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The effect of changes in temperature and food on the development of *Calanus finmarchicus* and *Calanus helgolandicus* populations

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Abstract:

We studied the response in development times of *Calanus finmarchicus* and *Calanus helgolandicus* to changes in temperature and food conditions. Grazing experiments were performed at different temperatures for both species, and the results were implemented in a stage-resolved zooplankton population model that predicted development times from biomass increments controlled by ingestion and metabolic losses. Predictions were validated against development data from the literature, and show that *C. finmarchicus* develops faster than *C. helgolandicus* below 11°C and slower above. The different relative development rates of the species are related to different temperature responses in ingestion rates. A temperature increase of 1°C to 2°C may have consequences for the relative contribution of *C. helgolandicus* and *C. finmarchicus* to the copepod community, and both seasonal and spatial displacements of the *Calanus* populations can be expected under climate change.

1. Introduction

Copepods of the genus *Calanus* are key species in the North Atlantic Ocean. They are central for the trophodynamics of the system and a change in abundance is likely to influence food web dynamics, energy transfer efficiency and the biological carbon pump (Hirche and Kosobokova 2007; Beaugrand 2009; Falk-Petersen *et al*. 2009). *Calanus* has been shown to be a crucial prey for fish species such as cod, haddock, herring and mackerel (Gaard and Reinert 2002; Gislason and Astthorsson 2002; Ringuette et al. 2002), as well as for marine birds and marine mammals (Laidre et al. 2007; Karnovsky et al. 2003). Four *Calanus* species exist in the North Atlantic. *Calanus glacialis* and *Calanus hyberboreus* dominates in arctic waters, while *Calanus finmarchicus* has its center in the North Atlantic and *Calanus helgolandicus* prevails further south (Beaugrand et al. 2002; Bonnet et al. 2005; Falk-Pedersen et al. 2009). Here we consider the latter two species, their responses in feeding and development time to changing temperature and food conditions and how this may affect the competition between them.

In the North Atlantic, occurrence of cod has been shown to be associated with high abundances of *Calanus finmarchicus* (Beaugrand and Kirby 2010). In the North Sea, a shift in the spatial distribution of *C. finmarchicus* and *C. helgolandicus* is believed to have caused lower recruitment of Atlantic cod due to changes in mean prey size, seasonal timing and abundance (Beaugrand et al. 2003). Observed decadal changes in the spatial distribution of *C. finmarchicus* between 1960 and 2005 in the North Sea suggest a decrease in the occurrence of the species at this southern edge of its distribution (Reygondeau and Beaugrand 2011). In a changing climate such changes are assumed to be more prominent and substantial efforts have been put into research on *Calanus* biogeography, biology, and ecology (Beaugrand et al. 2003; Bonnet et al. 2005; Jónasdóttir and Koski 2011).

Temperature is considered as a key factor for species development (Calbet et al. 2001; Halsband-Lenk et al. 2002, 2004) and *C. finmarchicus* and *C. helgolandicus* show a very distinct distribution in relation to temperature both horizontally and vertically (Bonnet et al. 2005; Jónasdóttir and Koski 2011). In the North Sea *C. finmarchicus* are more abundant than *C. helgolandicus* at temperatures below 11ºC, while *C. helgolandicus* generally dominates at temperatures above 12ºC (Bonnet et al. 2005).

Distribution of a s pecies is determined by a balance between recruitment, growth and mortality. The development time of *Calanus* is decisive for which species will succeed in a given environment. Moreover, for many of its predators the size of prey, i.e., *Calanus,* is important and it is therefore crucial to know at what time of the year *Calanus* reaches a suitable size as a prey item (Beaugrand et al. 2003). Thorough experiments with both *C. finmarchicus* and *C. helgolandicus* have been carried out showing a general increase in development times with decreasing food concentration and temperature (Campbell et al. 2001; Cook et al. 2007; Bonnet et al. 2009). However, due to the interaction between food and temperature on development (Cook et al. 2007) these studies have not been able to point out a solid difference between the two species.

A critical issue for understanding development is how ingestion depends on temperature. However, very few laboratory studies on ingestion have focussed on the natural temperature range of a given species. Typically, ingestion vs. in situ temperature relationships are extracted from field data. This is problematic because in situ ingestion rates will also be affected by other factors such as prey type and size, micro-scale patchiness, and predator avoidance (Carlotti and Poggiale 2010).

We hypothesize that different temperature responses of ingestion for the two species *C. finmarchicus* and *C. helgolandicus* will lead to differences in their development times. Therefore, we performed grazing experiments at different temperatures for both *C. finmarchicus* and *C. helgolandicus*. The results from those experiments were used in the parameterisation of a stage resolved zooplankton population model adapted for the two species. The model predicted development time from biomass increments controlled by ingestion and metabolic losses. This allowed us to test the response in development times of

the two *Calanus* species to changes in temperature and food concentrations. Predictions were validated against independent data of development from the literature. The developed *Calanus* stage structured population model can be implemented in future ecosystem models where it can provide information on the grazing and development rate of *C. finmarchicus* and *C. helgolandicus* as well as the prey size available for higher trophic levels.

2. Methods

2.1. Experiments

The ingestion response to temperature was determined in the laboratory, where the copepods *Calanus finmarchicus* and *Calanus helgolandicus* were fed the diatom *Thalassiosira weissflogii.* The diatom cultures were cultivated at 18-20ºC in filtered seawater enriched with B_1 medium with added silicate (Hansen 1989). Light was provided by cool white fluorescent bulbs set on a 12:12 light:dark cycle. Cultures were all the time kept at exponential growth by diluting the batch cultures daily.

Calanus finmarchicus were obtained for experiments from the Gullmar fjord (58° 19.2'N, 11° 32.8' E) 06 April 2009. *Calanus finmarchicus* was incubated at in situ temperature (5ºC) until the experiments were performed.

Calanus helgolandicus females were obtained from Sta. L4 off Plymouth UK (50º 15' N, 4º 13' W) in June 2009 and shipped in a cooler to Denmark. First generation cultures were grown in the laboratory at 15ºC from the eggs from the L4 females. During growth both *C. finmarchicus* and *C. helgolandicus* cultures were fed a mixture of the cryptophyte *Rhodomonas salina*, the diatom *Thalassiosira weissflogii* and the dinoflagellate *Prorocentrum minimum*.

Five 600 mL glass bottles containing 1400 cells mL^{-1} or 5 *µ*g chlorophyll a (Chl *a*) L^{-1} of *T. weissflogii* (~200 *µ*g C) and 1-2 *C. finmarchicus* or *C. helgolandicus* copepodite stage five (CV) or females were incubated in darkness at series of temperatures between 1ºC and 21 ± 0.5ºC. Three bottles without copepods served as control. In the *C. helgolandicus* experiment, *T. weissflogii* cells were counted at the beginning and end of the experiment in the grazing bottles and controls using a Coulter Counter® (Multisizer™ 3, Beckman Coulter). In the *C. finmarchicus* experiment, phytoplankton reduction was determined by Chl *a* measurements. 200 mL from each bottle were filtered onto GF/F filters in the beginning and end of the experiment. The filters were extracted overnight in 5 mL 96% ethanol (Jespersen and Christoffersen 1987) and measured on a Turner Design Model 700 fluorometer before and after acid addition. The reduction in phytoplankton during any of the experiments was generally below 20% and never more than 32%. Clearance rates were calculated following Båmstedt et al. (2000).

2.2. Model concept and parameterization

The model of development times of *C. finmarchicus* and *C. helgolandicus* were based on the model developed by Fennel (2001) for *Pseudocalanus* and later modified by Stegert et al. (2007). The model considered five life stages namely 1) eggs to nauplii 1-2 (egg-NI-II), 2) nauplii 3-6 (NIII-NVI), 3) copepodites 1-3 (CI-CIII), 4) copepodites 4-5 (CIV-CV), and 5) adults. The general scheme used two sets of equations, one to describe the flux of biomass *Zi* through each stage *i*, the other one to describe the flux of abundance of individuals *N*:

$$\frac{dZ_i}{dt_i} = T_{i\text{-}1,i} \cdot Z_{i\text{-}1} + g_i \cdot Z_i - l_i \cdot Z_i - T_{i,i+1} \cdot Z_i \quad (1)$$

$$\frac{dN_i}{dt} = T_{i\text{-}1,i} \cdot N_{i\text{-}1} - T_{i,i,+1} \cdot N_i \quad (2)$$

with rates of transfer $T_{i,i+1}$ from stage i to the next, grazing g_i and losses l_i. Stage-specific processes control the metabolism of a 'mean individual' using the mean individual mass for each stage, defined as stage biomass divided by the number of individuals (Z_i/N_i). Thus, simulated abundances and biomasses are connected as functions of time (Stegert et al. 2007). Mean individual weight change through grazing (ingestion) and losses (egestion, respiration, excretion) of matter and moulting depends on a critical moulting weight. Development is therefore dependent on the how gains and loss are described and the choice of moulting weights. As the present study considers only development times, mortality is not included.

The weight thresholds were derived from compilation of data available from the literature (Table 1). *Calanus* may store large amounts of lipids causing the carbon content to vary considerably within each stage. Lipids may be considered as a 'passive' biomass, i.e., processes normally related to body size will not vary with lipid stores. Lipids do not contain much nitrogen (Harris et al 2000) and therefore variation in lipid content will not result in as strong variation in nitrogen content as in carbon. Thus, nitrogen content is more related to 'active' biomass and we have chosen to use nitrogen weights in our models. Below, the parameterization of the different processes is described in more details. For units *see* Table 1.

2.3. Ingestion

Grazing (g_i) is controlled by maximum ingestion (I_{max}), dependency of ingestion on temperature ($f1$), availability of food ($f2$) and body weight ($f3$), respectively:

$$g_i = I_{\max} \cdot f1 \cdot f2 \cdot f3 \quad (3)$$

Maximum ingestion rates for the females were obtained from a compilation of maximum ingestion rates for calanoid copepods as a function of carbon weights (Saiz and Calbet 2007), assuming a C :N ratio of 5.7 the average for the studies used for the biomass estimates (Campbell et al. 2001; Rey et al. 2001; Rey-Rassat et al. 2002) and similar N-specific ingestion rates to C-specific ingestion rates. The ingestion for the smaller stages was obtained assuming an allometric scaling of 0.25 (Fenchel 1974).

The dependency of ingestion to food concentration (F) is described by Type 3 response (Gentleman and Neuheimer 2008):

$$f1 = \frac{F^2}{\left(F^2 + K_m^{\,2}\right)} \quad (4)$$

where K_m is the half saturation coefficient. K_m was initially chosen to be 4.4 μg N L^{-1} (equal to 25 μg C L^{-1}). The dependency of ingestion on temperature (T, in Kelvin) was obtained by fitting the results of the present experiments to a parabolic threshold function (Kooijman 2000) where P_1 and P_2 are the lower and upper boundaries of the tolerance range and P_3 and P_4 are the Arrhenius temperatures for the rate of the decrease at both boundaries. P_5 is a coefficient applied after the fitting procedure to set the maximum to 1. For parameter values *see* Table 1:

$$f2 = \frac{P_5}{\left(1 + \exp\left(\frac{P_3}{T} - \frac{P_3}{P_1}\right) + \exp\left(\frac{P_4}{P_2} - \frac{P_4}{T}\right)\right)} \quad (5)$$

For copepods which do not moult, ingestion will be inhibited due to limited body volume of the cuticle (Carlotti and Sciandra 1989; Stegert et al. 2007). This is described by a parabolic function allowing individuals to feed at maximum rate until their mean weight (W_i) reaches the critical weight Xt_i, and then decreases for higher weights down to zero at Xg_i (Table 1) (Stegert et al. 2007).

$$f3 = 1,\ W_i < Xt_i$$

$$f3 = 1 - \frac{(W_i - Xt_i)^2}{(Xg_i - Xt_i)^2}, W_i \geq Xt_i \quad (6)$$

Losses

Of the food ingested (g_i) 65% is assimilated (*AE*), while the rest is egested (Thor and Wendt 2010). Of the assimilated food between 25% and 35% is assumed to be lost by active metabolism (R_A) depending on stage. Furthermore, a basal metabolism (R_B) of 2% to 5% of the biomass is assumed (Table 1) (Stegert et al. 2007). Thus, the daily loss (l_i) is described as:

$$l_i = (1 - AE) \cdot g_i + R_A \cdot g_i + R_B \quad (7)$$

Transfer

Transfer from each group of feeding stages to the next is initiated when the mean weight exceeds the reference weight (Rt_i). At the critical moulting weight (Xt_i), the transfer rate is 50%:

$$f4 = \frac{(W_i - Rt_i)^4}{(W_i - Rt_i)^4 + (Xt_i - Rt_i)^4}, W_i \geq Rt_i \quad (8)$$

The transfer from the non-feeding group (egg-NII) to the first feeding group (NIII-NVI) were described by the Bělehrádeks function that assumes that the time from egg to the end of the *i*th stage, ES_i, is a non-linear temperature function (T):

$$ES_i = \frac{1}{P_6 \cdot (T + P_7)^{2.05}} \quad (9)$$

where P_6 is a stage-dependent coefficient and P_7 is a characteristic temperature constant. The exponent, 2.05, has been shown to characterize the temperature response of most copepod species (McLaren et al 1969; Corkett et al. 1986).

2.3.1. Model validation and scenarios

The model was initiated by 1000 eggs; the other stages were set to zero. The model was forced by a constant temperature and a constant food concentration during each experiment. Model runs were conducted for temperatures of 0ºC to 20ºC, at 1ºC increments and at food concentrations between 25 μg C L^{-1} and 400 μg C L^{-1} at 25 μg C increments, assuming a molar C:N ratio of 6.6. The mean development time (MDT) from egg to adult was calculated as the time when 500 of the 1000 copepods in the model had reached adulthood. The MDT for eggs to CI was calculated as the time when the cumulated abundance of Egg-NII and NIII-NVI was 500.

The model calculation of development time from egg to CI and from egg to adult were validated against data derived from experiments with *C. helgolandicus* (Rey et al. 2001; Rey-Rassat et al. 2002; Cook et al. 2007; Bonnet et al. 2009) and *C. finmarchicus* (Diel and Klein Breteler 1986; Cook et al. 2007; Campbell et al. 2001). Bonnet et al. (2009) did experiments with *C. helgolandicus* at 9ºC, 12ºC, and 15ºC. However, these copepods were not growing well at 9ºC and only reached naupliar stage 5. To be able to include this data point in our validation, the development time of NVI at 9ºC was assumed to constitute the same proportion of the development time from egg to NVI as the average proportion at 12ºC and 15ºC.

The effect of changing the half saturation coefficient K_m (Eq. 4) at different food levels is illustrated for *C. helgolandicus*. Furthermore the effect on the competition between the two species was tested in two sets of scenarios where *C. helgolandicus* had 20% higher or lower K_m than *C. finmarchicus*.

Results

The observed *C. helgolandicus* clearance rate was zero at 4ºC, and increased to 90±15 mL copepod^{-1} d^{-1} at 14ºC before decreasing again and reaching 35±20 mL copepod^{-1} d^{-1} at 24ºC, the highest temperature in the experiment (Fig. 1A). The shape of the response

was similar for *C. finmarchicus*. However, at the lowest temperature of 0.6ºC *C. finmarchicus* clearance rate was 20±10 mL copepod^{-1} d^{-1}. Thus, *C. finmarchicus* was more effective at lower temperatures than *C. helgolandicus* (Fig. 1B). The highest clearance rate of 164±48 mL copepod^{-1} d^{-1} for *C. finmarchicus* occurred at 14ºC followed by a decrease to 26±18 mL copepod^{-1} d^{-1} at 21ºC. Function *f*1 was obtained by fitting data to the parabolic threshold function (Eq. 5) and normalized by dividing by the maximum clearance rate (Fig. 1C). This was done as the fraction of maximum ingestion is expected to be the same as the fraction of maximum clearance at the same food concentrations, which was the case in all our experiments (parameter values in Table 1). This normalization also means that any effect on the absolute clearance rate measured due to the two different methods used can be disregarded, since we now only consider the shape of the temperature response. The optimum temperature obtained by the fitting procedure was 12.2ºC and 13.6ºC, for *C. finmarchicus* and *C. helgolandicus* respectively.

Development time calculated by the model decreased with increasing temperature until 12-13ºC for *C. finmarchicus* and 13-15ºC for *C. helgolandicus* (Fig. 2). At higher temperatures development time increased reflecting the decrease in ingestion. Below 8ºC, the loss processes (l_i, Eq. 7) for *C. helgolandicus* were larger than the grazing (g_i, Eq. 3) and the copepods did not develop. *Calanus finmarchicus* also developed at temperatures below 8ºC, indicating that living at these temperatures can be advantageous for that species.

Data for validation of the model calculations at different temperatures were mainly available at food concentrations above 200 μg C L^{-1}, i.e., at food saturation. Generally, the model and experimental results corresponded well (Fig. 2), although the data for *C. helgolandicus* were somewhat scattered, and were limited at the temperature intervals where the model calculates large changes in development times (<7ºC). This may be a result of the difficulties to grow this species in the laboratory at these low temperatures (Bonnet et al. 2009).

Decreasing food concentrations led to increasing development times (Fig. 3). Data for validation of the model response in development time to various food concentration were only available at 8ºC and 15ºC for *C. finmarchicus* and *C. helgolandicus*, respectively. For *C. finmarchicus,* data and model results were in correspondence (Fig. 3). For *C. helgolandicus* the available data fitted the model at food concentrations that lead to the minimum development times at 15ºC, but no data were available at the low food concentrations, where the model calculated increased development times (Fig. 3).

Calanus finmarchicus grew faster than *C. helgolandicus* below 11ºC and the difference in development time for the two species increased drastically below this temperature in the model (Fig. 4). Above 11ºC the opposite pattern emerged although the difference in development time between the two species was not as pronounced. Lower food availability caused more pronounced difference between the species in the mean development time with temperature enhancing the growth advantage of the favored species at a gi ven temperature (Fig. 4). Changing the half saturation K_m clearly affects the development time; higher K_m results in slower development. The effect is most pronounced at the lowest food concentration, and decreases with increasing food concentration (Fig. 5). Changing only K_m of one of the species moved the temperature threshold of transition between species. Allowing *C. helgolandicus* to have 20% higher or lower half saturation coefficient than *C. finmarchicus* resulted in a ~1ºC and 1.3ºC displacement of transition in growth benefit between species, respectively, at a food concentration of 25 μg C L^{-1} (Fig. 6).

3. Discussion

Development times of *C. finmarchicus* and *C. helgolandicus* are highly dependent on temperature and the displacement in the response curves to temperature presented here offers an explanation on observed patterns in their phenology and biogeography in the North Atlantic (Beaugrand et al. 2002; Bonnet et al. 2005; Helaouët and

Beaugrand 2007). The present study suggests that the differences in the development rates are related to the species differences in their response of ingestion rates to temperature, and that *C. finmarchicus* develops faster than *C. helgolandicus* below 11ºC and slower above this threshold.

Our results are obtained from a model parameterised by experimental data. In the model, the ingestion responses to temperature were derived from new experiments and values on ingestion functional responses, whereas loss rates and threshold biomasses were derived from the literature. Development times were calculated from biomass increments controlled by ingestion and metabolic losses and the model was successful in reproducing the development times measured experimentally (Figs. 2, 3). The model results agree with an earlier model of *C. finmarchicus* development (Carlotti and Radach 1996) at the temperatures below optimum. However, at higher temperatures there is an important divergence. Carlotti and Radach (1996) parameterised the temperature dependency following a constant Q_{10} law. Thus in their model the ingestion rate continues to increase and the development time to decrease with increasing temperatures, in contrast to our model that predicts decreasing ingestion and increasing development time with increasing temperatures.

When we use our experimental results on the dependency of grazing on temperature in the model, two assumptions had to be made. Linearity in the temperature response of ingestion is assumed across food concentrations, and we assume that the temperature response will be the same for younger stages as our grazing experiments were carried out on late *Calanus* copepodite stages. Few other experimental studies have systematically evaluated the effect of temperature on grazing rates, allowing estimation of the optimum temperature for *Calanus* or other copepod species but no data are available for young copepodites or nauplii. For adult *Temora stylifera,* however, the optimum was determined at several different food concentrations (Theubault 1985). This study may suggest that the temperature optimum is lower at the lowest food concentration. However, our parameterisation produces results that agree well with experimentally determined development times derived from the literature. Thus, based on the available information our assumptions seem reasonable.

The model suggests that for *C. helgolandicus* the loss (l_i) will exceed ingestion (g_i) for the larger stages below 8ºC and the copepods will not develop to adulthood. Similarly, Bonnet et al. (2009) found that *C. helgolandicus* did not grow very well at 9ºC while *C. finmarchicus* was observed to develop at 0ºC (Tande 1988) in accordance with our model. We were not able to find any data in the literature on development time for the two species above 15ºC. The model can therefore not be validated at these temperatures. While the clearance rates used to parameterize the model were clearly different at the lower temperatures for the two species (Fig. 1), the differences between the species were smaller at the higher temperatures. Thus, there is obviously a need for more experiments at temperatures in the range from 12ºC to 18ºC.

Most of the experiments on development time have been carried out at saturating food conditions. The model allows us to explore what will happen at lower and non-saturating food conditions. The model output suggests that the rate of change in the difference in development times between *C. helgolandicus* and *C. finmarchicus* with temperature will be more pronounced at lower food levels (Fig. 4). The validation of the response of development time to food concentration was carried out at the temperatures where data was available. For *C. finmarchicus* development rates were available at low food concentrations (Campbell et al 2001) and the model was able to reproduce these. For *C. helgolandicus* however, few data exist and none at the food levels that the model suggest as being limiting. Thus, while the existing data support the model, the choice of half saturation coefficient could not be validated. Furthermore, the experiments are often carried out with only one type of food item, and the half saturation coefficient obtained does not necessarily reflect in situ conditions. We therefore explored the effect of changing K_m on our conclusion. As expected, changes in the K_m had the largest effect at low food concentrations; i.e., increasing K_m 20% from the standard run (Table 1) at 25 μg C L^{-1} caused an increase in the mean development time of 25%, while at the 50 μg C L^{-1} the increase was 9% and at 200 μg

C L^{-1} it was negligible (Fig. 5). We furthermore evaluated how changes in K_m could affect the threshold for the shift of favorable development from the one *Calanus* species to the other. At food concentrations of 25 μg C L^{-1}, the effect of allowing *C. helgolandicus* to have 20% higher or lower half saturation coefficient than *C. finmarchicus* was a displacement of ~1ºC and 1.3ºC, respectively of the point where the two species have the same development rate (Fig. 6). This effect decreases with increasing food levels, since the copepods become less food limited (Fig. 5). At 50 μg C L^{-1} the displacement of the shift would only be ~0.3ºC, and no changes will occur at 200 μg C L^{-1}.

Parameter values for ingestion and loss were chosen from the literature (Table 1) for the two *Calanus* species. When nothing else was evident the simplest solution was preferred i.e., parameterisation was chosen to be similar for the two species. Thus, apart from the dependency of ingestion on temperature from the present study, only copepod weights and maximum specific ingestion rates that scale with size were different. The parameterisation we chose resulted in good outcome compared to the experimentally measured development times. However, a similar result may have been achieved with a different choice of parameter values, i.e., by decreasing or increasing both ingestion rates and losses. In a parameterisation of a similar zooplankton population model for *Pseudocalanus elongates,* a sensitivity analysis revealed that the particularly sensitive parameters were maximum ingestion rate, assimilation efficiency and active metabolism (Stegert et al. 2007). The two latter are related to the first one; ingestion rate, and therefore this sensitivity reflects the inherent dependency of development on biomass increment.

The dry weight of *C. finmarchicus* (stages C1-C6) has been shown to depend on temperature with 5-10% decrease with 1ºC increase in temperature and, with the largest decrease for the younger stages (Carlotti et al 1993). In the present study, temperatures are kept constant in the model runs, and the effect of neglecting this dependency of weight on temperature is minor. It may cause a slightly faster development at the higher temperatures than if the above mentioned effect were considered, due to the uneven decrease across the stages. However, if the model is run with changing temperatures (i.e., if it is incorporated in an ecosystem model) the effect may be important to consider (Carlotti and Radach 1996).

At low food concentrations, the basal metabolism constitutes a larger proportion of the losses than at higher food concentrations, since active metabolism and egestion are a proportion of ingestion. Furthermore, the model assumes that the basal metabolism is independent of temperature. This means that the parameterisation of the basal metabolism is especially important when the temperature is far from the optimal temperature and the food concentration is low.

In our experiments, *Calanus* were obtained from in situ temperatures that have been suggested to be close to their preferred temperature based on abundance and kept at this temperature until the start of the experiment (Bonnet et al. 2005; Jónasdóttir and Koski 2011). No acclimatization was carried out on the animals prior to exposing them to the experimental temperatures. In the sea, adaption to changing temperatures may take place. The experiments may therefore be seen as the copepod response to short time temperature changes experienced for instance during diel vertical migration in the water column. On a longer time scale some degree of adaption could be expected. For *Temora longicornis* it was suggested that the peak egg production was different in populations experiencing different temperatures during the growing season (Holste et al. 2009). More studies on the plasticity of the different *Calanus* species are certainly needed.

The distribution of the two *Calanus* species depends on the development time but obviously also on factors such as advection, reproduction and mortality. Nevertheless, there seems to be a correspondence between the temperature threshold calculated by our model for which species has the fastest development and general distribution patterns. By considering the abundance of *C. finmarchicus* and *C. helgolandicus* in relation to temperature in all available North Atlantic Continuous Plankton Recorder (CPR) samples Bonnet et al. (2005) defined their thermal niches. *Calanus helgolandicus* was generally found in 9–20ºC water, with maximum abundance between 13ºC and 17ºC. In contrast, *C. finmarchicus* was found in cooler waters, generally between 0ºC and 15ºC, with peak abundances from 0ºC to

9ºC. *Calanus helgolandicus* was the most abundant above 11ºC, while *C. finmarchicus* was most abundant below these temperatures, the same threshold temperatures as found in the present study. Further, analyses of the vertical distribution of the two species at Dogger Bank in the North Sea showed a similar picture. *Calanus finmarchicus* were primarily found in and below the thermocline (<10ºC), and *C. helgolandicus* in and above (>12ºC) (Jónasdóttir and Koski 2011).

This study shows that relatively small temperature changes can have consequences for the competition between *C. helgolandicus* and *C. finmarchicus* due to changes in the development rates. The sea surface temperature is expected to increase in the North Atlantic in the years to come (Beaugrand et al. 2008). If temperatures increase to above 11ºC, *C. helgolandicus* may take over the habitat currently dominated by *C. finmarchicus* with potential consequences for higher trophic levels (Beaugrand et al. 2003). If the temperature is around 11ºC, we predict that the two species will develop at similar rates. Compared to a situation with lower temperatures both species will develop faster. This may lead to higher biomass but could also lead to temporal mismatch between *Calanus* and their predators (Yang and Rudolf 2010). Thus, both temporal and spatial displacements of the *Calanus* populations can be expected with potential consequences for their predators. The current findings should be considered together with changes in circulation patterns and changes at other levels of the food web to make better predictions of the future distribution patterns of *Calanus*.

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Tables

Table 1: Parameter values for *Calanus helgolandicus* and *Calanus finmarchicus* used for the standard run of the model.

					Calanus finmarchicus					*Calanus helgolandicus*					
Process	Equation	Parameter	Unit	Abbreviation	Egg-NII	NIII-NVI	CI-CIII	CIV-CV	Adult	Egg-NII	NIII-NVI	CI-CIII	CIV-CV	Adult	Note
Ingestion dependency on food concentration	4	Maximum ingestion	μg N μg N^{-1} d^{-1}	I_{max}	-	1.41	0.81	0.47	0.41	-	1.35	0.89	0.54	0.45	Saiz and C albet 2007 plus 0.25 scaling
	4	Half saturation	μg N L^{-1}	K_m	-	4.4	4.4	4.4	4.4	-	4.4	4.4	4.4	4.4	partly fitted
Ingestion dependency on temperature	5	Temperature threshold	Kelvin	P_1	-	293	293	293	293	-	289	289	289	289	this study
	5	Temperature threshold	Kelvin	P_2	-	284	284	284	284	-	275	275	275	275	this study
	5	Temperature threshold	Kelvin	P_3	-	13282	13282	13282	13282	-	39429	39429	39429	39429	this study
	5	Temperature threshold	Kelvin	P_4	-	29725	29725	29725	29725	-	14123	14123	14123	14123	this study
	5	Normalize factor		P_5	-	5.72	5.72	5.72	5.72	-	11.45	11.45	11.45	11.45	this study
Loss	7	Assimilation efficiency	μg N μg N ingested^{-1}	AE	-	0.65	0.65	0.65	0.65	-	0.65	0.65	0.65	0.65	Thor and Wendt 2010
	7	Active metabolism	μg N μg N ingested^{-1}	R_A	-	0.35	0.29	0.29	0.25	-	0.35	0.29	0.29	0.25	Stegert et al. 2007
	7	Basal metabolism	μg N μg N biomass^{-1} d^{-1}	R_B	-	0.05	0.02	0.02	0.02	-	0.05	0.02	0.02	0.02	Stegert et al. 2007
Transfer to feeding stages	9	Stage dependent coefficient		P_6	1747	-	-	-	-	826	-	-	-	-	Cook et al. 2007; Bonnet et al. 2009
	9	Temperature parameter		P_7	-9.75	-	-	-	-	-8.97	-	-	-	-	Cook et al. 2007; Bonnet et al. 2009
Transfer between feeding stages	8	Reference biomass	μg N	Rt_i	-	0.29	3.53	24.8	31.5	-	0.40	2.16	11.7	17.8	Campbell et al. 2001; Rey et al. 2001; Rey-Rassat et al. 2002
Transfer between feeding stages, cease feeding	6,8	Critical moulting mass	μg N	Xt_i	-	0.31	3.85	27.4	34.0	-	0.45	2.33	13.5	19.8	Campbell et al. 2001; Rey et al. 2001; Rey-Rassat et al. 2002
Cease feeding	6	Critical ingestion mass	μg N	Xg_i	-	0.33	4.17	30.0	36.5	-	0.49	2.49	15.3	21.7	Campbell et al. 2001; Rey et al. 2001; Rey-Rassat et al. 2002

Figures

Fig. 1: Experimental data and the fitted function on clearance rate (mL copepod (cop)$^{-1}$ day^{-1}) of (a) *Calanus helgolandicus* (R^2=0.57, p<0.001) and (b) *C. finmarchicus* (R^2=0.45, p<0.001) as a function of temperature. Error bars are SE. (c) Clearance rate for both species normalized to fraction of its maximum. For parameter values *see* Table 1.

Fig. 2: Mean development time of *C. helgolandicus* and *C. finmarchicus* from egg to CI and from egg to adult as a function of temperature. Lines are modeled results at 200 μg C L^{-1} and symbols are experimental data obtained from Diel and Klein Breteler (1986), Campbell et al. (2001), Rey-Rassat et al. (2002), Cook et al. (2007), and Bonnet et al. (2009) at food concentrations above 200 μg C L^{-1}.

Fig. 3: Mean development time from egg to CI and from egg to adult as a function of food concentration at 15ºC and 8ºC for *C. helgolandicus* and *C. finmarchicus*, respectively. Lines are model results and symbols are experimental data obtained from Campbell et al. (2001), Rey-Rassat et al. (2002), Cook et al. (2007), and Bonnet et al. (2009).

Fig. 4: Differences in the mean development times of *C. helgolandicus* (CH) and *C. finmarchicus* (CF) from egg to adult as a function of temperature at 25 μg C L^{-1}, 50 μg C L^{-1}, and 200 μg C L^{-1} food.

Fig. 5: The mean development times from egg to adult of *C. helgolandicus* at 15ºC as a function of the chosen K_m at 25 μg C L^{-1}, 50 μg C L^{-1} and 200 μg C L^{-1}.

Fig. 6: Differences in the mean development times of *C. helgolandicus* and *C. finmarchicus* from egg to adult as a function of temperature at 25 μg C L^{-1} with equal K_m for the two species and with K_m for *C. helgolandicus* (CH) being 20% larger or smaller than K_m of *C. finmarchicus* (CF).

Figure 1

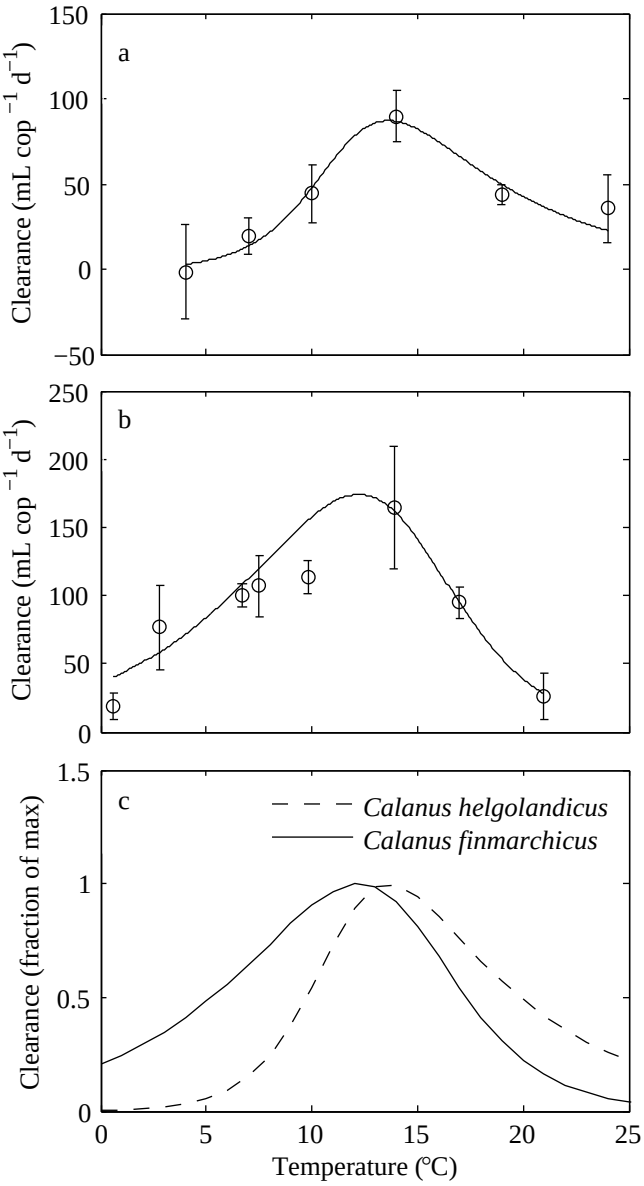

a
b
c
Clearance (mL cop $^{-1}$ d^{-1})
Clearance (fraction of max)
Temperature (°C)
Calanus helgolandicus
Calanus finmarchicus
150
100
50
0
−50
250
200
150
100
50
0
1.5
1
0.5
0
0
5
10
15
20
25

Figure 2

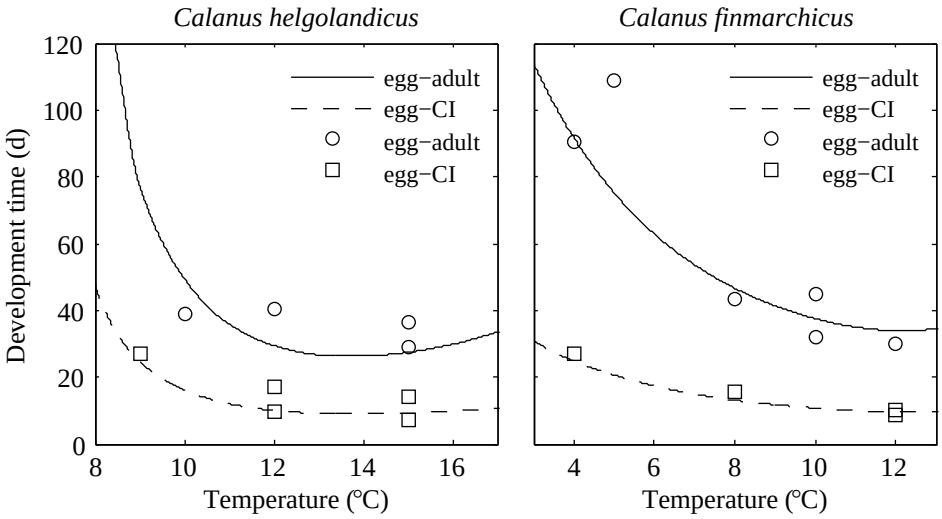

Calanus helgolandicus
Calanus finmarchicus
Development time (d)
Temperature (°C)
Temperature (°C)
egg−adult
egg−CI
egg−adult
egg−CI
egg−adult
egg−CI
egg−adult
egg−CI
0
20
40
60
80
100
120
8
10
12
14
16
4
6
8
10
12

Figure 3

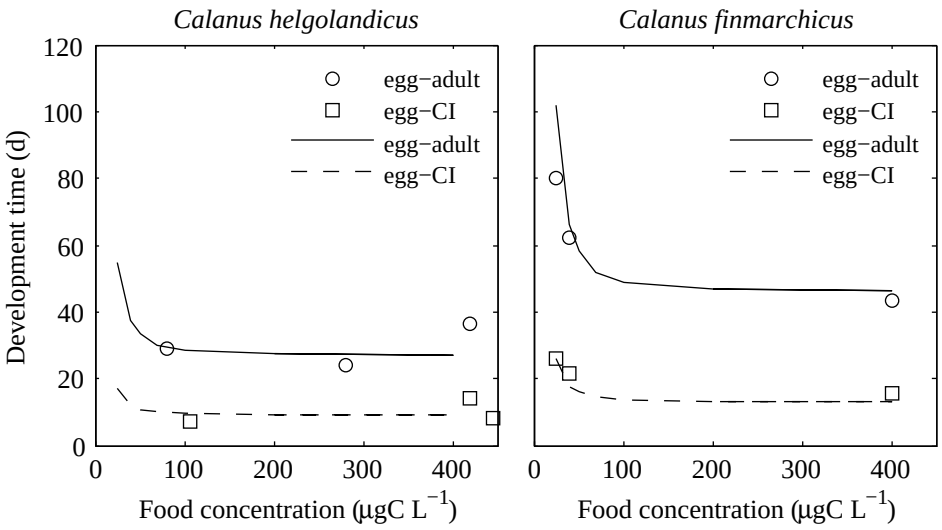

Calanus helgolandicus
Calanus finmarchicus
Development time (d)
Food concentration (µgC L−1)
egg−adult
egg−CI
egg−adult
egg−CI
0
20
40
60
80
100
120
0
100
200
300
400

Figure 4

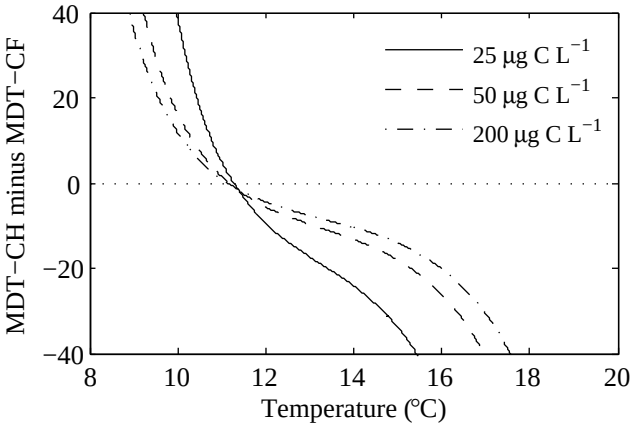

40
20
0
−20
−40
8
10
12
14
16
18
20
MDT−CH minus MDT−CF
Temperature (°C)
25 µg C L−1
50 µg C L−1
200 µg C L−1

Figure 5

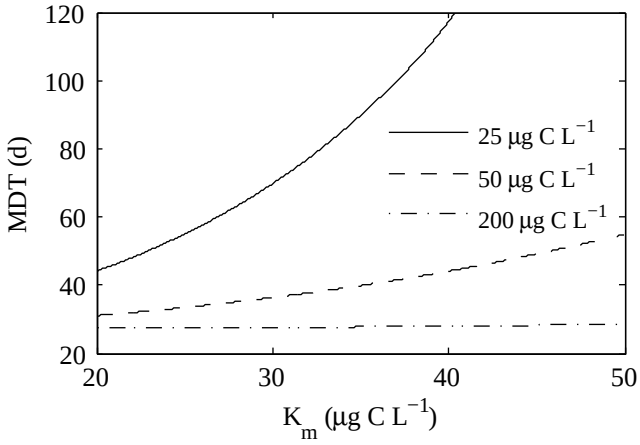
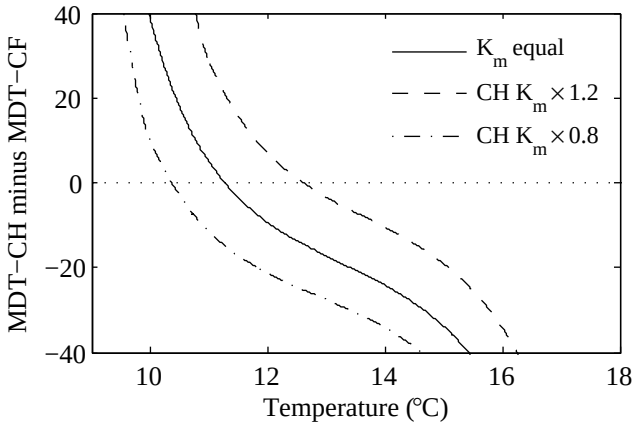

120
100
80
60
40
20
MDT (d)
20
30
40
50
K_m (µg C L^-1)
25 µg C L^-1
50 µg C L^-1
200 µg C L^-1

Figure 6


40
20
0
−20
−40
10
12
14
16
18
MDT−CH minus MDT−CF
Temperature (°C)
K_m equal
CH K_m × 1.2
CH K_m × 0.8