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# Spatial modelling of *Calanus finmarchicus* and *Calanus helgolandicus*: parameter differences explain differences in biogeography

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## ABSTRACT

The North Atlantic copepods *Calanus finmarchicus* and *C. helgolandicus* are moving north in response to rising temperatures. Understanding the drivers of their relative geographic distributions is required in order to anticipate future changes. To explore this, we created a new spatially explicit stage-structured model of their populations throughout the North Atlantic. Recent advances in understanding *Calanus* biology, including U-shaped relationships between growth and fecundity and temperature, and a new model of diapause duration are incorporated in the model. Equations were identical for both species, but some parameters were species-specific. The model was parameterized using Continuous Plankton Recorder Survey data and tested using time series of abundance and fecundity. The geographic distributions of both species were reproduced by assuming that only known interspecific differences and a difference in the temperature influence on mortality exist. We show that differences in diapause capability are not necessary to explain why *C. helgolandicus* is restricted to the continental shelf. Smaller body size and higher overwinter temperatures likely make true diapause implausible for *C. helgolandicus*. Known differences were incapable of explaining why only *C. helgolandicus* exists southwest of the British Isles. Further, the fecundity of *C. helgolandicus* in the English Channel is much lower than we predict. We hypothesize that food quality is a key influence on the population dynamics of these species. The modelling framework presented can potentially be extended to further *Calanus* species.

**Keywords: copepods**$_1$**, zooplankton**$_2$**, modelling**$_3$**, biogeography**$_4$**, diapause**$_5$

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## 1 INTRODUCTION

Zooplankton communities are now reorganizing throughout the North Atlantic (Chust et al., 2013; Beaugrand et al., 2009). Rising temperatures are causing species to expand at the northern edge of

their distribution, while they are retreating at the southern edge (Beaugrand, 2012). As a consequence, communities are changing and many species are being replaced by their southern congenerics (Beaugrand et al., 2002).

Changes in communities dominated by the calanoid copepods *Calanus finmarchicus* and *C. helgolandicus* are among the most well-studied (Wilson et al., 2015). *C. finmarchicus* is an oceanic species that is found from the Gulf of Maine to the North Sea (Melle et al., 2014). In contrast, *C. helgolandicus* is a shelf species that lives from the North Sea to the Mediterranean Sea (Bonnet et al., 2005). Both species are now moving north, which has caused *C. helgolandicus* to replace *C. finmarchicus* as the dominant calanoid copepod in the North Sea (Reid et al., 2003). Future temperature rises will likely cause this to be repeated further north (Villarino et al., 2015). We must therefore understand differences in the impacts of climate change on congeneric zooplankton species, so that we can anticipate changes in communities and their consequences.

A key test of our understanding of the interspecific differences in demography of these species is whether we can simulate their population dynamics in such a way that the relative geographic distributions of both species are a result of the differences in biology. An inability to do this can highlight important knowledge gaps that must be filled to make projections of the impact of climate change on *Calanus* communities more biologically credible.

In this spirit, we tested the ability of known interspecific differences to explain the geographic distributions of both species by creating a new unified model. We created a stage-structured model which represents each life stage of *C. finmarchicus* and *C. helgolandicus*, and that represents body size by dividing each stage into a set of size classes. This work is based on the previous model of *C. finmarchicus* in the North Atlantic of Speirs et al. (2005, 2006). Continuous Plankton Recorder survey data was used to parameterize the model and simulated annual cycles of abundance and fecundity were compared with empirical time series in a number of North Atlantic locations.

Recently, an increasing number of researchers have taken a trait-based approach to understanding zooplankton communities (Litchman et al., 2013; Barton et al., 2013). Key traits such as body size, development rate and fecundity are identified, and the functional role of species in ecosystems is thus thought to be a function of their positions within trait-space. A trait-based approach has previously been used to model copepod communities in Cape Cod Bay, Massachussetts (Record et al., 2010). We used this approach to understand the biogeography of two species, under the assumption that where species lie in trait-space is the fundamental determinant of relative biogeography.

Our underlying philosophy is that the equations describing the population dynamics of both species should be identical, but with potential differences in parameters. This constraint will arguably result in suboptimal models for each species when viewed separately. However, it enables us to more clearly understand the biological differences that drive the large-scale differences in distribution. Fundamentally, this work is based on the assumption that if knowledge of key interspecific differences is sufficient, then known interspecific differences are all that is needed for a model to reproduce the geographic distributions of both species. The only known difference between the species that could influence population dynamics is the response of ingestion rate, and thus growth, development and fecundity, to temperature (Wilson et al., 2015). We therefore begin with the hypothesis that this difference alone can explain most of the differences in geographic distribution.

# 2 MODEL

## 2.1 Model background and framework

We present an extension of the previous work by Speirs et al. (2005, 2006), who modelled the population dynamics of *C. finmarchicus* over the entire North Atlantic. This extension took two key forms. First, we incorporated recent developments in our understanding of *Calanus* biology. Second, we modified the model of Speirs et al. (2006) so that it could represent the population dynamics of both *C. finmarchicus* and *C. helgolandicus*. Full mathematical details of the model, along with relevant parameters, are given in Appendix 1. Here we will summarize the modelling framework of Speirs et al. and then the extensions to it.

The model of Speirs et al. was discrete in time and space. It covered the entire North Atlantic, ranging from 30 to 80°N and 80°W to 90°E. The population of *C. finmarchicus* was distributed over a regular grid of cells of size 0.5°longitude by 0.25°latitude. They had two update processes. First, the population of each cell was updated to account for development, reproduction and mortality. After these updates, the population is redistributed between cells to account for physical population transport. A separate physical model was used to create the flow-field and temperature drivers for the relevant biological and physical update. The annual cycle of food in each cell was estimated by deriving phytoplankton carbon fields from satellite sea-colour observations. 1997 was used as the target year for simulations because this was the year when the Trans-Atlantic Study of *Calanus* (TASC) collected a large number of time series of *C. finmarchicus* abundance in the North Atlantic. The framework of Speirs et al. was as follows. Surface developers are made up of eggs (E), naupliar stages (N1 to N6), and copepodite stages (C1 to C5). Finally, there are diapausers (C5d) and adults (C6).

*Calanus* development follows the equiproportional rule, that is relative stage duration is independent of temperature (Campbell et al., 2001). Development from egg to adult can therefore be divided into a fixed number of steps, with each having identical time duration under identical environmental conditions (Gurney et al., 2001). In total, there were 57 development steps, which cover the 13 stages of *Calanus* development.

This framework allows the entire population to be updated simultaneously, and for the entire population to be simulated with high computational efficiency (Speirs et al., 2006). However, modelling the populations of *C. finmarchicus* and *C. helgolandicus* required one modification.

We began with the hypothesis that differences in the response of growth and development to temperature are sufficient to explain the geographic distributions of both species. In other words, all equations and parameters would be the same, except for those related to growth and development. This could not be satisfactorily achieved in the original framework. Large-scale patterns of fecundity are not only the result of the effects of environmental conditions, but also of body size. Further, the ability of animals to diapause is strongly influenced by size (Wilson et al., 2016). We therefore incorporated body size into the framework. Large-scale patterns of fecundity and diapause duration could therefore be represented as the combined effects of body size and the environment, and did not require the introduction of interspecific differences. The geographic domain used by Speirs et al. covers all regions of high *C. helgolandicus* abundance (Bonnet et al., 2005), and was therefore maintained.

## 2.2 Biological processes: a new view of *Calanus* biology

The following biological processes are represented in our model: development, egg production, diapause and mortality. In each case, we modified the model of Speirs et al. to account for recent developments in the understanding of *Calanus* biology.

A recent review of the differences between the two species found that the only known relevant difference was the influence of temperature on ingestion, and thus growth, development and fecundity (Wilson et al., 2015). We therefore constrained the model by making a number of assumptions about the differences between the species based on this review. These assumptions were as follows:

- There is a dome-shaped response of ingestion rate to temperature for both species, with ingestion rate higher for *C. finmarchicus* than *C. helgolandicus* below a temperature of 13 °C.
- An emergent property of this is that there are dome-shaped relationships between growth and egg production rate and temperature, and a U-shaped relationship between development time and temperature for both species.
- Under identical conditions, both species will grow to the same size.
- There are no differences in the ability to accumulate lipids or diapause.

Further, we take the following assumptions and simplifications about the biology and ecology of both species.

- There are no interactions between the two species.
- The species do not hybridize. However, hybridization has been observed among other *Calanus* species (Gabrielsen et al., 2012; Parent et al., 2011, 2012).
- The relationships between traits and the environment do not vary in time or space.

The key modelled relationships between body size, development time, egg production rate and diapause duration with temperature are shown in Fig. 1.

There are no apparent interspecific differences in body size, and large-scale geographic patterns of body size are largely driven by temperature (Wilson et al., 2015). We therefore modeled body size under the simplified assumption that it is determined by temperature experienced at birth for all development classes (Fig. 1(a)). This assumption is derived from the fact that egg size is determined by temperature (Campbell et al., 2001) and that the existence of an exo-skeleton likely greatly constrains size over all development classes. The temperature-prosome length relationship of Campbell et al. (2001) was used with a multiplier, which was fitted based on the relationship between predicted and observed female prosome length. Prosome length reduces linearly with increasing temperature. This approach contrasts with Speirs et al., which did not represent size.

Egg-adult development time was assumed to be influenced purely by temperature and food concentration. The relationship between egg-adult development time and temperature under food-saturated conditions is assumed to follow that derived by the model of Wilson et al. (2015). Development time saturates at high food levels, and we use the relationship between food concentration and development time of Campbell et al. (2001). There is a U-shaped response of development time to temperature (Fig. 1(b)), which contrasts with the monotonically decreasing form used by Speirs et al. The computational approach is that of Gurney et al. (2001) and uses dynamic time-step constraints. This is the same approach as in Speirs et al. (2005,

2006) and it is effective in minimizing numerical diffusion (Gurney et al., 2001; Record and Pershing, 2008).

Fecundity was related to temperature, food concentration and body size. We assumed that egg production and growth are equivalent (McLaren and Leonard, 1995). Egg laying females have stopped growing and we therefore assume that carbon previously directed to growth will be used to make eggs. The growth rate equation of Wilson et al. (2015) forms the basis of our egg production rate (EPR) model for both species, with the food saturation component taken from Hirche et al. (1997). EPR therefore has a dome-shaped response to temperature (Fig. 1(c)). Further, EPR has a saturating response to food concentration and we use a conventional allometric relationship between EPR and carbon weight, i.e. EPR $\sim$ carbon weight$^{0.75}$. This contrasts with Speirs et al., who represented EPR as a monotonically increasing function of temperature, but using the same food response as we have assumed. We assume that 50% of adults are female.

A recent modelling study, which synthesized empirical findings, showed that maximum potential diapause duration is largely determined by prosome length and overwintering temperature (Wilson et al., 2016). We therefore modelled diapause duration using the maximum potential diapause duration equation from that study (Fig. 1(d)). Diapause duration declines at higher temperature because of increased metabolic rates, and is shorter at smaller prosome lengths because of lower relative lipid levels and higher relative metabolic costs. We assumed that a fraction of the C5 population enters diapause at the end of the C5 stage. This fraction is dependent on growth rate, with it increasing at lower growth rates, so that more animals diapause when development conditions are poor. In the model, animals exit diapause at the end of their potential diapause duration. This differs from Speirs et al., who assumed that diapause exit was triggered by a photoperiod cue.

Mortality is modelled using a stage-dependent background rate, alongside a starvation and density dependent term. Field studies indicate that mortality in both species is stage-dependent (Eiane et al., 2002; Ohman et al., 2004; Hirst et al., 2007). These estimates of stage-dependent mortality include all sources of mortality. However, we need to distinguish between different sources of mortality to properly represent population dynamics. We therefore used a fraction of the stage-specific mortality rates calculated by Eiane et al. (2002) as the background mortality rate, with additional temperature, starvation and density dependent terms. Starvation dependent mortality was modelled in the same way for both species by assuming that it relates to growth rate; with starvation mortality only occurring below a threshold growth rate and increasing as growth rate decreases. Background mortality is temperature dependent, with mortality increasing with temperature and the relationship taking the form mortality $\sim (T/8)^z$. Density dependent mortality is assumed to be proportional to total biomass. Mortality was represented the same way as in Speirs et al., with the exception of starvation-dependence. Speirs et al. represented this purely as a function of food concentration. However, the differences in ingestion rate between the two species (Møller et al., 2012) show that *C. helgolandicus* is likely to face much greater starvation levels at temperatures below approximately 11 °C. We therefore viewed growth rate as a better indicator of starvation than food concentration.

## 2.3 Environmental drivers

Seasonal cycles in food concentration, temperature and oceanic circulation drive the model. The only data with sufficient spatial and temporal coverage of food concentration are satellite estimates of sea surface colour. SeaWIFS satellite estimates of chlorophyll were therefore used to derive food fields.

Insufficient observations are available for 1997. We therefore used a climatological 8 day mean of chlorophyll concentration from 1998-2000. There is a poor relationship between time series derived from SeaWIFS and field estimates of chlorophyll (Speirs et al., 2005; Clarke et al., 2006). We used the estimates

of Clarke et al. (2006), who developed a statistical methodology, where thin plate regression splines modelled local estimates of chlorophyll concentration in relation to SeaWIFS estimates, bathymetry and time of year. Field estimates of chlorophyll concentration in the top 5 m were used, assuming they reflect chlorophyll concentration throughout the vertical distribution of *Calanus*. However, it is possible that this does not fully capture deep-water chlorophyll concentrations. Phytoplankton abundance was calculated assuming that 1 mg $m^{-}3$ of Chl *a* is equivalent to 40 mg $Cm^{-3}$ (the approximate median of the values reported by Parsons et al. (1984). Estimates of food extend to regions covered by sea ice, where we masked food levels to zero. This mask was derived from 1997 satellite percentage ice cover from the Defence Meteorological Satellite Program's (DMSP) spatial sensor microwave/imager (SSM/I) (Comiso, 1997). The approach taken to food was the same as in Speirs et al.

Temperature and velocity fields come from the Nucleus for European Modelling of the Ocean (NEMO) Ocean General Circulation Model (OCGM) (version 3.2) (Madec, 2012). The forcings and model implementation are described in Yool et al. (2011). NEMO is resolved at 64 vertical levels, and it resolves the primitive equations on a C-type Arawkawa grid. Ocean surface forcing comes from the DFS4.1 fields produced by the European DRAKKAR collaboration. This differs from Speirs et al., who used the OCCAM model to derive temperatures and flow fields. Computation of the NEMO model was performed using the free Java tool Ichthyop version 3.2 (Lett et al., 2008).

We assumed that surface developers experience the temperatures and velocities which occur at a depth of 20 m. Diapause depth varies in space. We therefore derived a map of diapause from the data reported by Heath et al. (2004). A loess smooth was used to estimate the median diapause depth in regions close to where Heath et al. (2004) reported data. Where the smoothed estimate exceeded bathymetry, we used a depth 10 metres shallower than the bathymetry at a location. In other regions we assumed that if bathymetry was greater than 800 m that diapause depth was 800 m. For locations where bathymetry was shallower than 800 m we used the predictions of a general additive model which related median diapause depth with bathymetry using the data of Heath et al. (2004). Transport updates occurred every seven days. At the start of each time step, 100 seeds were placed at the centre of each model cell. Particle trajectories over a 7-day period were then calculated, and transition matrices were calculated to show the proportion of particles which move to each nearby cell. The approach outlined above was in agreement with Speirs et al.

## 2.4 Data sources

### The Continuous Plankton Recorder Survey

The Continuous Plankton Recorder Survey (CPR) is made up of data collected by devices attached to ships which traverse commercial shipping lanes. It is designed for towing depths of 10 m at the operating speeds of vessels (Batten et al., 2003). Water enters the CPR through a 1.27 $cm^2$ opening and is filtered by a 270 $\mu$m silk mesh. Abundance estimates are semi-quantitative, with each observation being placed in one of 12 distinct abundance categories (Rae, 1952). CPR provides reliable temporal and spatial measures (Batten et al., 2003; Hélaouët et al., 2016) of abundance. We used CPR data from 1958-2002.

### Time series

The EU TASC project collected time series of *C. finmarchicus* copepodite abundance in 1997 at three locations (Planque and Batten, 2000). Data was collected at Ocean Weather Ship Mike (OWS M) (66°N, 2°E) from 24 February to 17 December 1997 (Heath et al., 2000; Hirche et al., 2001) using a 180 $\mu$m mesh opening and closing multinet. Concentrations of copepodite stages ($m^{-3}$) were converted to stage abundances ($m^{-2}$) at 0-100 and 100-1600 m. During autumn and winter the population largely resided in

the deep layer. We assume that deep animals were diapausing at that time. Per-capita egg production rates were also recorded at this station (Niehoff et al., 1999).

Data was collected at 2 locations near the Westmann Islands (63°27.25'N, 20°00.00'W, depth 100 m, and 63°22.20'N, 19°54.85'W, depth 200 m) (Gislason and Astthorsson, 2000). This site was visited 29 times, with *C. finmarchicus* being collected by vertically integrating hauls from 5 m above the seabed to the surface with a 200 $\mu$m mesh, 56 cm Bongo net. In addition, data was collected from Murchison (61°30.00' N, 01°40.00' E, depth 160 m) on 29 occasions, using a 200 $\mu$m mesh with a 30 cm Bongo net from a depth of 150 m to the surface.

We include data from Ocean Weather Ship India (OWS I) (59°N, 19°E), which was collected between 1971 and 1975 (Irigoien, 1999). This time series is used because we lack data for a truly oceanic location in 1997. Sampling occurred at approximately weekly intervals from 1971 to 1975 using oblique hauls of a Longhurst-Hardy plankton recorder (280 $\mu$m mesh). Stage-resolved copepod samples were then collected from a depth of 500 m to the surface, with a resolution of 10 m. We used data from the top 100 m.

The US GLOBEC program started in 1995 (Durbin et al., 2000), and includes extensive zooplankton sampling in the Gulf of Maine and Georges Bank. *C. finmarchicus* densities ($m^{-3}$) were estimated during the first half of the year at varying depths using a 1 $m^2$ MOCNESS fitted with 0.15 mm mesh nets. Estimates of density ($m^{-2}$) were calculated for the top 100 m and from 100 m to the sea floor by considering regions where bathymetry exceeded 200 m.

*C. helgolandicus* abundance data has been collected of Stonehaven, Scotland (56°57.8' N, 2°6.2'W) since 1997. Sampling uses fine mesh nets, which collect an integrated sample of zooplankton throughout the water column (Bresnan et al., 2015). Integrated abundance data is provided for C5, female and male stages.

Station L4 in the English Channel (50°15'N, 4°13'W) is one of the longest standing zooplankton time series in European waters (Harris, 2010), with monitoring beginning in 1988. Seabed depth is 51 m, while observations typically range between 40 and 45 times each year (Harris, 2010). This time series contains information on the abundance of male, female and total copepodites, and egg production rate (Irigoien et al., 2000).

## 2.5 Parameter derivation and sensitivity experiments

Our underlying goal was to reproduce the biogeography of both species displayed by the CPR. We therefore carried out an extensive set of simulations to assess how well different parameter sets could reproduce the geographic distributions of both species.

As discussed in section 2.2, laboratory and field data were used to derive the following traits: development time, growth, fecundity, diapause duration, background mortality and body size. The remaining free, i.e. unknown, parameters related to the equations for diapause entry and starvation and biomass dependent mortality. We initially sought a single parameter set for mortality and diapause entry that would result in credible predictions of geographic distributions for both species. However, a large number of exploratory runs showed that this was not possible. We therefore sought parameter sets that reproduce the geographic distributions of both species while minimizing the differences between the model parameters of both species. A suite of runs showed that this was only achievable by assuming that mortality responded differently to temperature in both species.

Model parameters were derived by simultaneously altering the terms for mortality and diapause entry for both species and recording each parameterization's fit to CPR abundance data. First, CPR data was split

into cells of dimension 2°E and 1°N, and we then removed cells without a CPR abundance record for each month of the year. Annual mean abundance was then calculated by averaging the mean abundance of the mean monthly abundance for C5 and adults in each cell.

This resulted in 333 cells for model comparisons. Each CPR abundance record represents approximately 3 $m^3$ of filtered seawater (Richardson et al., 2006). Therefore, CPR data must be divided by 3 to get estimates of abundance per $m^3$. This must then be multiplied by a further conversion factor of 20 (Speirs et al., 2006) to provide estimates of abundance ($m^{-2}$) over the top 100 m of the water column.

Simulations began by seeding a large number of eggs over the entire North Atlantic and in the eastern North Atlantic for *C. finmarchicus* and *C. helgolandicus* respectively. The model was then run to a quasi-stable state and we then calculated the correlation coefficient ($r$) between predicted annual surface abundance ($m^{-2}$)) and CPR abundance ($m^{-2}$)).

We report two sensitivity experiments. First, we show the geographic distributions of both species when there are no interspecific differences in free parameters, i.e. only differences in growth, development and fecundity are assumed. In this case we are using the diapause entry and starvation and temperature dependent mortality parameters for *C. helgolandicus* for both species.

Our initial model of diapause duration used a model of maximum potential diapause duration (Wilson et al., 2016), which possibly results in diapause durations which are unrealistically long. We therefore carried out a sensitivity analysis which relates the ability to reproduce the geographic distributions of both species to the assumptions for diapause duration and temperature dependent mortality. Temperature dependent mortality is proportional to $(T/8)^z$ for temperature T (°C). The parameterization assumed different values of $z$ for each species.

## 3 RESULTS

### 3.1 Model results

Fig. 2 and Fig. 3 compare the model predictions and CPR estimates of bimonthly abundance for *C. finmarchicus* and *C. helgolandicus* respectively. Table 1 shows the correlation coefficients between monthly modelled and CPR abundance for both species. The large-scale geographic pattern of *C. finmarchicus* abundance was successfully reproduced in comparison with CPR. The correlation coefficient between simulated mean annual abundance and CPR abundance over the 2°E by 1°N cells is 0.75. Bimonthly comparisons between *C. finmarchicus* predictions and the CPR abundance are shown in Fig. 2. Importantly, we reproduced the relatively high abundance of *C. finmarchicus* in the West Atlantic in autumn. In addition, the model predicts a year round surface population in coastal waters in the West Atlantic, in accordance with CPR. However, it perhaps over-predicted abundance in November and December.

A comparison of bimonthly predictions of *C. helgolandicus* abundance with the CPR abundance is shown in Fig. 3. The correlation coefficient between predicted mean annual abundance and CPR abundance over the 2°E by 1°N cells was 0.76. Importantly, *C. helgolandicus* was restricted to the continental shelf. The autumn bloom of *C. helgolandicus* in the North Sea was also reproduced. However, predicted abundance in November and December in the region to the south west of the British Isles appears too high.

Fig. 4 shows simulated combined abundance for stage C5 and adult *C. finmarchicus* compared with those from the time series. Predicted peak abundances are within a factor of 2 of those recorded in the time series, with the exception of the Westmann Islands. OWS I is notable for getting the scale of the first generation very accurate, but we predicted a much larger second generation than is apparent in the time series. We

failed to show the apparent sharp increase in C5 and adult at OWS M before day 100. Additionally, the second peak in C5 and adult abundance at OWS M appears to be time shifted by approximately 50 d.

We compare predictions for *C. helgolandicus* with field time series and time series derived from CPR in Fig. 5. The timing of the autumn peak of *C. helgolandicus* abundance at Stonehaven was successfully reproduced. However, we failed to reproduce the small spring bloom. Predicted time and the magnitude of peak abundance was close to that in the L4 time series. However, abundance appeared to be over-predicted during winter.

Predicted EPR is compared with field time series at OWS M and L4 for *C. finmarchicus* and *C. helgolandicus* respectively in Fig. 6. Predicted *C. helgolandicus* EPR is lower in the first half of the year of the time series, and is slightly time shifted compared with the time series. Predictions depart significantly from the times series in the second half of the year, with EPR being significantly higher than in the time series. The *C. finmarchicus* EPR time series at OWS M is of short duration. We can therefore only make a limited comparison. However, the predicted EPR is approximately the same as the median EPR in the time series.

### 3.2 Sensitivity experiments

In the results shown in section 3.1, the only differences between the species are the relationship between growth, development and fecundity and temperature, and a parameterized difference in the response of mortality to temperature. Fig. 7 shows the predicted geographic distribution of *C. finmarchicus* when the temperature-dependent mortality parameter for *C. helgolandicus* was used. The geographic distribution in the west Atlantic is successfully reproduced. However, the geographic distribution in the east Atlantic is too southerly, with a large population predicted to exist in the Celtic Sea.

Exploratory simulations showed that the *C. helgolandicus* predictions were sensitive to diapause assumptions. First, the model performed well if *C. helgolandicus* was assumed to remain at the surface year round and to never diapause. In fact, this simplified model arguably performed better than the original. The key features of the distribution of *C. helgolandicus* were largely reproduced, with the correlation coefficient (0.78) of model performance compared with CPR actually improving in comparison with our original model.

Further exploratory simulations showed that the state of populations of *C. helgolandicus* is sensitive to diapause duration. A sensitivity analysis showed that small changes to diapause or mortality assumptions can result in *C. helgolandicus* becoming an oceanic species. Fig. 8 shows the correlation coefficient between predictions and CPR abundance of *C. helgolandicus* under varying assumptions for diapause duration and the scaling of mortality with temperature. A small reduction in how steeply mortality scales with temperature results in a reduction in model performance, with *C. helgolandicus* becoming an oceanic species. Likewise, an increase in diapause duration can result in *C. helgolandicus* becoming an oceanic species. Notably, the high sensitivity to changes in temperature dependent mortality was not evident diapause duration is reduced by 60%, which is potentially a more biologically realistic assumption for diapause duration.

## 4 DISCUSSION

This study can be framed by a single question. What differences between *C. finmarchicus* and *C. helgolandicus* explain the relative geographic distributions of these two species? Alternatively, we can ask how much we need to change *C. finmarchicus*'s traits before it effectively becomes *C. helgolandicus*.

In this setting, the model equations can be viewed as describing a generic *Calanus* species, while the parameters determine where a species lies in trait space. We showed that the geographic distributions of both species can be reproduced by assuming only two interspecific differences. These were the temperature response of mortality and the temperature influence on ingestion rate, which in turn influences growth, development and fecundity. In other words, we can effectively turn *C. finmarchicus* into *C. helgolandicus* by modifying those two traits. This framework has the potential to be applied to a number of *Calanus* species, and represents a complimentary approach to that taken by others (e.g. Record et al. (2010, 2013); Maps et al. (2012)).

A key assumption underlying almost all population models of *Calanus* is that growth and egg production rate increase monotonically with temperature. This is the second study after Maar et al. (2013) to assume they do not. Instead, we use a dome-shaped relationship between growth and fecundity and temperature. Similar responses have now been established for a number of zooplankton species (Halsband-Lenk et al., 2002; Holste and Peck, 2006; Holste et al., 2009; Rhyne et al., 2009; White and Roman, 1992; Koski and Kuosa, 1999; Pasternak et al., 2013).

The relationships between fecundity and development time and temperature were derived from the experimental ingestion rate data of Møller et al. (2012). A review of the literature shows that we have little knowledge of the key traits of *C. finmarchicus* such as development, growth and fecundity above 12 °C (Table 2). Further, we are not aware of published evidence of the influence of temperature on *C. helgolandicus*'s fecundity. Clarifications of the relationship between growth and temperature are therefore a priority of *Calanus* research. Importantly, conventional models of development are problematic in the context of climate change, where they may falsely predict ever increasing growth rates as temperatures rise. This is highlighted in the Gulf of Maine, where despite summer surface temperatures now often exceeding 20 °C (Mills et al., 2013) there have recently been record high levels of *C. finmarchicus* abundance (Runge et al., 2014).

Understanding the relative geographic distributions of both species can arguably be answered by asking why only *C. helgolandicus* exists in the region south west of the British Isles. On the basis of our models of growth and fecundity, this region is not noticeably favourable to *C. helgolandicus*. However, the population model's performance is instructive. Simulated abundance of *C. helgolandicus* is much higher in winter at L4 than in reality, and we significantly over-predicted EPR in the second half of the year compared with the long-term seasonal pattern (Maud et al., 2015). This is potentially related to food quality. Resolving the apparent contradictions in understanding of the influence of food quality on fecundity (Maud et al., 2015; Niehoff et al., 1999; Jønasdøttir et al., 2002) and development time (Diel and Klein Breteler, 1986) may therefore be the key to fully explaining the relative biogeographies of both species.

Measuring mortality in copepods is commonly viewed as an intractable problem (Ohman, 2012), and therefore models of mortality are inherently uncertain and difficult to validate. This problem is highlighted by our formulation of starvation mortality, where it was related to growth rate. The formulation was similar to that used by other modellers (e.g. Tittensor et al. (2003)), however it was ad-hoc and impossible to validate. Importantly, the modelled biogeography of *C. helgolandicus* was dependent on starvation mortality, where it plays a key role in reducing post-diapause populations in oceanic regions to a low enough level to eliminate long-term persistence. However, alternative formulations of mortality could potentially achieve this. Some zooplankton modellers have used U-shaped relationships between mortality and temperature (Rajakaruna et al., 2012), which could act as a limit on the north-western distribution of *C. helgolandicus*. Further, allee effects (Kiørboe, 2006) and the impact of starvation on long-term fecundity (Niehoff, 2004) could significantly deplete the populations of low-abundance post-diapause *C.*

*helgolandicus* populations. Including these mortality effects in our model would result in a more complete representation of copepod ecology. However, there is little evidence to quantify the relative magnitude of these sources of mortality. Further advances in understanding copepod mortality (Gentleman et al., 2012; Ohman, 2012) are therefore likely necessary to justify increasingly complex mortality models. However, the influence of mortality should be considered if the model is to be applied, particularly in climate change contexts where changes might be dependent on the specific mortality formulation.

There is a spring bloom of *C. helgolandicus* in the North Sea (Bresnan et al., 2015), which we did not predict. However, the apparent phenology of *C. helgolandicus* in the North Sea is difficult to reconcile with the known influence of temperature on its development time (Cook et al., 2007; Bonnet et al., 2009). The first Stonehaven bloom typically occurs before day 130, and temperatures are below 9 °C before then. Evidence indicates that *C. finmarchicus* either cannot develop from egg to adult (Bonnet et al., 2009) or has a development time greater than 120 d at these temperatures (Møller et al., 2012). Research is therefore needed to reconcile development time studies of *C. helgolandicus* and phenology in the North Sea. Further, additional model runs (not shown) indicated that most of the modelled autumn bloom in the northern North Sea resulted from animals that are advected into the North Sea from the North. The importance of advection for North Sea *C. finmarchicus* populations has been previously been studied (Heath et al., 1999), however the role of advection in influencing year to year North Sea *C. helgolandicus* abundance has not. It may be possible that *C. helgolandicus* phenology in the North Sea can be explained by the existence of hybrids of *C. helgolandicus* and *C. finmarchicus*. This is a speculative hypothesis. However, at the fringes of its northern distribution, *C. finmarchicus* hybridizes with *C. glacialis* (Berchenko and Stupnikova, 2014; Parent et al., 2011; Gabrielsen et al., 2012), and we cannot rule out a similar phenomenon for *C. finmarchicus* and *C. helgolandicus*.

Finally, our model highlights the importance of lipid dynamics and deep-water temperatures as influences on the distribution of *Calanus*. Existing statistical models of *Calanus* biogeography (Helaouët and Beaugrand, 2007; Chust et al., 2013; Hinder et al., 2013) and projections of future distributions (Reygondeau and Beaugrand, 2011; Villarino et al., 2015) have only considered surface conditions. However, the distribution of *C. helgolandicus* appears to be strongly influenced by deep-water temperatures. Conditions in large parts of the North Atlantic are sufficient to support at least one generation of *C. helgolandicus*, but high overwintering temperatures result in the inability of a sufficiently large overwintering population to maintain a persistent population. Recent work showed that projected potential diapause duration of *C. finmarchicus* in the Norwegian Sea under a high emissions scenario was largely unchanged this century, whereas surface temperature increases significantly (Wilson et al., 2016). Development conditions will therefore improve significantly for *C. helgolandicus* in the Norwegian Sea, whereas diapause conditions would remain largely unchanged. There is therefore potential for *C. helgolandicus* to become an oceanic species as a result of deep-water warming lagging that at the surface. Similarly, these marginal changes in potential diapause duration may act as a brake on the northward retreat of *C. finmarchicus*. However, the expected temperature increases across the North Atlantic will reduce lipid levels of animals (Wilson et al., 2016) and the consequences are poorly understood. The future evolution of lipid dynamics may therefore be pivotal in determining the fate of *Calanus* communities and will have important consequences for the fish, seabirds and marine mammals that depend on the lipids provided by copepods (Beaugrand and Kirby, 2010; Frederiksen et al., 2013).

## DISCLOSURE/CONFLICT-OF-INTEREST STATEMENT

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

## AUTHOR CONTRIBUTIONS

RJW, MRH and DCS contributed to the design of the model. RJW implemented and analyzed the model and led the writing of the paper. All authors contributed to the editing and refining of the paper.

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## TABLE CAPTIONS

Table 1: The correlation coefficient (r) between modelled monthly abundance and the mean CPR abundance in each cell.

Table 2: Temperature ranges for measurement of key *C. finmarchicus* traits. * indicates the reference with the highest report temperature. References: Ingvarsdøttir et al., 1999; 2. Rey et al., 1999; 3. Harris, 2000; 4. Campbell et al., 2001 5. Hygum et al., 2000b; 6. Saumweber and Durbin, 2006; 7. Runge and Plourde, 1996; 10. Hirche, 1983; 11. Meyer et al., 2002; 12. Hirche et al., 1997; 13. Hirche, 1987; 14. Møller et al., 2012; 15. Preziosi and Runge, 2014; 16. Kjellerup et al., 2012; 17. Rey-Rassat et al., 2002; 18. Cook et al., 2007; 19. Hygum et al., 2000a; 20. Ikeda et al., 2001; 21. Corkett et al., 1986; 22. Tande, 1988; 23. Diel and Klein Breteler, 1986

## FIGURE CAPTIONS

Figure 1: Influence of temperature on Calanus's body size, development and growth in the model. Body size and diapause duration are assumed to be the same in both species. Development time is based on the model of Wilson et al. (2015), and the EPR model is derived from that model's growth equation assuming that female's use carbon for egg production instead of growth. Egg-adult development times assume an animal is of size 280 $\mu$g C.

Figure 2: Comparison of bimonthly *C. finmarchicus* abundance as recorded by CPR and by the model. Density is mean C5 and adult abundance.

Figure 3: Comparison of bimonthly *C. helgolandicus* abundance as recorded by CPR and by the model. Density is mean C5 and adult abundance.

Figure 4: Comparison of modelled *C. finmarchicus* abundance for combined states C5 and adult with time series data. Solid lines represent model output; dashed lines represent smooths of CPR abundance; points represent time series data. Abundance is depth integrated over the top 100 m of the water column.

Figure 5: Comparison of modelled abundance of *C. helgolandicus* for combined states C5 and adult with time series data. Solid lines represent model output; dashed lines represent smooths of CPR abundance; points represent time series data. Abundance is depth integrated over the top 100 m of the water column.

Figure 6: Predicted EPR for *C. helgolandicus* at L4, English Channel and for *C. finmarchicus* at OWS M compared with field estimates. Solid lines are modelled EPR; points are field estimates.

Figure 7: Mean annual abundance of C5 and adult *C. finmarchicus* under the assumption that temperature scaling of mortality, $z = 7$ and $z = 4.1$. A higher value of $z$ means that mortality scales much more steeply with temperature.

Figure 8: Sensitivity of *C. helgolandicus* model to diapause duration. Diapause duration was altered by a fixed percentage throughout the model domain, and the temperature scaling of mortality was varied. Abrupt changes in model fit close to the optimum indicates that *C. helgolandicus* switches from being a shelf to an oceanic species.

Table 1

| Month | *C. finmarchicus* | *C. helgolandicus* |
|---|---|---|
| January | 0.52 | 0.56 |
| February | 0.31 | 0.61 |
| March | 0.54 | 0.32 |
| April | 0.50 | 0.55 |
| May | 0.32 | 0.70 |
| June | 0.64 | 0.65 |
| July | 0.67 | 0.67 |
| August | 0.61 | 0.49 |
| September | 0.60 | 0.55 |
| October | 0.47 | 0.57 |
| November | 0.27 | 0.65 |
| December | 0.22 | 0.69 |

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Table 2

| Trait | Maximum temperature (°C) | Reference |
|---|---|---|
| Growth | 12 | 3,4, 5, 9,19, 23 |
| Development | 12 | 4, 18, 19, 21, 23 |
| Fecundity | 13.5 | 2,3, 7*, 8, 12, 16 |
| Egg hatching success | 22 | 15 |
| Ingestion rate | 21 | 3, 11, 14* |
| Respiration rates | 17.9 | 1,6, 10, 13*, 20 |
| Costs of gonad formation | 8 | 17 |

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# 5 APPENDIX: MODEL SUMMARY

## 5.1 State variables

The model is adapted from Speirs et al. (2006), which modelled *C. finmarchicus* over the entire North Atlantic. The geographic domain covers the North Atlantic from 30 to 80°N and from 80°W to 90°E. This domain is further divided into cells of size 0.25°N by 0.5°E. Each cell is represented by a vector address **x** = {N,E}, where N and E represent the latitude and longitude of the centre of each cell. In each model cell, we divide the population into 3 groups: surface developers, diapausers, and adults. Surface developers include all development stages from egg to the end of the C5 stage. Diapausers are C5 individuals overwintering in deep waters. Adults (C6s) are animals in the surface who have completed development and can reproduce. Each group is further divided into 10 body size classes. For the surface developers, we define a development class $q$, which takes a value of 0 for eggs and 1 at the end of C5. This allows us to divide the surface developers into a set of $n$ classes of equal width $\Delta q$, and each overwintering body size class into $m$ classes of width $\delta q$. Egg to adult development time is dependent on food and temperature. However, the relative durations of the inter-molt period remains constant. There is therefore a one-to-one relationship between the constant-width classes of the model and the observable physiological stages, shown in Table 1.

$$C_{i,B,x,t} \equiv \text{No. of class i developers of body size B in surface cell } \mathbf{x} \text{ at time } t \quad (1)$$

$$D_{i,B,x,t} \equiv \text{No. of class j diapausers of body size B in surface cell } \mathbf{x} \text{ at time } t \quad (2)$$

$$A_{i,B,x,t} \equiv \text{No. of adults of body size B in surface cell } \mathbf{x} \text{ at time } t \quad (3)$$

**Supplementary Table 1.** Stage classes and mortality parameters

| Stage | E | N1 | N2 | N3 | N4 | N5 | N6 | C1 | C2 | C3 | C4 | C5 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *C. finmarchicus* | | | | | | | | | | | | |
| **Surface** | | | | | | | | | | | | |
| last class | 2 | 5 | 8 | 11 | 14 | 17 | 20 | 25 | 30 | 35 | 41 | 57 |
| **Diapause** | | | | | | | | | | | | |
| last class | - | - | - | - | - | - | - | - | - | - | - | 100 |
| *C. helgolandicus* | | | | | | | | | | | | |
| **Surface** | | | | | | | | | | | | |
| last class | 1 | 4 | 6 | 11 | 15 | 19 | 27 | 31 | 36 | 42 | 47 | 57 |
| $\mu_q^E(d^{-1} \times 100)$ | 18.2 | 33.6 | 33.6 | 14.9 | 2.6 | 2.6 | 2.6 | 1.5 | 0.0 | 2 | 2 | 15 |
| $w_q^C(\mu$g | 0.5 | 0.33 | 0.49 | 1.0 | 1.5 | 2.1 | 2.8 | 4.2 | 13 | 23 | 64 | 170 |

## 5.2 Body size

Adult prosome length (mm) is assumed to be determined at birth. For computational efficiency purposes we have 10 body size classes. First we divide temperature space into 10 equally spaced classes between lower and upper ecologically relevant temperature thresholds $T_{B_L}$ and $T_{B_U}$. Eggs are then placed into the relevant temperature class, with body size being determined by the mean temperature in the temperature class. If the temperature at birth is below the lower threshold or above the upper threshold we place the egg into the first or last temperature class respectively. The relationship between adult length, $L$ (mm) and temperature, $T$ (°C) is that reported by Campbell et al. (2001), with a rescaling to account for non food-saturated conditions.

$$L = \frac{\alpha_L(m_L T + c_L)}{1000} \tag{4}$$

For adults we convert length to body weight, $w_c^A$ ($\mu$g C) using the equation from Runge et al. (2006),

$$w_c^A = 4.39L^3.57 \tag{5}$$

We follow Speirs et al. (2006) and use the dry weights, $w_{B,q}^C$, of each stage from Lynch et al. (2001) as our body weights for each pre-adult stage. However, these numbers are adjusted for the temperature scaling of body size above, assuming that the animals caught by Lynch et al. (2001) (weights shown in Table 1) developed at a temperature of 10 °C.

## 5.3 Transport updates

We simulate the physical transport of animals from one cell to another by redistributing the contents of each cell to a set of destination cells a set of times separated by the transport update interval $\Delta g$. Using subscript - and + to denote the system state infinitesimally before and after the update, we can write:

$$C_{i,B,x,t}^{+} = \sum_{\text{all y}} \Psi_{x,y,t}^{S} C_{i,B,y,t}^{-} \tag{6}$$

$$D_{i,B,x,t}^{+} = \sum_{\text{all y}} \Psi_{x,y,t}^{S} D_{i,B,y,t}^{-} \tag{7}$$

$$A_{i,B,x,t}^{+} = \sum_{\text{all y}} \Psi_{x,y,t}^{S} A_{i,B,y,t}^{-} \tag{8}$$

$\Psi^S_{x,y,t}$ and $\Psi^S_{x,y,t}$ are the transfer distributions, representing the proportion of individuals in the surface and deep layers of cell **y** at time $t - \Delta t$ that are transported to the same layer of cell **x** by time $t$. Thus, using $L \in [S, D]$, we define:

$$\Psi^L_{\mathbf{x},\mathbf{y},t} \equiv \Pr\{\text{particle at } \mathbf{y} \text{ at time } t - \Delta t \text{ is at } \mathbf{x} \text{ at time } t\}$$

This quantity was determined by releasing 100 particles at the centre of each cell and tracking their positions from $t - \Delta t$ to $t$, assuming that the deterministic part of velocity is given by the NEMO model (Madec, 2012).

## 5.4 Biological updates

The state of the surface developer population in cell **x** is updated at a set of times $\{u^c_{\mathbf{x}}\}$, such that:

$$\Delta q = \int_{u^C_{x,i-1}}^{u^C_{x,i}} g^C_{\mathbf{x}}(\tau) d\tau$$

where $g^C_{\mathbf{x}}(\tau)$ is the development rate of surface developers in cell **x** at time $\tau$ (see equation 15). At the end of each update time, individuals are moved one class to the right. In the case of final stage CV, individuals are either moved to adult or diapause stage. The egg stage then receives the eggs produced by surviving adults. Diapause entry is described using a function $\theta_{i,x,t}$ which returns the fraction of individuals who transfer to the first diapause class. We let $Ex, t$ denote the per capita egg production from the previous update to the one taking place at time $t$ in cell **x**. Further, if $\xi^A_{B,x,t}$ and $\xi^C_{i,B,x,t}$ denote the respective survival of adults and surface developers, then we can write the surviving developers and adults as: $S^C_{i,B,\mathbf{x},t} \equiv \xi^C_{i,B,x,t} C^-_{i,B,\mathbf{x},t}$ and $S^A_{B,\mathbf{x},t} \equiv \xi^A_{B,x,t} A^-_{\mathbf{B},x,t}$. We therefore have:

$$C_{i,j} = \begin{cases} E_{B,\mathbf{x},t} S^C_{i-1,\mathbf{x},t} & i = 1 \\ (1 - \theta_{i-1,\mathbf{x},t}) S^C_{i-1,\mathbf{x},t} & \text{otherwise} \end{cases} \tag{9}$$

$$D^+_{0,B,\mathbf{x},t} = D^+_{0,B,\mathbf{x},t} + \sum_{i=1}^{n} \theta_{i,\mathbf{x},t} S^C_{i,B,\mathbf{x},t} \tag{10}$$

$$A^+_{B,\mathbf{x},t} = (1 - \theta_{n,\mathbf{x},t}) S^C_{B,n,\mathbf{x},t} + S^A_{B,\mathbf{x},t} \tag{11}$$

The diapausing population of cell **x** is updated, in a similar way, at a set of times $(u^D_{B,x})$ related to each other such that:

$$\delta q = \int_{u^D_{B,x,i-1}}^{u^D_{B,x,i}} g^D_{\mathbf{x}}(\tau) d\tau \tag{12}$$

where $g^D_{B,x}$ is the development rate of diapausing individuals of body size class B in cell **x** at time $\tau$. Our update process requires that all survivors in all classes, but the last, are moved one class to the right. Diapausers become adults when they have reached the end of the final diapause stage. Let $\xi_{B,x,t}$ be the survival of individuals in class $j$ in model cell **x** from the last update to the one at time $t$, so that

$S^{+D}_{j,B,\mathbf{x},t} \equiv \xi^{D}_{j,B,\mathbf{x},t} D^{-}_{j,B,\mathbf{x},t}$ is the number of surviving diapausers just before the update. Diapausers are therefore updated according to:

$$D^{+}_{j,B,\mathbf{x},j} = \begin{cases} 0 & j = 1 \\ S^{D}_{j,B,\mathbf{x},t} & \text{otherwise} \end{cases} \tag{13}$$

and at the same time, adults are updated:

$$A^{+}_{0,B,\mathbf{x},t} = A^{-}_{0,B,\mathbf{x},t} + D^{+}_{m,B,\mathbf{x},t} \tag{14}$$

## 5.5 Update strategy

We have two types of updates: biological and transportation. Transportation updates occur at a set time, every 7 days. In between this there are a number of biological updates that must occur. This is performed by updating the biological state of each cell until the next update time is after the next transportation time. Once the biological updates are complete, we then perform the transport update.

## 5.6 Growth and development

Development times under food saturated conditions for both species are as calculated by Wilson et al. (2015).

Carbon weight is defined as $w_c$, and growth rate under food saturated conditions is defined as follows:

$$\dot{w}_c = {w_c}^{0.75} \left( \frac{P_5 A E \mu}{1 + \exp\left(\frac{P_3}{T+273.15} - \frac{P_3}{P_1}\right) + \exp\left(\frac{P_4}{P_2} - \frac{P_4}{T+273.15}\right)} - Q_{10}^{S\ (T/10)} \lambda \right) \tag{15}$$

First we parameterize our model completely for *C. finmarchicus*, using the development times at 4, 8 and 12°C under food-saturated conditions reported by Campbell et al. (2001). The parameterization of development to C5 was performed by minimising the least squares of our model fit. Development time for *C. helgolandicus* was estimated assuming that the only inter-species difference is the response of ingestion to temperature.

Individuals were assumed to molt to the next stage when their carbon weight reaches the respective critical molting weight. We estimated the relationship between molting weight for C5 individuals and temperature using published data on length-weight (Hygum et al., 2000b) and temperature-length relationships (Campbell et al., 2001). C5 molting weight was therefore assumed to relate to temperature using the equation $C_m = 2.307 \cdot 10^{-10} \cdot (-27.4 * T + 2084)^{3.52}$, where $C_m$ is the C5 molting carbon weight ($\mu$g), and $T$ is temperature (°C).

Development time to adult under food saturated conditions, DT, was calculated assuming the equiportionality defined by Campbell et al. (2001). Finally, we define the development rate $g^{C}_{\mathbf{x}}(t)$ to be

$$g_{\mathbf{x}}^{C}(t) = \frac{1}{\mathrm{DT}}\left(1 - \exp\left[-\frac{F_{\mathbf{x}}(t)}{F_G}\right]\right) \tag{16}$$

where $F_G$ is the half saturation coefficient from Campbell et al. (2001).

## 5.7 Diapause duration

Diapause duration is modelled using the maximum potential diapause model of Wilson et al. (2016). Here we will summarize that model. We model diapause duration assuming that individuals start diapause with length dependent wax ester levels implied by the upper 95th percentile reported by Pepin and Head (2009). Diapause is assumed to end when wax ester levels are three times nitrogen weight. This is an approximate estimate derived from the limited data for the energetic requirements of molting and gonad formation (Rey-Rassat et al., 2002). Respiration rates are assumed to have allometric scaling of 0.75 (Maps et al., 2014) and to have a $Q_10^D$ of 2.8 (the mean value from (Hirche, 1983; Saumweber and Durbin, 2006; Ingvarsdøttir et al., 1999)).

The relationship between prosome length and wax esters available for respiration during diapause, $\mathrm{WE}_d$, is therefore

$$\mathrm{WE}_d = aL^y \tag{17}$$

where $a = 3.66$ and $y = 4.6$, and $L$ is prosome length.

Metabolism is assumed to relate strictly to structural (nitrogen) weight, which is assumed that structural weight is fixed throughout diapause. This assumption means that respiration rates are constant throughout diapause under fixed temperatures, which results in a more elegant model formulation.

Respiration rate, $r$ ($\mu$mol $O_2$gN$^{-1}$hr$^{-1}$) is estimated using the data of Saumweber and Durbin (2006), and follows the equation:

$$r = \mu_d {w_N}^{0.75} Q_{10}^{d\ T/10} \tag{18}$$

where $\mu_d$ is a constant, $w_N$ is nitrogen weight ($\mu$g), and $T$ is temperature in °C.

Nitrogen weight, $w$ ($\mu$g), is related to prosome length, $L$ (mm) using the following equation derived from Runge et al. (2006),

$$w_N = \alpha L^\beta \tag{19}$$

where $\alpha = 2.014$ and $\beta = 2.7$.

Using the weight-specific respiration data of Saumweber and Durbin (2006), we get the following estimate, $\mu_d$ = 280.

We then convert the oxygen respiration rate into a carbon respiration rate,

$$R = \frac{24 \cdot \text{RQ} \cdot 12.011 \cdot r}{10^6} \tag{20}$$

where $R$ is the carbon respiration rate ($\mu$g C$\mu$N$^{-1}$d$^{-1}$) and RQ is the respiratory quotient.

This can be simplifed to the form

$$R = \xi {w_N}^{0.75} {Q_{10}^d}^{T/10} \tag{21}$$

where

$$\xi = \mu * 24 * RQ * 12.011 * 10^{-6} = 0.06$$

Therefore diapause duration is of the form

$$\begin{aligned} \text{Duration} &= \frac{aL^y}{\xi {w_N}^{0.75} \cdot {Q_{10}^d}^{T/10}} \\ &= \frac{aL^y}{\xi (\alpha L^\beta)^{0.75} \cdot {Q_{10}^d}^{T/10}} \\ &= \frac{a \cdot L^{y-0.75\beta}}{\xi \alpha^{0.75} {Q_{10}^d}^{T/10}} \end{aligned} \tag{22}$$

We then have the final equation which relates diapause duration with body size and temperature,

$$\text{Duration } = \gamma_d L^{\lambda_d} \cdot {Q_{10}^d}^{-T/10}$$

where $\gamma_d = 36.08$ and $\lambda = 2.58$.

## 5.8 Diapause entry

Individuals are assumed to enter diapause at the end of stage C5, and that the fraction, $\theta_{q,\mathbf{x},t}$, of the population entering diapause is related to growth rate. The proportion of animals that stay at the surface, $F_s$ relates to a reference growth rate $\dot{w}_{de}$

$$\theta_{q,\mathbf{x},t} = \begin{cases} 0 & \text{if } \dot{w} < 0 \\ 1 & \text{if } \dot{w} > \dot{w}_{de} \\ \frac{\dot{w}_c}{\dot{w}_{de}} & \text{otherwise} \end{cases} \tag{23}$$

## 5.9 Mortality

Let $u_n$ denote the $n$th update time in $u_{\mathbf{x}}^K$, where $K \in [A, C, D]$ denotes the target population. We write:

$$\xi_{q,B,\mathbf{x},u_i} = \exp[-m^K_{q,B,\mathbf{x},u_i}(u_{i-1})] \tag{24}$$

We assume that there is simply a constant background mortality rate for diapausers:

$$m^D_{i,B,\mathbf{x},t} = \mu^D \tag{25}$$

We assume that mortality for surface developers and adults consists of a temperature dependent background rate, together with density-dependent and starvation elements. Let $T^s_{\mathbf{x}}(t)$, $W_{\mathbf{x},t}$, and $F_{\mathbf{x},t}$ are surface temperature, biomass of *C. finmarchicus* or *C. helgolandicus*, and food in cell $\mathbf{x}$ at time $t$, then:

$$m^C_{i,B,\mathbf{x},t} = \gamma(T^S_{\mathbf{x}}(t))\mu^C_i(1+\phi W_{\mathbf{x},t}) + \mu_F \tag{26}$$

$$m^A_{B,\mathbf{x},t} = \gamma(T^A_{\mathbf{x}}(t))\mu^C_i(1+\phi W_{\mathbf{x},t}) + \mu_F \tag{27}$$

with temperature dependence being given by:

$$\gamma(T^S_{\mathbf{x}}(t)) = \gamma_0 + (1-\gamma_0)(T/T_c)^z \tag{28}$$

The parameter $\lambda_0$ is the fraction of the mortality at some characteristic temperature $T_c$ that is experienced at 0°C, and $z$ determines how quickly mortality increases with temperature.

We relate starvation mortality to weight specific growth rate. If weight specific growth rate is above a threshold, there is no starvation mortality. However, below this threshold, starvation mortality increases linearly as growth rate decreases.

$$\mu_F(F_{\mathbf{x}}(t), T(t)) = \begin{cases} 0 & \text{if } \dot{w} > \dot{w}_c \\ \frac{w_c - w^{-1}\dot{w}}{\mu_c} & \text{otherwise} \end{cases} \tag{29}$$

Total biomass density in cell $\mathbf{x}$ is given by the sum over all develop classes of the number of individuals in each class multiplied by the dry weight of each individual plus a similar sum over the adult population, divided by the surface area of the cell ($\alpha_{\mathbf{x}}$):

$$W_{\mathbf{x},t} = \frac{1}{\alpha_{\mathbf{x}}}\left[\sum_{i=1}^{n}\sum_{j=1}^{B} w^C_{i,j}C_{i,j,x,t} + \sum_{j=1}^{B} w^A_j A_{j,x,t}\right] \tag{30}$$

## 5.10 Egg production

We assume that egg production is equivalent to growth, as defined above. Furthermore, we assume that the carbon weight of eggs is related to temperature as reported by Campbell et al. (2001). Thus

$$E_{B,x,t} - \beta_{B,x,t}(u_n - u_{n-1}) \tag{31}$$

where $\beta_{B,x,t}$ is the per capita EPR. This is modelled assuming a saturating function of food.

$$E_{B,x,t} = \frac{F_{\mathbf{x}}(t)}{F_h + F_{\mathbf{x}}(t)} \dot{w} \frac{1}{-0.00255T + 0.216} \tag{32}$$

This model provides a very close fit with the experimental data of Hirche et al. (1997).

**Supplementary Table 2.** Summary of model equations.

| Equation | Comment |
|---|---|
| **State variables** | |
| $C_{i,B,x,t} \equiv$ No. of class i developers of body size B in surface cell **x** at time *t* | |
| $D_{i,B,x,t} \equiv$ No. of class j diapausers of body size B in surface cell **x** at time *t* | |
| $A_{i,B,x,t} \equiv$ No. of adults of body size B in surface cell **x** at time *t* | |
| **Body size** | |
| $L = \frac{\alpha_L(m_L T + c_L)}{1000}$ | $L$ is adult prosome length (mm) |
| | We assume that $L$ is determined by temperature at birth |
| $w_c^A = 4.39 \times L^{3.57}$ | $w_c^A$ is carbon weight of adults ($\mu$g C) |
| **Growth and development** | |
| $\dot{w}_c = {w_c}^{0.75}\left(\frac{P_5 AE\mu}{1+\exp\left(\frac{P_3}{T+273.15}-\frac{P_3}{P_1}\right)+\exp\left(\frac{P_4}{P_2}-\frac{P_4}{T+273.15}\right)} - {Q_{10}^S}^{(T/10)}\lambda\right)$ | $\dot{w}_c$ is carbon growth rate ($\mu$gC h$^{-1}$) |
| $C_m = 2.307 \cdot 10^{-10} \cdot (-27.4 * T + 2084)^{3.52}$ | $C_m$ is molt weight ($\mu$g C) assumed for CV in development model |
| DT = development time (d) under food saturated conditions | |
| $g_{\mathbf{x}}^C(t) = \frac{1}{\mathrm{DT}}\left(1 - \exp\left[-\frac{F_{\mathbf{x}}(t)}{F_G}\right]\right)$ | $g_{\mathbf{x}}^C$ is development rate (d$^{-1}$), $F$ is food concentration (mg C m$^{-3}$) and $F_G$ = half saturation of food (mg C m$^{-3}$) |
| $\Delta q = \int_{u_{x,i-1}^C}^{u_{x,i}^C} g_{\mathbf{x}}^C(\tau) d\tau$ | Update times, $\{u_{\mathbf{x}}^c\}$ satisfy this equation |
| **Fecundity** | |
| $E_{B,x,t} = \frac{F_{\mathbf{x}}(t)}{F_h + F_{\mathbf{x}}(t)} \dot{w} \frac{1}{-0.00255T+0.216}$ | $\beta_{B,x,t}$ is the per capita EPR (eggs$^{-1}$individual$^{-1}$d$^{-1}$) |
| **Diapause** | |
| Duration $= \gamma_d L^{\lambda_d} \cdot {Q_{10}^d}^{-T/10}$ | Diapause duration (d) is related to size and temperature |
| $\theta_{q,\mathbf{x},t}(F_{\mathbf{x}}(t), T(t)) = \begin{cases} 0 & \text{if } \dot{w} < 0 \\ 1 & \text{if } \dot{w} > \dot{w}_{de} \\ \frac{\dot{w}_c}{\dot{w}_{de}} & \text{otherwise} \end{cases}$ | $\theta_{q,\mathbf{x},t}$ is proportion diapausing at the end of C5 |
| **Mortality** | |
| $\xi_{q,B,\mathbf{x},u_i} = \exp[-m_{q,B,\mathbf{x},u_i}^K(u_{i-1})]$ | $\xi$ is proportion surviving, $m$ is mortality rate |
| $m_{i,B,\mathbf{x},t}^D = \mu^D$ | Simple background mortality rate, $\mu^D$, is assumed for for diapausers |
| $m_{i,B,\mathbf{x},t}^C = \gamma(T_{\mathbf{x}}^S(t))\mu_i^C(1 + \phi W_{\mathbf{x},t}) + \mu_F$ | $m_{i,B,\mathbf{x},t}^C$ is mortality rate for developers, $\phi$ is density dependence |
| $m_{B,\mathbf{x},t}^A = \gamma(T_{\mathbf{x}}^A(t))\mu_i^C(1 + \phi W_{\mathbf{x},t}) + \mu_F$ | $m_{B,\mathbf{x},t}^A$ is mortality rate for adults, $\phi$ is density dependence |
| $\gamma(T_{\mathbf{x}}^S(t)) = \gamma_0 + (1-\gamma_0)(T/T_c)^z$ | $\gamma$ gives the temperature dependence of mortality |
| $\mu_S(F_{\mathbf{x}}(t), T(t)) = \begin{cases} 0 & \text{if } \dot{w} > \dot{w}_c \\ \frac{\dot{w}_c - w^{-1}\dot{w}}{\mu_c} & \text{otherwise} \end{cases}$ | $\mu_S$ is starvation mortality |
| $W_{\mathbf{x},t} = \frac{1}{\alpha_{\mathbf{x}}}\left[\sum_{i=1}^n \sum_{j=1}^B w_{i,j}^C C_{i,j,x,t} + \sum_{j=1}^B w_j^A A_{j,x,t}\right]$ | $W_{\mathbf{x},t}$ is biomass ($\mu$g C) for density dependence. See table 1 for stage biomasses. |

## FIGURE CAPTIONS

Figure A1: Derivation of synthetic map of median diapause depth. The top-left shows locations where we have vertical distribution data for diapausers (Heath et al., 2004). Median diapause depth was related to bathymetry using a general additive model (top right). In regions close to where we have median diapause depth data we use the results of a loess smooth through the observed median diapause depths. Elsewhere, for depths less than 1000 m, we use predictions from the general additive model, and for depths greater than 1000 m we assume a median diapause depth of 800 m.

**Supplementary Table 3.** Model parameters. Bracketed value shows *C. helgolandicus* parameter.

| Parameter | Symbol | Value | Units | Reference |
|---|---|---|---|---|
| **Surface developers** | | | | |
| Ingestion scaling with temp. | $P_1$ | 293 (289) | - | Møller et al. (2012) |
| | $P_2$ | 284(275) | - | Møller et al. (2012) |
| | $P_3$ | 13,282 (14,123) | - | Møller et al. (2012) |
| | $P_4$ | 29,725 (39,429) | - | Møller et al. (2012) |
| | $P_5$ | 6.05 (12.12) | - | Møller et al. (2012) |
| Assimilation efficiency | AE | 0.488 | - | Wilson et al. (2015) |
| $Q_{10}$ of surface respiration | $Q_{10}^S$ | 3.19 | - | Wilson et al. (2015) |
| Ingestion scaling | $\mu$ | 0.0415 | - | Wilson et al. (2015) |
| Respiration scaling | $\lambda$ | 0.000101 | $\mu$gC$\mu$gC$^{-1}$d$^{-1}$ | Wilson et al. (2015) |
| Development saturation coeff. | $F_g$ | 29.2 | mg C m$^{-3}$ | Campbell et al. (2001) |
| Nominal mortality | $\mu_q^E$ | Table 1 | d$^{-1}$ | Eiane et al. (2002) |
| **Starv. and density dependence** | | | | |
| Starv. growth threshold | $\dot{w}_c$ | 0.0012 | $\mu$gC$\mu$gC$^{-1}$d$^{-1}$ | Fitted |
| Starv. ref. growth | $\mu_c$ | 0.01 | | Fitted |
| Density dependence | $\phi$ | $3 \times 10^{-6}$ | d$^{-1}$m$^3$$\mu$g$^{-1}$ | Fitted |
| Fraction back. mort. at 0 °C | $\gamma_0$ | 0.65 | - | Speirs et al. (2006) |
| Characteristic temp. | $T_C$ | 8 | °C | Fitted |
| Temp. power coeff. | $z$ | 7 (4.1) | - | Fitted |
| Stage specific dry weight | $w_q^C$ | Table 1 | $\mu$g | Lynch et al. (2001) |
| **Adults** | | | | |
| Fecundity half saturation food | $F_h$ | 82.02 | mgCm$^{-3}$ | Hirche et al. (1997) |
| **Body size** | | | | |
| Temperature-body size coeff. | $\alpha_L$ | 0.9 | - | Fitted |
| | $m_L$ | -39.1 | - | Campbell et al. (2001) |
| | $b_L$ | 3073 | - | Campbell et al. (2001) |
| Lower temp. threshold | $T_{B_L}$ | 0 (7) | °C | Fitted |
| Upper temp. threshold | $T_{B_L}$ | 15 (20) | °C | Fitted |
| Adult mortality | $\mu_y^A$ | 0.01 | d$^{-1}$ | Speirs et al. (2006) |
| **Diapausers** | | | | |
| Diapause reference growth | $\dot{w}_{de}$ | 0.1 | $\mu$gCgC$^{-1}$d$^{-1}$ | Fitted |
| Diapause duration factor | $\gamma_d$ | 36.08 | d | Wilson et al. (2016) |
| All. scaling of diapause dur. | $\lambda_d$ | 2.58 | - | Wilson et al. (2016) |
| Diapause temperature scaling | $Q_10^d$ | 2.8 | - | Wilson et al. (2016) |
| Mortality rate | $\mu_D$ | 0.05 | d$^{-1}$ | Speirs et al. (2006) |