
82 are the main influences on lipid levels. Furthermore, field evidence shows that there is a steep
83 allometric scaling of lipid reserves with prosome length (Miller et al., 2000; Saumweber and
84 Durbin, 2006; Pepin et al., 2011; Bergvik et al., 2012). The two key influences on metabolic

85 costs are temperature (Saumweber and Durbin, 2006) and the scaling of metabolism with
86 body size (Maps et al., 2014).

87 Quantitative knowledge is only sufficiently advanced to explicitly incorporate the influence
88 of body size and temperature into a model of diapause duration. Body size varies
89 geographically and is largely determined by temperature (Wilson et al., 2015). We can
90 therefore model the geographic variation of body size and overwintering metabolism with
91 reasonable credibility using depth resolved spatial temperature data. However, there is
92 currently insufficient data to model the impact of geographic variations of food quality and
93 quantity on body size and lipid reserves of animals. We therefore produced a model that
94 relates potential diapause duration to body size and overwintering temperature.

95 A recent large-scale analysis of field data showed that diapause duration is 200-250 days in
96 the North Atlantic, with a median duration of approximately 200 and 250 days in the
97 Northwest and Northeast Atlantic respectively (Melle et al., 2014). Temperature variation
98 was put forward as an explanation for the difference between the eastern and western North
99 Atlantic. However, no existing study has modelled the potential diapause duration of *C.*
100 *finmarchicus* populations and compared model predictions with field estimates. The present
101 study marks the first attempt to do so and to consider the geographic variation in changes that
102 will result from climate change.

103

104

105 **Materials and methods**

106 **Potential diapause duration model**

107 We define potential diapause duration as the maximum time an animal can diapause for. This
108 was calculated under the following biological and ecological assumptions. Temperature
109 experienced during development determines prosome length. Body size determines maximum
110 pre-diapause lipid reserves. Animals must have sufficient lipid reserves remaining after
111 diapause for molting and gonad formation. Structural body mass and temperature determine
112 metabolism, and hence the rate at which animals deplete their reserves. Potential diapause
113 duration is therefore the time taken for an animal to deplete its lipid reserves to the level
114 required for post-diapause gonad formation and molting. The model's mathematical
115 equations are detailed in Table 1 and the literature used to derive relevant biological
116 parameters is given in Table S1. Here we will provide an overview of the biological and
117 ecological rationale for the model, while referencing the relevant equations.

118 We assume a linear relationship between prosome length and temperature (equation 1). Food
119 quantity also influences body size (Campbell et al., 2001), however large scale patterns of *C.*
120 *finmarchicus* body size can be successfully reproduced with a linear relationship between
121 prosome length and temperature (Wilson et al., 2015). Furthermore, existing knowledge of
122 the influence of food on body size is insufficient to credibly model body length in terms of
123 food and temperature. Structural, i.e. nitrogen, weight is then calculated using the relevant
124 allometric scaling (equation 2).

125 Maximum pre-diapause oil sac volume scales allometrically with prosome length (equation
126 3). Oil sac volume is then converted to wax ester carbon (equation 4). There is limited
127 knowledge of the lipid requirements for post-diapause molting and gonad formation. We
128 therefore assume that there is a simple linear relationship between post-diapause lipid

129 requirements and nitrogen weight (equation 5). This is estimated using the laboratory data of
130 Rey-Rassat et al. (2002). Lipid reserves available for metabolism during diapause, WE_{α} , is
131 thus defined as the difference between maximum pre-diapause lipid reserves and the lipid
132 requirements for post-diapause molting and gonad formation (equation 6). This is then
133 simplified to an allometric relationship with length (equation 6).

134 Respiration rates are related to structural weight and temperature (equations 7-10). The
135 oxygen respiration rate (equation 7) is converted to a carbon respiration rate (equation 8).
136 This is then converted from being related to nitrogen weight to being related to length
137 (equation 8).

138 Potential diapause duration is then the time taken to deplete WE_{α} (equation 11). Finally, we
139 simplify the relationship and relate potential diapause duration to prosome length and
140 overwintering temperature (equation 14).

141

142 Table 1: Outline of potential diapause duration model

143	Definitions	
	T_S = Surface (development) temperature (°C)	T_D = Diapause temperature (°C)
144	L = prosome length of diapausers (mm)	w = Nitrogen weight (μg)
	OSV_{max} = Maximum oil sac volume (mm ³)	WE_{max} = Maximum pre-diapause WE ($\mu\text{g C}$)
145	WE_{ω} = Post-diapause WE requirements ($\mu\text{g C}$)	WE_{α} = WE for diapause metabolism ($\mu\text{g C}$)
	r = Respiration rate ($\mu\text{mol O}_2\text{g N}^{-1}\text{h}^{-1}$)	R = Respiration rate ($\mu\text{g C } \mu\text{N}^{-1}\text{d}^{-1}$)
	RQ = Respiratory quotient ($\mu\text{mol CO}_2\mu\text{mol O}_2^{-1}$)	Q_{10} = Q_{10} of overwinter respiration
Equation		Remark
	$L = a \times T_S + b$	(1) Length assumed to be determined by temperature (Wilson et al. 2015).
	$w = c \times L^d$	(2) Nitrogen weight assumed to be structural weight.
	$OSV_{max} = e \times L^f$	(3) Derived from Pepin and Head (2009).
	$WE_{max} = 0.74 \times \frac{900 \times OSV_{max} + 10.8}{1.44}$	(4) Formula from Miller et al. (1998).
	$WE_{\omega} = 3 \times w$	(5) Approximation from Rey-Rassat et al. (2002).
	$WE_{\alpha} = WE_{max} - WE_{\omega} \cong \alpha L^{\beta}$	
	$r = \mu w^{0.75} Q_{10}^{T_D/10}$	(6) Derived from Saumweber and Durbin (2006).
	$R = \frac{24 \times RQ \times 12.011 \times r}{10^6}$	(7) Respiration rate converted to a carbon rate.
	$R = \xi w^{0.75} Q_{10}^{T_D/10}$	(8) Respiration rate related to length.
	where $\xi = \mu \times 24 \times RQ \times 12.011 \times 10^{-6}$	
	$t_d = \frac{\alpha L^{\beta}}{\xi w^{0.75} Q_{10}^{T_D/10}}$	(9) Defined as time taken to deplete available reserves
	$t_d = \frac{\alpha L^{\beta}}{\xi (c L^d)^{0.75} Q_{10}^{T_D/10}}$	
	$t_d = \frac{\alpha L^{\beta}}{\xi c^{0.75} Q_{10}^{T_D/10}}$	
	$t_d = \lambda L^{\theta} Q_{10}^{-T_D/10}$	

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151 **Model scenarios**

152 We report two model scenarios. First, we estimated potential diapause duration in the North
153 Atlantic under current environmental conditions (2005-2012). This scenario was used to
154 validate the model compared with field estimates of current diapause duration. We then
155 estimated changes in potential diapause duration throughout the North Atlantic under the
156 IPCC Representative Concentration Pathway 8.5 (RCP 8.5) (Riahi et al., 2011). RCP 8.5 is a
157 high emissions scenario; however, current greenhouse gas emissions are closely tracking this
158 scenario (Sanford et al., 2014).

159 The ecological assumptions for the scenarios are as follows. Field estimates show that
160 diapause begins in late summer (Melle et al., 2014). We therefore assume that animals enter
161 diapause in late summer, with prosome length being determined by the mean temperature at a
162 depth of 20 m in July and August. A biological map of diapause depth was created using a
163 loess smooth through the median diapause depths reported by Heath et al. (2004), who
164 collated an extensive spatial data set of 13th, 50th and 83rd percentile of diapause depths.

165 Oceanic temperatures for the period 2005-2012 were obtained from NOAA's World Ocean
166 Atlas 2013 (WOA13) (Locarnini et al., 2013). WOA13 is resolved at a geographic resolution
167 of 1 °W by 1 °N and depths are resolved at a resolution of 5, 25 and 50 m in the intervals 0-
168 100, 100-500 and 500-1500 m. We use the statistical mean temperature at the surface and
169 diapause depths for the relevant months over the period 2005-2012, with overwintering
170 temperature being the mean temperature between September and March.

171 The physical model used to project changes in oceanic temperature in the 21st century was
172 version 3.2 of the state of the art Nucleus for European Modelling of the Ocean (NEMO)
173 model (Madec, 2012). Complete details of forcings etc. are given in Yool et al. (2013). The
174 horizontal resolution of NEMO is approximately 1 °× 1 °, with an increased resolution at the
175 equator to provide a more realistic representation of equatorial upwelling. There are 64
176 vertical levels, with the thickness of levels increasing with depth. Projected temperatures for
177 the decades 2000-2009 and 2090-2099 were calculated by forcing the NEMO model using
178 RCP 8.5. Mean temperature at the surface and diapause depth for each decade were used to
179 estimate mean potential diapause duration for each location in the two decades.

180 Diapause duration is potentially sensitive to the overwintering depth of animals because of
181 temperature variation, and thus respiration rate, with depth. We therefore projected the
182 change in temperature profile at a series of locations in the North Atlantic which have depth
183 profiles of diapausing populations (locations shown in Fig. S1), and then compared the
184 evolution of the temperature profile between 2000-09 and 2090-99 in relation to the current
185 depth profiles of diapausing populations.

186

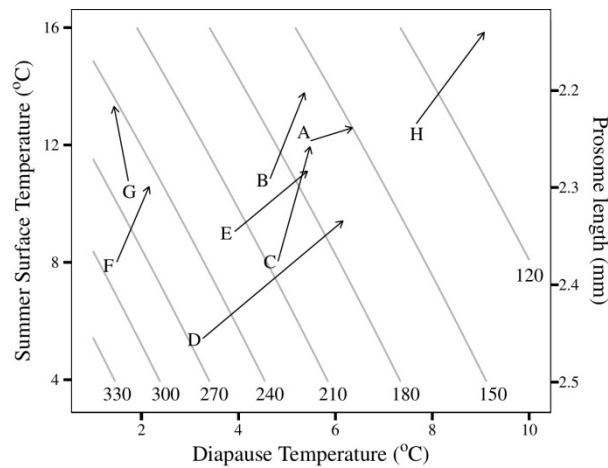
187 **Results**

188 **Relationship between potential diapause duration and prosome length and**
189 **overwintering temperature**

190 Fig. 1 shows the modelled relationship between potential diapause duration and prosome
191 length and overwintering temperature. Field data indicates that typical temperatures
192 experienced by diapausing animals range from 0 to 5 °C (Heath et al., 2004), whereas
193 prosome length typically varies from 2.1 to 2.7 mm (Miller et al., 2000; Arashkevich et al.,
194 2004; Tarrant et al., 2008; Pepin and Head, 2009).

195 Diapause duration is relatively sensitive to body length. An animal of prosome length 2.7 mm
196 will have potential diapause duration 91% longer than that of an animal of prosome length
197 2.1 mm. This difference is principally driven by the fact that bigger animals have relatively
198 higher energy reserves than do small animals, with the allometric scaling of overwintering
199 metabolism a lesser component. Weight-specific metabolism is 16% lower for a 2.7 mm
200 animal than for a 2.1 mm individual, which will, in itself, result in potential diapause duration
201 being 19% longer in a 2.7 mm animal. Temperature has a large effect of diapause duration
202 because of its influence on metabolism. A 1 °C increase in overwintering temperature will
203 result in a 10% reduction in potential diapause duration, while a 2 °C temperature increase
204 will reduce diapause duration by 19%.

205



206

207 Figure 1: Modelled relationship between potential diapause duration (days) and prosome
 208 length and overwinter temperature. Field data was used to derive the relationship between
 209 prosome length and energy reserves. Potential diapause duration is the time taken for an
 210 animal to use up its energy reserves while maintaining sufficient reserves for post-diapause
 211 molting and gonad formation. Arrows show projected changes in the temperatures and length
 212 in locations throughout the North Atlantic under IPCC RCP 8.5 as projected using the NEMO
 213 ocean model. Starting and end points are the means for 2000-09 and 2090-99 respectively.
 214 Letters refer to the following regions: A - Faroe-Shetland Channel, B - Iceland Basin, C -
 215 Irminger Basin, D - Labrador Sea, E - Mid-Atlantic Ridge, F - Northeast Iceland, G -
 216 Norwegian Sea, H - Rockall Basin.

217

218 **Current diapause duration**

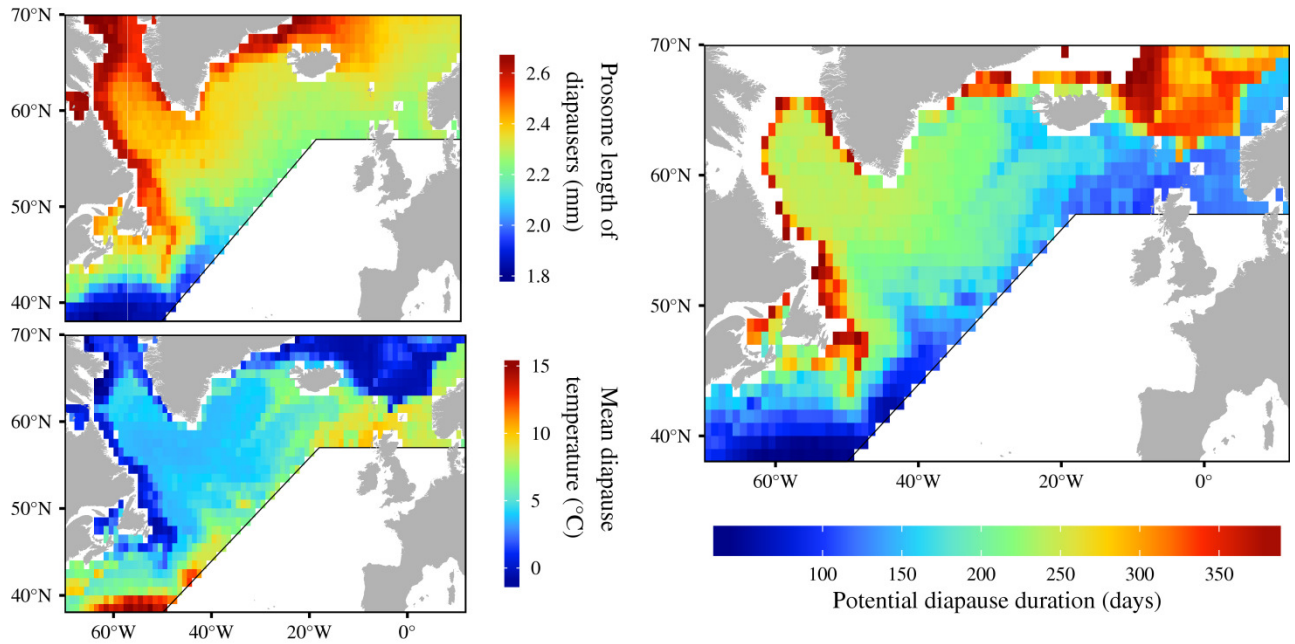
219 Modelled potential diapause duration in the North Atlantic between 2005 and 2012 are show
220 in Fig. 2. Potential diapause duration shows significant geographic variation. In particular,
221 there is a marked difference between the overwintering centres in the Norwegian and
222 Labrador Seas. The Labrador Sea has potential diapause durations of between 200 and 250
223 days. The Norwegian Sea has potential diapause durations of between 300 and 350 days.

224 The main cause of this difference is overwintering temperatures. Fig. 2 shows modelled
225 prosome lengths and estimated temperatures experienced during winter by diapausers.
226 Surface temperatures during summer in the Norwegian Sea are higher than in the Labrador
227 Sea, which results in smaller animals. However, the relatively lower potential diapause
228 duration induced by smaller body size is overwhelmed by the effects of overwintering
229 temperature. Overwintering temperatures in much of the Norwegian Sea are 4 °C lower than
230 in the Labrador Sea. In itself a 4 °C reduction in temperature results in a 50% increases in
231 diapause duration.

232 Modelled potential diapause durations are consistent with field knowledge of diapause
233 duration. The model shows potential diapause duration of 330 days in the central Norwegian
234 Sea, in comparison with approximately 250 days as shown by field studies (Hind et al., 2000;
235 Speirs et al., 2006; Melle et al., 2014). A range of field studies indicate that diapause duration
236 in the Gulf of Maine is approximately 6 months (Durbin et al., 2000; Johnson et al., 2006).
237 This matches our model, which indicates that potential diapause duration in this region is
238 approximately 220 days. Furthermore, our model implies that higher temperatures are the
239 principal reason for *C. finmarchicus* having significantly lower diapause durations in the Gulf
240 of Maine than in Northeast Atlantic regions. Field data shows that diapause duration is 250-
241 270 days in Disko Bay, west Greenland (Madsen et al., 2001), which compares with

242 modelled potential diapause duration of approximately 330 days. Field estimates of median
243 diapause duration are therefore approximately 20-30% lower than modelled potential
244 diapause duration.

245



246

247 Figure 2: Modelled potential diapause duration of *C. finmarchicus*. Potential diapause
 248 duration was estimated assuming that body size was determined by mean surface temperature
 249 in July and August. Overwintering temperatures were estimated by creating a synthetic map
 250 of median diapause depths using field data, and then calculating the temperature at that depth.
 251 The solid line demarcates the approximate southern extent of *C. finmarchicus*'s geographic
 252 distribution. Regions with high sea-ice cover where population modelling (Speirs et al. 2006)
 253 indicates *C. finmarchicus* is not viable were excluded.

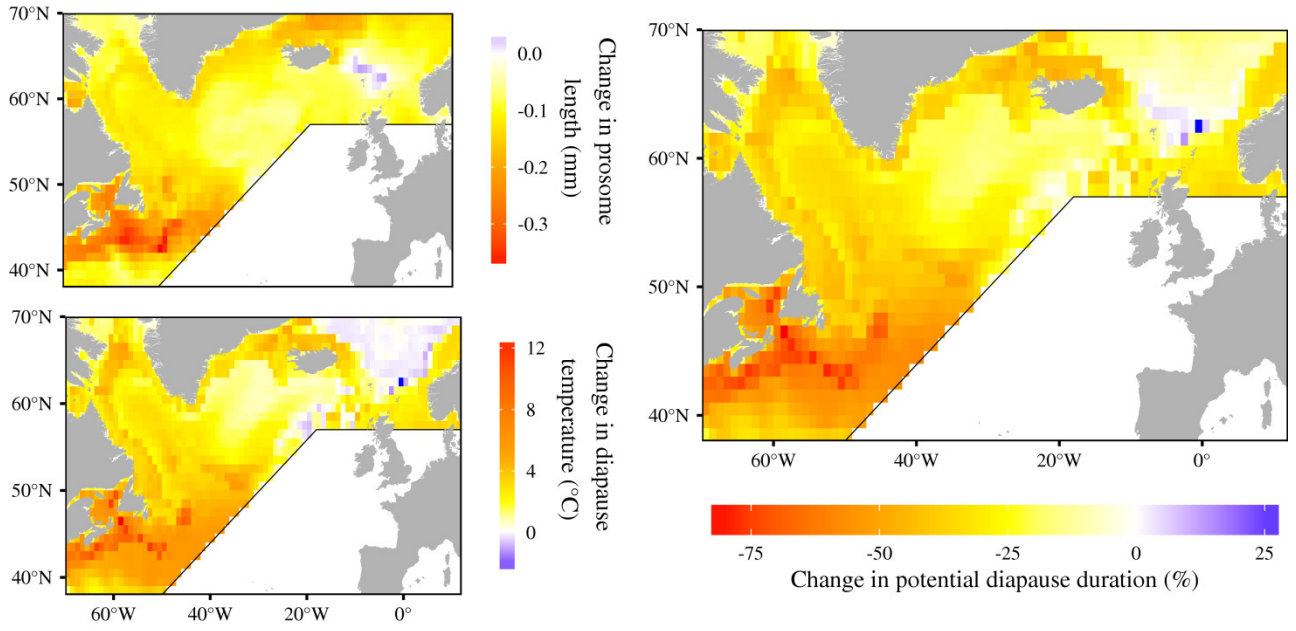
254 **Projected changes under climate change**

255 Fig. 3 shows projected changes in prosome length of diapausers, overwintering temperature
256 and potential diapause duration between 2000-2009 and 2090-2099. Most of the North
257 Atlantic area studied sees significant increases in summer surface temperatures, which induce
258 a reduction in prosome length. Prosome lengths typically reduce by 0.1-0.2 mm in the
259 Labrador Sea. Parts of the Norwegian Sea have similar reductions in prosome length,
260 however regions north and east of the Faroe Islands see only marginal changes. The most
261 pronounced changes in prosome length are in the region south of the Gulf of St. Lawrence,
262 where there are declines of 0.3-0.4 mm.

263 Changes in overwintering temperature are not uniform throughout the North Atlantic.
264 Temperature experienced by diapausing animals only changes marginally in the Norwegian
265 Sea, whereas projected increases in overwintering temperature in the Labrador Sea are
266 between 2 and 3 °C.

267 Estimated percentage changes in potential diapause duration are shown in Fig. 3. Model
268 results indicate that changes in diapause duration will vary significantly. The Norwegian Sea
269 witnesses marginal reductions in diapause duration, with maximum changes of less than 20%.
270 In fact, parts of the Norwegian Sea witness increases in diapause duration.

271



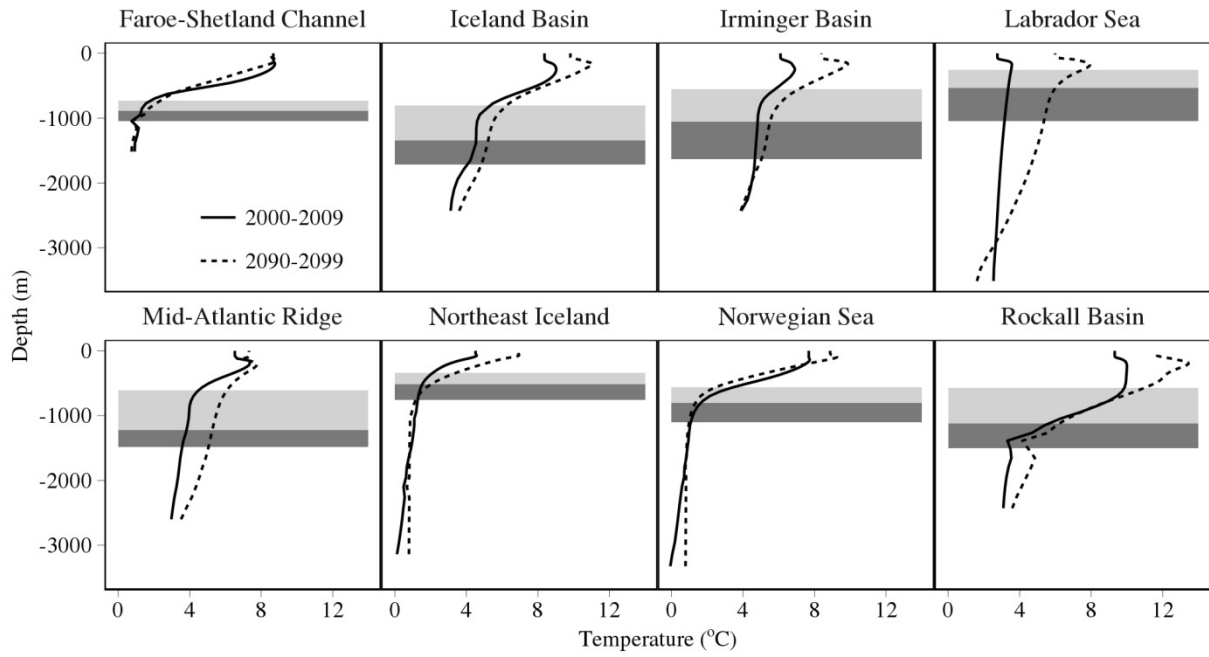
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273 Figure 3: Projected changes in mean prosome length, overwintering temperature and potential
 274 diapause duration of *C. finmarchicus* populations (2000-2009 to 2090-2099), under IPCC
 275 RCP 8.5.

276 In contrast, potential diapause duration shortens significantly in the Labrador Sea. The central
277 Labrador Sea witnesses a shortening of diapause duration of almost 100 days, with reductions
278 of 30-40%. The region south of the Gulf of St. Lawrence and the Gulf of Maine, with
279 reductions of at least 50%, see the most pronounced reduction in potential diapause duration.

280 Projected changes in summer surface and overwintering temperature and thus prosome length
281 and potential diapause duration are shown for a number of locations in Fig. 2. The relative
282 influence of summer surface and diapause temperature on the change in potential diapause
283 duration varies significantly. In the Rockall Basin, Irminger Basin, Northeast Iceland and the
284 Iceland Basin the influence of surface and overwintering temperature changes is
285 approximately the same. In contrast, in the Labrador Sea, the Mid-Atlantic Ridge and the
286 Faroe-Shetland Channel the influence of overwintering temperature changes is much more
287 pronounced. The Norwegian Sea is the only region where overwintering temperature
288 declines, with potential diapause duration staying almost unchanged this century.

289



290

291 Figure 4: Changes in temperature profiles in the first week of January in regions considered.
 292 Solid lines are temperatures in 2000 and 2009 using IPCC RCP 8.5. The light grey bar shows
 293 the depths of the 17th to 50th percentile of diapausing populations and the dark grey bar
 294 shows the depths of the 50th to the 83rd percentile as derived from field data.

295

296 Fig. 4 shows the projected changes in the vertical temperature profile in a number of
297 locations in the North Atlantic and compares them with the current vertical distribution of
298 diapausing *C. finmarchicus* populations. Changes in the temperature profile show a
299 noticeable east-west pattern. Temperature changes in deep waters in the Northeast Atlantic
300 are marginal and have minimal impact on diapause duration. However, changes in deep water
301 temperatures in the overwintering centre of the Labrador Sea are pronounced.

302 Notably, the impacts of increased overwintering temperatures could be almost entirely offset
303 in some regions if animals diapause in deeper waters. In the Labrador Sea, animals currently
304 diapause at depths of between 500 and 1000 m. However, overwintering at depths of greater
305 than 2000 m would result in minimal changes in overwintering metabolic costs. This is also
306 true for the Mid-Atlantic Ridge, where temperatures at a depth of 2000 m in 2090-2099 are
307 projected to be similar to those at 1000 m today, where animals currently diapause.

308

309 **Discussion**

310 The ecological consequences of the projected reductions in potential diapause duration in
311 large parts of the North Atlantic will likely be significant. However, because we have a poor
312 understanding of the causes of diapause exit timing (Johnson et al., 2008) they are difficult to
313 predict. Diapause exit may be triggered by an environmental cue such as photoperiod (Hind
314 et al., 2000) or relate largely to lipid metabolism (Irigoien, 2004). In the first case, animals
315 could exit diapause before they have low lipid levels. Diapause duration will therefore only
316 be reduced when potential diapause duration is less than current diapause duration. However,
317 reductions in post-diapause lipid levels will also reduce the ability of females to lay eggs in
318 the absence of food (Richardson et al., 1999) and lower post-diapause survival, which will
319 influence population dynamics.

320 On the other hand, if diapause duration is related purely to lipid metabolism, reductions in
321 potential diapause duration will automatically reduce actual diapause duration. Evidence
322 suggests this is the case in the Gulf of Maine. Animals currently exit diapause at the end of
323 the year in this region (Durbin et al., 2000), and our model shows that this is likely triggered
324 by low lipid levels. In our model scenario diapause exit time for populations in this region
325 will be in September and October by the end of this century. Overwinter persistence of
326 locally produced populations will therefore be extremely challenging, which makes
327 understanding the role of advection of populations from colder waters into this region (Runge
328 et al., 2015) important. Reductions in diapause duration are therefore likely to have
329 ecological consequences regardless of what causes animals to exit diapause.

330 One of the most notable aspects of our results is that the large reduction in diapause duration
331 in the Labrador Sea could be significantly mitigated if animals diapause in deeper waters.
332 Diapausing at a depth of 2000 m greater than at present will increase diapause duration by
333 approximately 25% in the Labrador Sea at the end of the century. However, it is unclear if
334 animals can diapause in waters of this depth. All studies of overwintering populations show
335 that they never diapause at depths greater than 1500 m (Heath and Jónasdóttir, 1999; Heath
336 et al., 2000; Bagøien et al., 2001; Heath et al., 2004; Bonnet et al., 2006; Edvardsen et al.,
337 2006; Head and Pepin, 2008; Pepin and Head, 2009). Furthermore, it may be physically
338 implausible for animals to diapause at these depths. Visser and Jónasdóttir (1999) used the
339 biophysical properties of lipids and animal dry matter to derive the buoyancy properties of
340 diapausing animals. Their results imply that animals will be negatively buoyant at the depths
341 required to offset increased temperatures in the Labrador Sea, which may make them
342 incapable of diapausing at these depths. Furthermore, the reduction in prosome length will
343 make animals more negatively buoyant in future than they are today due to the combined

344 effects of lower relative lipid content and non-lipid body mass having higher density than
345 lipids (Visser and Jónasdóttir, 1999).

346 The importance of lipid reserves has been disputed by some researchers, who have argued
347 that they are mostly used for activities other than metabolism (Jónasdóttir, 1999; Fiksen,
348 2004; Irigoien, 2004). However, our model shows that use of lipid reserves during diapause is
349 of vital importance. Potential diapause duration is typically 50-100 days greater than
350 observed diapause durations in the Northeast and Northwest Atlantic (Melle et al., 2014);
351 therefore our model implies that over half of pre-diapause lipid reserves are used to meet
352 metabolic costs. This is consistent with field studies in the Labrador Sea (Pepin and Head,
353 2009), Irminger Sea (Heath et al., 2008) and Malengen, Northern Norway (Pasternak et al.,
354 2001), which showed that over half of lipid reserves are used up during diapause.

355 Lipid quality can influence diapause because of energy density variations (Kattner and
356 Hagen, 1995) and the effect of wax ester un-saturation level (Pond, 2012). There is some
357 evidence that animals in temperate regions have fewer long chain fatty acids than more
358 northern animals (Kattner, 1989), which may have an impact on diapause duration. However,
359 the close resemblance of lipid composition in diapausing animals across latitudes (Kattner
360 and Hagen, 2009) means geographic variations in energy density will be relatively low.

361 Liquid to solid phase transitions in copepods may influence diapause depth (Pond, 2012). The
362 temperature and depth at which these occur are related to wax ester un-saturation level, but
363 they are not likely to be of ecological significance for *C. finmarchicus* (Wilson et al., 2013).
364 However, for higher latitude species, for example *Calanoides acutus* (Pond and Tarling,
365 2011), these phase transitions may play a critical role in influencing the impact of climate
366 change on diapause. Extending our model to other species may therefore require
367 consideration of lipid quality.

368 A fundamental uncertainty of our model is the reliability of experimental estimates of
369 overwintering respiration rates, which involve taking animals from depths of up to 1000 m
370 and then measuring their respiration rates in a laboratory at the surface. Changes in water
371 pressure, and the inevitable disturbance of animals, possibly cause animals to partially exit
372 diapause. However, there is a consistent pattern across *Calanus* species, with overwintering
373 metabolism typically 25% of that in surface animals (Maps et al., 2014). Our model uses the
374 experimental work of Saumweber and Durbin (2006), which did not measure respiration rates
375 at temperatures below 3.6 °C. However, the model provides a close fit to respiration rates
376 recorded at 0 °C by Ingvarsdóttir et al. (1999) (Saumweber and Durbin, 2006).

377 The significantly higher scaling of maximum lipid levels than structural weight with prosome
378 length used in our model is shown by all studies that report lipid levels and prosome length
379 (Miller et al., 2000; Saumweber and Durbin, 2006; Pepin et al., 2011; Bergvik et al., 2012).
380 Furthermore, a quantitatively similar relationship is found between median lipid levels and
381 prosome length of diapausers (Pepin and Head, 2009). The reasons for this relationship are
382 unclear. Miller et al. (2000) suggested that this was due to body organs taking up relatively
383 less space in larger individuals, however direct evidence for this is currently lacking. Other
384 influences could potentially explain a large part of this trend of bigger individuals having
385 relatively more lipid. Individuals can be smaller due to higher temperatures and lower food
386 concentrations (Hygum et al., 2000). Length relationships are also potentially biased by
387 animals who diapause later in the year being smaller due to higher temperatures. Reliable
388 estimates of lipids available for diapause would therefore benefit from advances in our
389 understanding of the biochemistry of animals, and on the development of methods to
390 determine when animals have entered diapause.

391 An important future enhancement to our model would be the ability to relate lipid reserves
392 explicitly to environmental conditions. We assumed a simplified relationship between

393 prosome length and lipid reserves based on field data. This data comes exclusively from the
394 Northwest Atlantic, and may not be reflective of other regions. Laboratory and field evidence
395 shows that lipid levels in Calanus are strongly influenced by food quantity and food quality
396 (Gatten et al., 1980; Hygum et al., 2000), and life history modelling shows that the timing of
397 prey availability may be of key importance (Varpe, 2012). Estimates of the large-scale
398 geographic variations of food quality, in particular lipid levels in phytoplankton, do not exist,
399 and a large-scale research programme would be required to attain them. However, a study on
400 the relationship between prosome length and lipid reserves and temperature and food
401 concentration would provide important clarifications on the relationship between
402 environmental conditions and potential diapause duration.

403

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411

412

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