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

Running title: Warming impacts on C. finmarchicus diapause

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Abstract

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

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

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

Oceanic warming will not be uniform in the North Atlantic (Collins et al., 2013). Some regions will warm significantly less than others (Drijfhout et al., 2012), while deep water warming will lag that at the surface (Li et al., 2013). In addition, weakening of the Atlantic Meridional Overturning Circulation (AMOC) could result in cooling in some regions (Banks and Gregory, 2006). These complexities result in difficult to predict regional changes, but it is clear that they will result in the general northward shift of species (Reygondeau and Beaugrand, 2011).
Research on the impact of climate change on C. finmarchicus’s biogeography has focused almost exclusively on changes in surface temperatures (e.g. Reygondeau and Beaugrand (2011); Hinder et al. (2013); Chust et al. (2013)). However, in response to low food in autumn and winter, C. finmarchicus populations spend over half of the year diapausing in deep waters (Svetlichny et al., 1998; Johnson and Checkley, 2004; Falk-Petersen et al., 2009). During diapause, animals reduce their metabolism (Maps et al., 2014) and do not feed (Hirche, 1996). C. finmarchicus is probably the only calanoid copepod species where quantitative empirical knowledge is advanced enough to allow modelling of diapause duration. Furthermore, diapause of C. finmarchicus acts as an important carbon sink in the North Atlantic (Jønasdóttir et al. 2015). C. finmarchicus is therefore an excellent target species if we want to understand the impacts of climate change on diapause.

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

Effective modelling of potential diapause duration therefore requires understanding the key determinants of lipid levels and overwintering metabolism. Evidence shows that body size (Miller et al., 2000) and food quantity and quality (Gatten et al., 1980; Hygum et al., 2000) are the main influences on lipid levels. Furthermore, field evidence shows that there is a steep allometric scaling of lipid reserves with prosome length (Miller et al., 2000; Saumweber and Durbin, 2006; Pepin et al., 2011; Bergvik et al., 2012). The two key influences on metabolic
costs are temperature (Saumweber and Durbin, 2006) and the scaling of metabolism with body size (Maps et al., 2014).

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

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

Potential diapause duration model

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

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

Maximum pre-diapause oil sac volume scales allometrically with prosome length (equation 3). Oil sac volume is then converted to wax ester carbon (equation 4). There is limited knowledge of the lipid requirements for post-diapause molting and gonad formation. We therefore assume that there is a simple linear relationship between post-diapause lipid
requirements and nitrogen weight (equation 5). This is estimated using the laboratory data of Rey-Rassat et al. (2002). Lipid reserves available for metabolism during diapause, $WE_{a}$, is thus defined as the difference between maximum pre-diapause lipid reserves and the lipid requirements for post-diapause molting and gonad formation (equation 6). This is then simplified to an allometric relationship with length (equation 6).

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

Potential diapause duration is then the time taken to deplete $WE_{a}$ (equation 11). Finally, we simplify the relationship and relate potential diapause duration to prosome length and overwintering temperature (equation 14).
Table 1: Outline of potential diapause duration model

<table>
<thead>
<tr>
<th>Definitions</th>
<th>Equation</th>
<th>Remark</th>
</tr>
</thead>
<tbody>
<tr>
<td>$T_S$ = Surface (development) temperature (°C)</td>
<td>$L = a \times T_S + b$</td>
<td>(1) Length assumed to be determined by temperature (Wilson et al. 2015).</td>
</tr>
<tr>
<td>$L$ = prosome length of diapausers (mm)</td>
<td>$w = c \times L^d$</td>
<td>(2) Nitrogen weight assumed to be structural weight.</td>
</tr>
<tr>
<td>$\text{OSV}_{\text{max}} = \text{Maximum oil sac volume (mm}^3)$</td>
<td>$\text{OSV}_{\text{max}} = e \times L^f$</td>
<td>(3) Derived from Pepin and Head (2009).</td>
</tr>
<tr>
<td>$\text{WE}_{\text{max}} = \text{Maximum pre-diapause WE}$</td>
<td>$\text{WE}<em>{\text{max}} = 0.74 \times \frac{900 \times \text{OSV}</em>{\text{max}} + 10.8}{1.44}$</td>
<td>(4) Formula from Miller et al. (1998).</td>
</tr>
<tr>
<td>$\text{WE}_{\omega} = \text{Post-diapause WE requirements}$</td>
<td>$\text{WE}_{\omega} = 3 \times w$</td>
<td>(5) Approximation from Rey-Rassat et al. (2002).</td>
</tr>
<tr>
<td>$r = \text{Respiration rate (}\mu\text{mol} \text{O}_2 \text{g}^{-1} \text{h}^{-1}$</td>
<td>$R = \xi , w^{0.75} \frac{T_D/10}{Q_{10}}$</td>
<td>(6) Derived from Saumweber and Durbin (2006).</td>
</tr>
<tr>
<td>$RQ = \text{Respiratory quotient}$</td>
<td>$R = \xi , w^{0.75} \frac{Q_{10} , T_D/10}{Q_{10}}$</td>
<td>(7) Respiration rate converted to a carbon rate.</td>
</tr>
<tr>
<td>$w = \text{Nitrogen weight (}\mu\text{g}$</td>
<td>$R = \xi , w^{0.75} \frac{T_D/10}{Q_{10}}$</td>
<td>(8) Respiration rate related to length.</td>
</tr>
<tr>
<td>$\text{WE}_{\alpha} = \text{WE for diapause metabolism (}\mu\text{g C}$</td>
<td>$\text{WE}<em>{\alpha} = \text{WE}</em>{\max} - \text{WE}_{\omega} \approx \alpha , L^\beta$</td>
<td>(9) Defined as time taken to deplete available reserves</td>
</tr>
</tbody>
</table>

$t_d = \frac{a \, L^\beta}{\xi \, w^{0.75} \, Q_{10} \, T_D/10}$
$t_d = \frac{a \, L^\beta}{\xi \, (c \, L^f)^{0.75} \, Q_{10}} \frac{T_D/10}{Q_{10}}$
$t_d = \frac{a \, L^\beta - 0.75 d}{\xi \, w^{0.75} \, Q_{10} \, T_D/10}$
$t_d = \frac{\lambda \, L^\beta \, Q_{10} \, T_D/10}{a \, L^\beta}$
$t_d = \lambda \, L^\beta \, Q_{10} \, T_D/10$
Model scenarios

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

The ecological assumptions for the scenarios are as follows. Field estimates show that diapause begins in late summer (Melle et al., 2014). We therefore assume that animals enter diapause in late summer, with prosome length being determined by the mean temperature at a depth of 20 m in July and August. A biological map of diapause depth was created using a loess smooth through the median diapause depths reported by Heath et al. (2004), who collated an extensive spatial data set of 13th, 50th and 83rd percentile of diapause depths. Oceanic temperatures for the period 2005-2012 were obtained from NOAA’s World Ocean Atlas 2013 (WOA13) (Locarnini et al., 2013). WOA13 is resolved at a geographic resolution of 1 °W by 1 °N and depths are resolved at a resolution of 5, 25 and 50 m in the intervals 0-100, 100-500 and 500-1500 m. We use the statistical mean temperature at the surface and diapause depths for the relevant months over the period 2005-2012, with overwintering temperature being the mean temperature between September and March.
The physical model used to project changes in oceanic temperature in the 21st century was version 3.2 of the state of the art Nucleus for European Modelling of the Ocean (NEMO) model (Madec, 2012). Complete details of forcings etc. are given in Yool et al. (2013). The horizontal resolution of NEMO is approximately 1 °× 1 °, with an increased resolution at the equator to provide a more realistic representation of equatorial upwelling. There are 64 vertical levels, with the thickness of levels increasing with depth. Projected temperatures for the decades 2000-2009 and 2090-2099 were calculated by forcing the NEMO model using RCP 8.5. Mean temperature at the surface and diapause depth for each decade were used to estimate mean potential diapause duration for each location in the two decades.

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

Relationship between potential diapause duration and prosome length and overwintering temperature

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

Diapause duration is relatively sensitive to body length. An animal of prosome length 2.7 mm will have potential diapause duration 91% longer than that of an animal of prosome length 2.1 mm. This difference is principally driven by the fact that bigger animals have relatively higher energy reserves than do small animals, with the allometric scaling of overwintering metabolism a lesser component. Weight-specific metabolism is 16% lower for a 2.7 mm animal than for a 2.1 mm individual, which will, in itself, result in potential diapause duration being 19% longer in a 2.7 mm animal. Temperature has a large effect of diapause duration because of its influence on metabolism. A 1 °C increase in overwintering temperature will result in a 10% reduction in potential diapause duration, while a 2 °C temperature increase will reduce diapause duration by 19%.
Figure 1: Modelled relationship between potential diapause duration (days) and prosome length and overwinter temperature. Field data was used to derive the relationship between prosome length and energy reserves. Potential diapause duration is the time taken for an animal to use up its energy reserves while maintaining sufficient reserves for post-diapause molting and gonad formation. Arrows show projected changes in the temperatures and length in locations throughout the North Atlantic under IPCC RCP 8.5 as projected using the NEMO ocean model. Starting and end points are the means for 2000-09 and 2090-99 respectively. Letters refer to the following regions: A - Faroe-Shetland Channel, B - Iceland Basin, C - Irminger Basin, D - Labrador Sea, E - Mid-Atlantic Ridge, F - Northeast Iceland, G - Norwegian Sea, H - Rockall Basin.
Current diapause duration

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

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

Modelled potential diapause durations are consistent with field knowledge of diapause duration. The model shows potential diapause duration of 330 days in the central Norwegian Sea, in comparison with approximately 250 days as shown by field studies (Hind et al., 2000; Speirs et al., 2006; Melle et al., 2014). A range of field studies indicate that diapause duration in the Gulf of Maine is approximately 6 months (Durbin et al., 2000; Johnson et al., 2006). This matches our model, which indicates that potential diapause duration in this region is approximately 220 days. Furthermore, our model implies that higher temperatures are the principal reason for C. finmarchicus having significantly lower diapause durations in the Gulf of Maine than in Northeast Atlantic regions. Field data shows that diapause duration is 250-270 days in Disko Bay, west Greenland (Madsen et al., 2001), which compares with
modelled potential diapause duration of approximately 330 days. Field estimates of median diapause duration are therefore approximately 20-30% lower than modelled potential diapause duration.
Figure 2: Modelled potential diapause duration of C. finmarchicus. Potential diapause duration was estimated assuming that body size was determined by mean surface temperature in July and August. Overwintering temperatures were estimated by creating a synthetic map of median diapause depths using field data, and then calculating the temperature at that depth. The solid line demarcates the approximate southern extent of C. finmarchicus’s geographic distribution. Regions with high sea-ice cover where population modelling (Speirs et al. 2006) indicates C. finmarchicus is not viable were excluded.
Projected changes under climate change

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

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

Estimated percentage changes in potential diapause duration are shown in Fig. 3. Model results indicate that changes in diapause duration will vary significantly. The Norwegian Sea witnesses marginal reductions in diapause duration, with maximum changes of less than 20%. In fact, parts of the Norwegian Sea witness increases in diapause duration.
Figure 3: Projected changes in mean prosome length, overwintering temperature and potential diapause duration of C. finmarchicus populations (2000-2009 to 2090-2099), under IPCC RCP 8.5.
In contrast, potential diapause duration shortens significantly in the Labrador Sea. The central Labrador Sea witnesses a shortening of diapause duration of almost 100 days, with reductions of 30-40%. The region south of the Gulf of St. Lawrence and the Gulf of Maine, with reductions of at least 50%, see the most pronounced reduction in potential diapause duration.

Projected changes in summer surface and overwintering temperature and thus prosome length and potential diapause duration are shown for a number of locations in Fig. 2. The relative influence of summer surface and diapause temperature on the change in potential diapause duration varies significantly. In the Rockall Basin, Irminger Basin, Northeast Iceland and the Iceland Basin the influence of surface and overwintering temperature changes is approximately the same. In contrast, in the Labrador Sea, the Mid-Atlantic Ridge and the Faroe-Shetland Channel the influence of overwintering temperature changes is much more pronounced. The Norwegian Sea is the only region where overwintering temperature declines, with potential diapause duration staying almost unchanged this century.
Figure 4: Changes in temperature profiles in the first week of January in regions considered. Solid lines are temperatures in 2000 and 2009 using IPCC RCP 8.5. The light grey bar shows the depths of the 17th to 50th percentile of diapausing populations and the dark grey bar shows the depths of the 50th to the 83rd percentile as derived from field data.
Fig. 4 shows the projected changes in the vertical temperature profile in a number of locations in the North Atlantic and compares them with the current vertical distribution of diapausing *C. finmarchicus* populations. Changes in the temperature profile show a noticeable east-west pattern. Temperature changes in deep waters in the Northeast Atlantic are marginal and have minimal impact on diapause duration. However, changes in deep water temperatures in the overwintering centre of the Labrador Sea are pronounced.

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

**Discussion**

The ecological consequences of the projected reductions in potential diapause duration in large parts of the North Atlantic will likely be significant. However, because we have a poor understanding of the causes of diapause exit timing (Johnson et al., 2008) they are difficult to predict. Diapause exit may be triggered by an environmental cue such as photoperiod (Hind et al., 2000) or relate largely to lipid metabolism (Irigoin, 2004). In the first case, animals could exit diapause before they have low lipid levels. Diapause duration will therefore only be reduced when potential diapause duration is less than current diapause duration. However, reductions in post-diapause lipid levels will also reduce the ability of females to lay eggs in the absence of food (Richardson et al., 1999) and lower post-diapause survival, which will influence population dynamics.
On the other hand, if diapause duration is related purely to lipid metabolism, reductions in potential diapause duration will automatically reduce actual diapause duration. Evidence suggests this is the case in the Gulf of Maine. Animals currently exit diapause at the end of the year in this region (Durbin et al., 2000), and our model shows that this is likely triggered by low lipid levels. In our model scenario diapause exit time for populations in this region will be in September and October by the end of this century. Overwinter persistence of locally produced populations will therefore be extremely challenging, which makes understanding the role of advection of populations from colder waters into this region (Runge et al., 2015) important. Reductions in diapause duration are therefore likely to have ecological consequences regardless of what causes animals to exit diapause.

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

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

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

Liquid to solid phase transitions in copepods may influence diapause depth (Pond, 2012). The temperature and depth at which these occur are related to wax ester un-saturation level, but they are not likely to be of ecological significance for C. finmarchicus (Wilson et al., 2013). However, for higher latitude species, for example Calanoides acutus (Pond and Tarling, 2011), these phase transitions may play a critical role in influencing the impact of climate change on diapause. Extending our model to other species may therefore require consideration of lipid quality.
A fundamental uncertainty of our model is the reliability of experimental estimates of overwintering respiration rates, which involve taking animals from depths of up to 1000 m and then measuring their respiration rates in a laboratory at the surface. Changes in water pressure, and the inevitable disturbance of animals, possibly cause animals to partially exit diapause. However, there is a consistent pattern across Calanus species, with overwintering metabolism typically 25% of that in surface animals (Maps et al., 2014). Our model uses the experimental work of Saumweber and Durbin (2006), which did not measure respiration rates at temperatures below 3.6 °C. However, the model provides a close fit to respiration rates recorded at 0 °C by Ingvarsðottir et al. (1999) (Saumweber and Durbin, 2006).

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

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