

1 Title: Projected impact of 21<sup>st</sup> 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 21<sup>st</sup>  
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 (Irigoién, 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.

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## 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,  $WE_{\alpha}$ , 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  $WE_{\alpha}$  (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	<b>Definitions</b>	
144	$T_S$ = Surface (development) temperature (°C)	$T_D$ = Diapause temperature (°C)
145	$L$ = prosome length of diapausers (mm)	$w$ = Nitrogen weight ( $\mu\text{g}$ )
	$OSV_{max}$ = Maximum oil sac volume (mm <sup>3</sup> )	$WE_{max}$ = Maximum pre-diapause WE ( $\mu\text{g C}$ )
	$WE_\omega$ = Post-diapause WE requirements ( $\mu\text{g C}$ )	$WE_\alpha$ = 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
<b>Equation</b>		<b>Remark</b>
	$L = a \times T_S + b$	(1) Length assumed to be determined by temperature (Wilson <i>et al.</i> 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 <i>et al.</i> (1998).
	$WE_\omega = 3 \times w$	(5) Approximation from Rey-Rassat <i>et al.</i> (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 13<sup>th</sup>, 50<sup>th</sup> and 83<sup>rd</sup> 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 21<sup>st</sup> 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  $1^\circ \times 1^\circ$ , 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

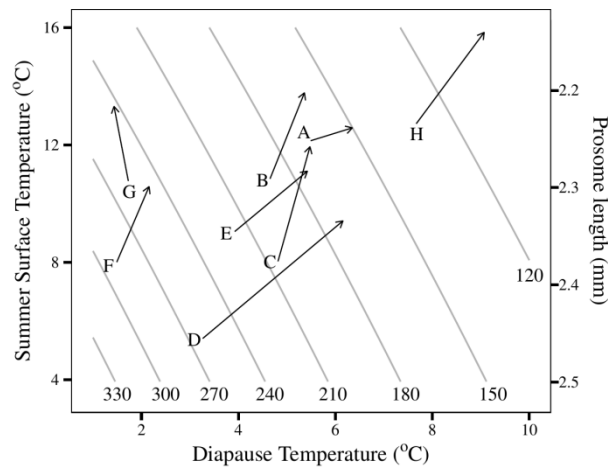
187 **Results**

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**

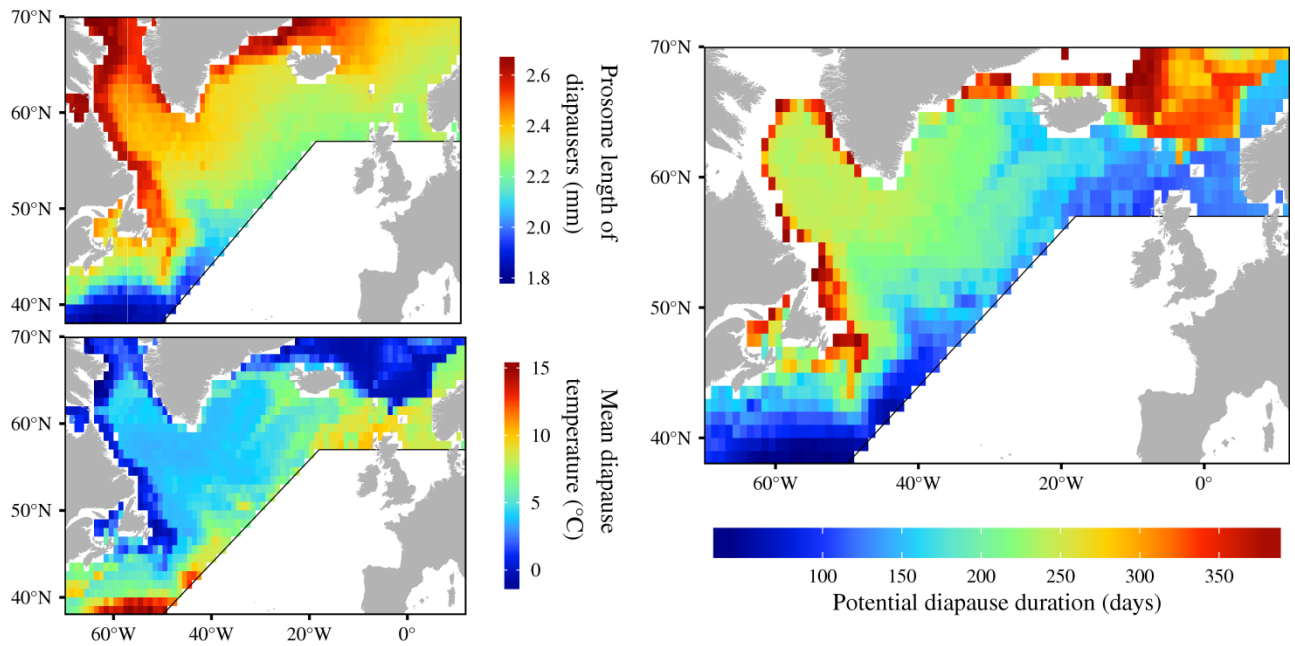
219 Modelled potential diapause duration in the North Atlantic between 2005 and 2012 are show  
220 in Fig. 2. Potential diapause duration shows significant geographic variation. In particular,  
221 there is a marked difference between the overwintering centres in the Norwegian and  
222 Labrador Seas. 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**

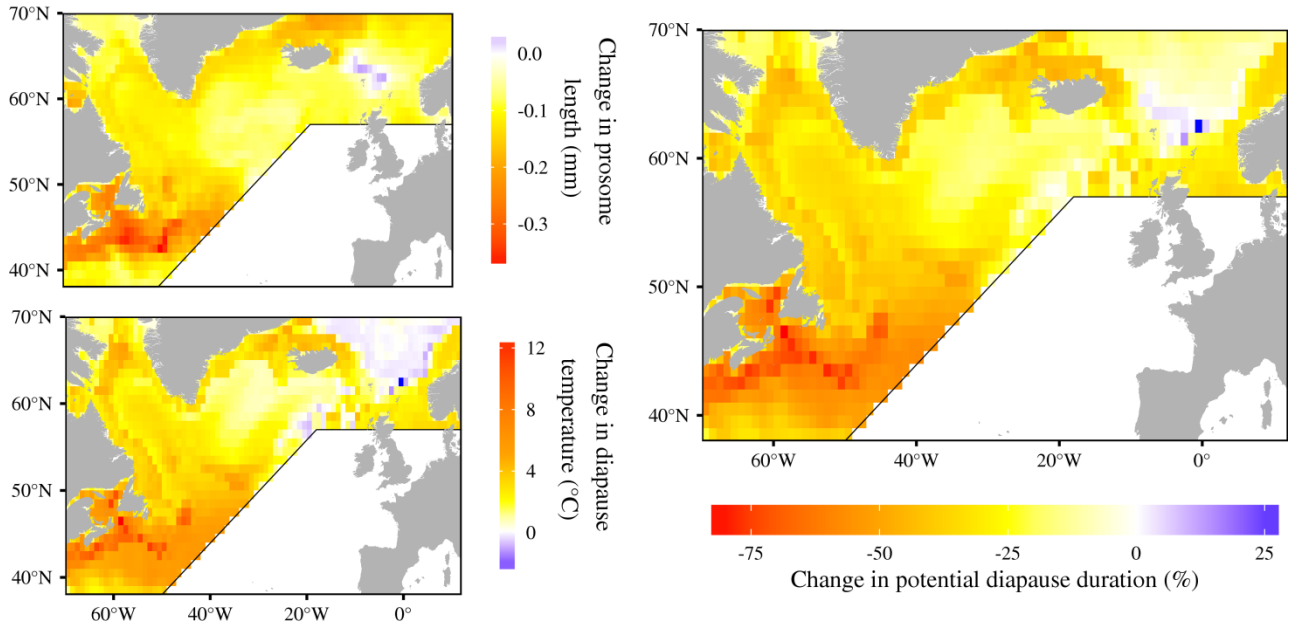
255 Fig. 3 shows projected changes in prosome length of diapausers, overwintering temperature  
256 and potential diapause duration between 2000-2009 and 2090-2099. Most of the North  
257 Atlantic area studied sees significant increases in summer surface temperatures, which induce  
258 a reduction 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





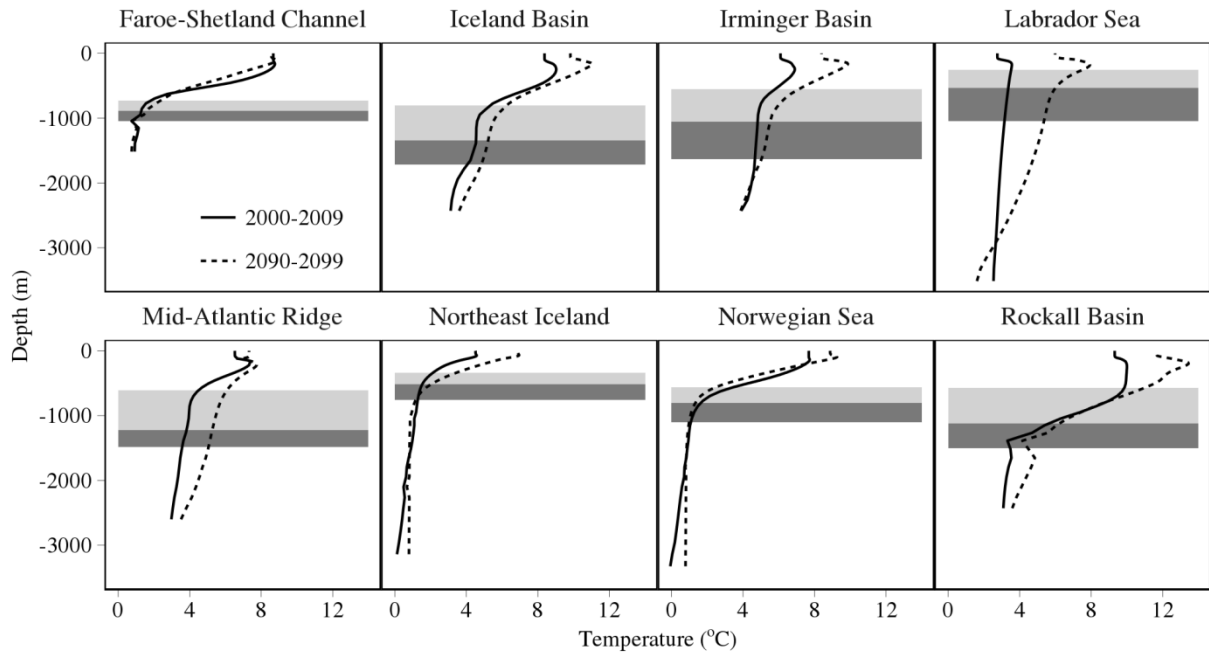
272

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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