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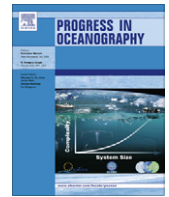
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# Influence of projected ocean warming on population growth potential in two North Atlantic copepod species

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## ABSTRACT

Copepods of the genera *Pseudocalanus* and *Centropages* play an important role in the North Atlantic ecosystems and have distinctive spatial and temporal patterns depending on physiological adaptation to different environmental conditions. To examine the possible impact of climate change on these biogeographic patterns, potential population growth rate was computed for each species using IPCC projections of sea surface temperature together with chlorophyll distributions from SeaWiFS climatology and published laboratory data on temperature and food-dependent life-history parameters. The results indicate that the predicted temperature increase throughout the North Atlantic will cause temporal and spatial shifts in copepod species population growth potential. The *Centropages* population is projected to increase in mid-latitudinal shelf areas, e.g. the Gulf of Maine and the North Sea, due to shorter generation times and a longer growing season, while *Pseudocalanus* is predicted to be less abundant in these regions after 2050. These shifts potentially have a significant impact on the future demographics of pelagic fish species for which the copepods are the major food source.

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## 1. Introduction

Recent investigations within regional GLOBEC programs (Global Ocean Ecosystem Dynamics, GLOBEC, 1997) have found that different fish species prefer to feed on specific copepod species. Changes in the abundance of *Acartia* and *Pseudocalanus* in the Baltic Sea coincided with shifts in the dominance of herring and cod (Hansen et al., 2006; Köster et al., 2001), respectively. In the northwestern Atlantic, Buckley and Durbin (2006) investigated the relationship of growth rates in larval fish on Georges Bank and copepod abundance and Neuheimer et al. (2009) showed that a shift in the timing of copepod growth could lead to food limitation of larval fish. These studies underscore the importance of copepods on the survival of larval fish, which undergoes strong inter-annual variability (Alheit et al., 2005; Mountain et al., 2008). Understanding the mechanisms driving this prey variability is critical for developing a capacity to ultimately forecast the recruitment strength of fishes.

More generally, planktonic copepods are a key component of marine ecosystems, dominating the North Atlantic zooplankton and linking lower and higher trophic levels. Their developmental and reproductive rates change significantly based on abiotic and biotic factors. Due to this sensitivity to environmental conditions,

copepods are considered key indicators for climate variability and change (Richardson, 2008). A strong impact of climate variation on the abundance and species composition of copepods in the North Atlantic has been found in long-term data sets like the Continuous Plankton Recorder (CPR) data (Edwards et al., 2002; Planque and Taylor, 1998) and MARMAP/ECOMON<sup>3</sup> surveys (Sherman, 1980; Meise and O'Reilly, 1996; Kane, 2007). Inter-annual to inter-decadal changes in temperature are correlated with variability in population abundance of several copepod species (e.g. Planque and Fromentin, 1996; Reid et al., 2003). The influence of temperature changes on those species varies geographically, as seen in zooplankton data from the NW Atlantic shelf (Kane, 2007; Kane and Prezioso, 2008). Time series of temperature and *Centropages typicus* anomalies from 1977 to 2007 reveal a significant increase of both variables in the Middle Atlantic Bight (Kane, 2007).

Throughout the North Atlantic Ocean a general increase in temperature has been observed in the past century (Beaugrand, 2009) and future ocean temperatures have been forecasted by coupled atmosphere–ocean general circulation models (GCM) as discussed in the Fourth Assessment Report (AR4) of the Intergovernmental Panel on Climate Change (IPCC). Simulations for the 21st century have been carried out based on different emission scenarios. These ranged from ‘if we don't change’ (emphasis on global economy, A2) to ecological awareness (emphasis on regional environment, B1) with a middle way (A1B) representing a future world of rapid economic growth with an introduction of new and more efficient technologies

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(Roeckner et al., 2006). The simulations provide forcing and boundary data for large scale ocean models, which aim to forecast future development of marine systems as done by Hollowed et al. (2009).

The present paper uses literature information from laboratory and field observations of life cycle processes of *Pseudocalanus* and *C. typicus*. Temperature predictions from IPCC simulations are incorporated into static models of copepod species population growth potential to estimate the impact of ocean warming on biogeographic patterns and phenology of these species. This study is the first empirical study of the effect of climate change on potential population growth rates in copepod species on a basin scale. This analysis provides a first-order assessment of possible changes in the population dynamics of copepods in a larger spatial context.

## 2. Material and methods

### 2.1. Biological estimations

Potential population growth was defined as the net reproductive rate (i.e. the average number of individuals surviving from spawning to maturity) divided by the net developmental time as introduced by Kiørboe and Sabatini (1994). They calculated it as:

$$r = \left[ \ln \left( \frac{m}{\beta} \right) - (\beta e - \beta)HT - \beta D \right] / (D + 1/\beta) \quad (1)$$

which incorporates the egg production  $m$ , the egg mortality  $\beta e$ , the post-hatching mortality  $\beta$ , the hatching time  $HT$  and the generation time  $D$ . These processes are calculated by temperature and food dependent functions from a copepod population model (Hu et al., 2008; Ji et al., 2009) with species specific parameter values reflecting their adaptation to different environmental conditions (the different life-history parameter values for *Pseudocalanus* sp. and *C. typicus* are listed in Table 1, the corresponding functions are given in the text and plotted in Fig. 3). For *Pseudocalanus* four dominant species exist in the North Atlantic Ocean: *P. minutus*, *P. newmani*, *P. moultoni*, and *P. elongatus* (Frost, 1989). To perform a basin-wide parameterization, a generic “*Pseudocalanus* spp.” was used, which has composite values that approximate its life-history parameters based on existing data. This can be justified as these species show similar sizes, reproduction rates (Halsband and Hirche, 2001; and references therein) and responses to temperature in development (Klein Breteler et al., 1995; their Fig. 4).

The development times decrease with temperature and are commonly estimated by the Belehradek function  $D = a(T - \alpha)^{-b}$  (Belehradek, 1935). Development can be impeded at low food concentrations (Davis, 1984a; Davis and Alatalo, 1992; Klein Breteler et al., 1995; Vidal, 1980). Thus, Ohman and Hsieh (2008) extended the Belehradek function by adding food dependence with a combined temperature-food effect (a stronger food-limiting effect at higher temperature):

$$D = a(T - \alpha)^{-b} \cdot [1 - \exp(-(qT^s) \cdot P)] \quad (2)$$

Food as carbon content was calculated from chlorophyll using a conversion of 50:1 (weight ratio). The parameter values for  $q$  and  $s$

**Table 1**

Parameter values for the processes involved in population growth.

| Parameter   | Parameter          | <i>Pseudocalanus</i>  | <i>C. typicus</i>     | Unit                                 |
|-------------|--------------------|-----------------------|-----------------------|--------------------------------------|
| $a$         | Development $f(T)$ | 22733.00 <sup>1</sup> | 10361.00 <sup>2</sup> | d                                    |
| $\alpha$    | Development $f(T)$ | −13.87 <sup>1</sup>   | −5.30 <sup>2</sup>    | °C                                   |
| $b$         | Development $f(T)$ | 2.05 <sup>3</sup>     | 2.05 <sup>3</sup>     | nd                                   |
| $q$         | Development $f(F)$ | 0.26 <sup>4</sup>     | 0.25 <sup>5</sup>     | μg C <sup>−1</sup>                   |
| $s$         | Development $f(F)$ | −1.14 <sup>4</sup>    | −0.50 <sup>5</sup>    | nd                                   |
| $g_a$       | Fecundity $f(T)$   | 17.56 <sup>1</sup>    | 46.63 <sup>7</sup>    | eggs f <sup>−1</sup> d <sup>−1</sup> |
| $g_b$       | Fecundity $f(T)$   | 19.48 <sup>1</sup>    | 7.63 <sup>7</sup>     | nd                                   |
| $T_0$       | Fecundity $f(T)$   | −42.83 <sup>1</sup>   | −18.65 <sup>7</sup>   | °C                                   |
| $kchl$      | Fecundity $f(F)$   | 0.86 <sup>6</sup>     | 1.70 <sup>5</sup>     | μg Chl l <sup>−1</sup>               |
| $\mu_0$     | Base mortality     | 0.06 <sup>8</sup>     | 0.09                  | d <sup>−1</sup>                      |
| $\mu_{e,0}$ | Base mortal. eggs  | 0.06 <sup>8</sup>     | 0.60                  | d <sup>−1</sup>                      |
| $q_{10\ m}$ | Mortality $Q_{10}$ | 3.50                  | 1.9                   | nd                                   |
| $T_{base}$  | Mortality $f(T)$   | 10.00                 | 10.00                 | °C                                   |
| $a_e$       | Development eggs   | 2312.00 <sup>1</sup>  | 922.00 <sup>9</sup>   | d                                    |

<sup>1</sup>Davis (1984b,c); <sup>2</sup>calculated from Fryd et al. (1991); <sup>3</sup>McLaren et al. (1969); <sup>4</sup>derived from Klein Breteler et al., (1995); <sup>5</sup>derived from Davis and Alatalo (1992); <sup>6</sup>Bunker and Hirst, (2004); <sup>7</sup>derived from Halsband-Lenk et al. (2002); <sup>8</sup>Ohman et al. (2002); <sup>9</sup>Carlotti et al. (2007); mortality inferred by adjusting to fit seasonal timing.

for *Pseudocalanus* were estimated from a comprehensive data set of Klein Breteler et al. (1995) who measured stage durations at various food and temperature conditions. Values for *C. typicus* were based on observations by Davis and Alatalo (1992) for the food effect, while an increase at lower temperatures was included in accordance to its adaptation to warmer waters.

As the eggs do not feed, the hatching time is dependent on temperature only with

$$HT = a_e(T - \alpha)^{-b} \quad (3)$$

The value of  $b = 2.05$  is based on an estimate by McLaren et al. (1969) for several copepods and widely used, while the values for  $a_e$  and  $\alpha$  are based on laboratory experiments from Corkett and McLaren (1978) (see Davis, 1984a,b,c) for *Pseudocalanus* and Fryd (1991) for *Centropages typicus*.

Egg production rate as a function of temperature was approximated using a Gaussian function with an optimum temperature for reproduction and decreasing in warmer environment (this curve was used for *Centropages* based on data by Halsband-Lenk et al. (2002) and was also adapted for *Pseudocalanus*). The food dependence term is a sigmoidal (Type III) function (Ji et al., 2009):

$$m = g_0 \cdot \exp[-(T - T_0)^2 / 2g_b^2] \cdot \left( \frac{P^2}{P^2 + kchl^2} \right) \quad (4)$$

Mortality was approximated by a  $Q_{10}$  function of temperature, which has been found to agree well with estimates using the vertical life-table method (Ji et al., 2009; Plourde et al., 2009). Mortality increases with increasing temperature indicating higher predation pressure in the warmer season. We used the same  $Q_{10}$  function for the eggs and post hatching stages and only distinguished the base mortality  $\mu_0$  and  $\mu_{e,0}$ , following Kiørboe and Sabatini (1994). They focused on the difference of free spawning

**Table 2**

Overview of six climate models shown in Fig. 1. Further detail in IPCC (2007).

| Model    | Institution            | Horiz. grid | Reference   |
|----------|------------------------|-------------|---|
| CNRM CM3 | CNR Meteo, France      | 64 × 128    | CNRM: IPCC DDC AR4 SREA1B run 1                               |
| GDGL CM2 | NOAA GDGL, USA         | 90 × 144    | GDGL contact, 2005: IPCC DDC AR4 GFDL-CM2.0 SRESA1B run1.     |
| HADGEM1  | HCCPR, MetOffice, UK   | 145 × 192   | Lowe, 2005: IPCC DDC AR4 UKMO-HadGEM SRESA1B run1             |
| MIROC3.2 | JAMSTEC, Tokyo, JAP    | 64 × 128    | Emori, 2005: IPCC DDC AR4 CCSR-MIROC3.2_(lo-res) SRESA1B run1 |
| MIROC3.2 | JAMSTEC, Tokyo, JAP    | 160 × 320   | Emori, 2005: IPCC DDC AR4 CCSR-MIROC3.2_(hi-res) SRESA1B run1 |
| ECHAM5   | MPI Met., Hamburg, GER | 96 × 192    | Roeckner, 2005: IPCC DDC AR4 ECHAM5/MPI-OM SRESA1B run2.      |

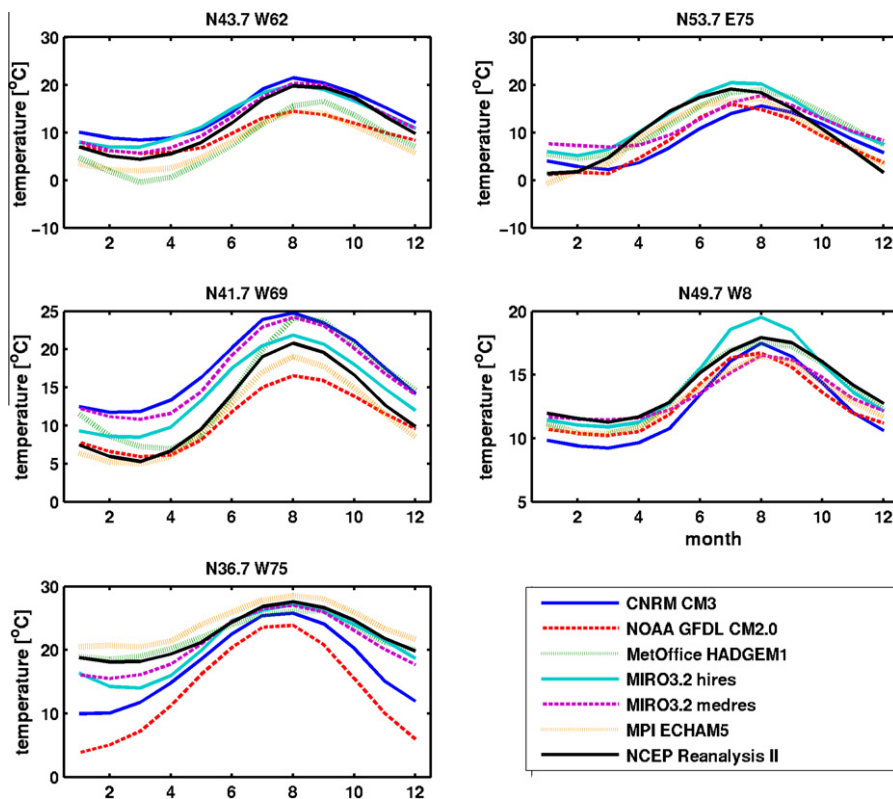


Fig. 1. Left: Simulated mean SST for 2001–2008 from the MIRO3.2 (hires) model run (°C). Right: Monthly mean climatology of SeaWiFS data for 1997–2007 (mg Chl m<sup>-3</sup>).

versus egg-carrying females and only compared to the influence of egg mortality and the post-hatch population. Though inter-stage variability exists (Ohman et al., 2002) the difference between eggs in free spawning individuals and the rest is significant. As in Kjørboe and Sabatini (1994), we assumed equal egg- and post-hatch mortality in *Pseudocalanus*.

$$\beta = \mu_0 \cdot q10^{(T-T_{base})/10} \quad (5)$$

$$\beta_e = \mu_{0,e} \cdot q10^{(T-T_{base})/10} \quad (6)$$

The mortality was inferred by adjusting the model to fit the general seasonal timing. As an approximation we chose the same reference temperature ( $T_{base}$ ) for both species (10 °C), while a higher  $Q_{10}$  (3.5) was chosen for the cold water species *Pseudocalanus*, which leads to stronger decrease in the warmer season. A lower value (1.9) was used for the warmer water preferring *C. typicus*.

## 2.2. Forcing data

We used monthly sea surface temperature (SST) data from the MIRO3.2 (hires) climate model (Hasumi and Emori, 2004), which provides highest resolution for the coupled ocean model of  $0.188^\circ \times 0.28^\circ$  among the models contributed to the 4th Assessment Report (IPCC, 2007). The model results for the years 2001–2100 though were provided on the grid of the coupled atmospheric model, which has a resolution of  $1.125^\circ \times 1.12^\circ$ .

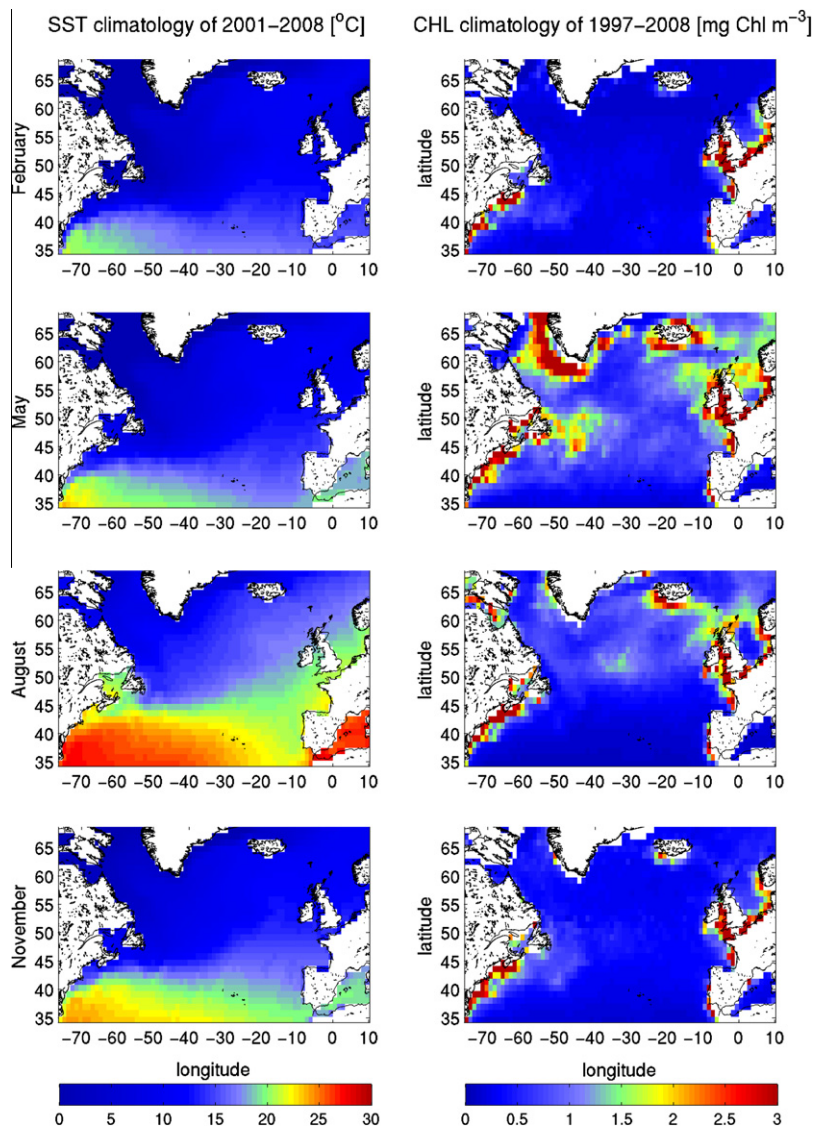
The modeled SST climatology (2001–2008) shows a strong gradient between  $40^\circ\text{N}$  and  $45^\circ\text{N}$  west of  $40^\circ\text{W}$  and a northwest to southeast gradient in the eastern part of the study area (Fig. 1). To assess the quality of these simulation data, we compared mean SST for the years 2001–2008 at five positions in the North Atlantic Ocean (see Fig. 8 for locations) from six GCM

models (see Table 2 for a list) to data from the National Centers for Environmental Prediction (NCEP)<sup>4</sup> (Fig. 2). The GCMs generally overestimated the amplitude of the annual cycle, and underestimated the mean. The divergence was higher in lower latitudes. The MIRO3.2 model calculated summer temperatures within  $\sim 1^\circ\text{C}$  except off the English Channel, whereas most other models estimated lower SST. In winter most models underestimated SST compared to NCEP data, and the difference for the MIRO model was within  $\pm 3^\circ\text{C}$ .

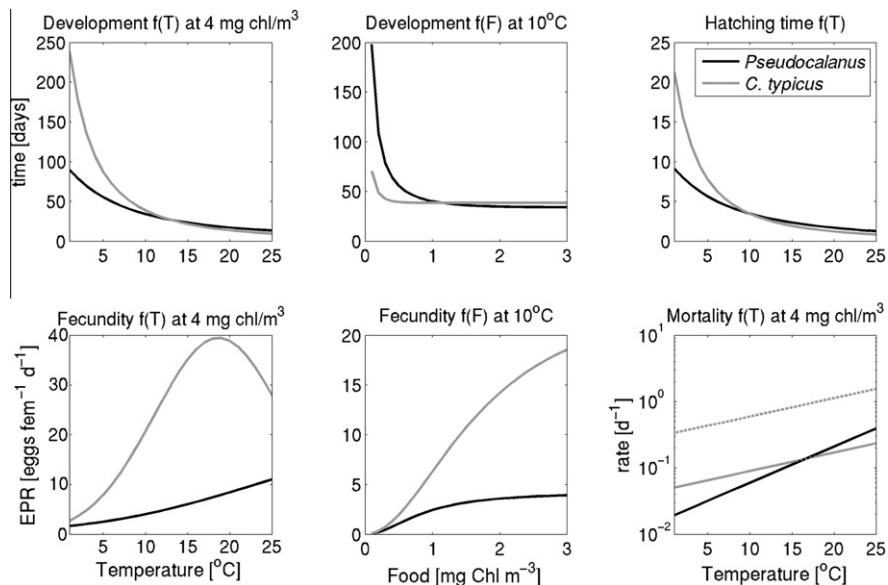
The food condition used in this study was derived from SeaWiFS satellite data and interpolated to the MIRO3.2 grid. Gaps due to sparse data at higher latitudes in fall and winter were filled by extrapolation of existing data from adjacent months scaled to fit the monthly data field. While coupled atmosphere–ocean general circulation models provide information on ocean temperature there is no clear information on the future development of annual chlorophyll cycles. Thus, a climatological annual cycle (monthly data) from the years 1997 to 2008 was used. Concentrations in the coastal area are high year-round ( $>2\text{ mg Chl m}^{-3}$ ). Spring concentrations were  $>1\text{ mg Chl m}^{-3}$  for most of the area north of  $40^\circ\text{N}$  and notably high in the Labrador Sea, around the Grand Banks and the Rockall Plateau (Fig. 1). For the future projection a change in the phytoplankton concentration is likely, as temperature influences the phytoplankton biomass directly (i.e. physiologically) and indirectly (e.g. through intensified stratification) (Scavia et al., 2002). The effect of changes in food supply was examined in a separate scenario testing.

<sup>4</sup> We used the NCEP\_Reanalysis 2 (1.875, 1979–present) data (Kanamitsu et al., 2002) provided by the NOAA/OAR/ESRL PSD, Boulder, Colorado, USA, from their Web site at <http://www.esrl.noaa.gov/psd/>.





**Fig. 2.** Mean annual cycle of sea surface temperature ( $^{\circ}\text{C}$ ) for 2001–2008 at five ecosystems in the North Atlantic Ocean (see Fig. 8 for a map) from six climate models and NCEP reanalysis II data.



**Fig. 3.** Life-history parameters as functions of food and temperature for *Pseudocalanus* sp. and *Centropages typicus* (equations are given in text). Dashed lines indicate egg mortality rates, which are identical to post-hatch mortality in *Pseudocalanus*.

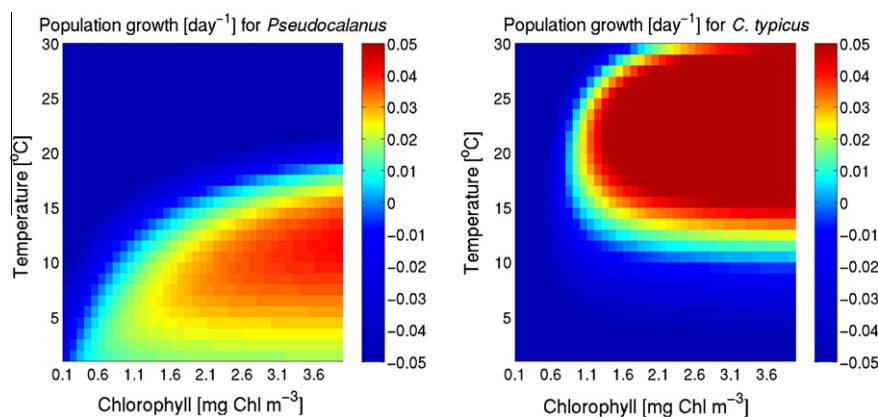


Fig. 4. Population growth potential of *Pseudocalanus* (left) and *C. typicus* (right) as a function of chlorophyll ( $\text{mg Chl m}^{-3}$ ) (x-axis) and temperature ( $^{\circ}\text{C}$ ) (y-axis) depending on model formulations.

### 3. Results

The potential of copepod population growth is affected by the combination of abiotic and biotic factors. Of the latter, the food concentration leads to a bottom-up control. The potential population growth of both species is limited by the combination of all involved processes (Fig. 4) based on the parameter values given in Table 1. Population growth of *Pseudocalanus* is positive, if  $T < 20^{\circ}\text{C}$ . The negative population growth at higher temperature is mainly caused by the increasing mortality. On the contrary, *C. typicus* has negative growth at  $T < 10^{\circ}\text{C}$  due to extended developmental times in cold waters (see Fig. 3) and has its optimum at ca.  $T = 20^{\circ}\text{C}$ . Compared to *C. typicus*, *Pseudocalanus* has higher growth potential at low food concentrations. The maximum values for population growth of  $0.05 \text{ d}^{-1}$  and  $0.10 \text{ d}^{-1}$  are of the same order as the estimate of  $0.07 \text{ d}^{-1}$  by Kiørboe and Sabatini (1994).

#### 3.1. Spatial analysis and parameter sensitivity

We calculated the population growth potential at monthly mean surface temperatures generated by the first 8 years (2001–2008) of the climate model to obtain a present state climatology and for comparison with changes throughout the simulated century. We determined the maximum biogeographic distribution as the area having a positive annual maximum population growth (Fig. 5). The spatial distributions of population growth rate generally coincide with abundances from CPR surveys (cf. CPR Atlas, CPRS, 2004). In the present study *Pseudocalanus* (panel A1), apart from shallow coastal areas, has its highest population growth in the Iceland region, on the northern European Shelf and at the Grand Banks area off Newfoundland. Estimated high abundances of *Pseudocalanus* in the deep ocean are not found in the CPR data. By contrast, population growth of *C. typicus* is strongly restricted to the shelf areas. The areas of high potential population growth rates of *C. typicus* on the US shelf coincide with CPR data, which show higher abundances in the warmer Middle Atlantic Bight compared to the northern areas (Fig. 6). Observed abundances in the Bay of Biscay off to  $30^{\circ}\text{W}$  are only represented in the coastal area by the potential population growth (Fig. 5, panel B1). A critical aspect is the representation of mortality. Using the temperature relation, mortality rates in the warmer southern part of the North Atlantic are generally high, which might not necessarily be right. So, how sensitive are the population growth rates towards the chosen parameter values?

The sensitivity of biogeographic boundaries to the parameter values is different between the two species (Fig. 5, panels 2–6).

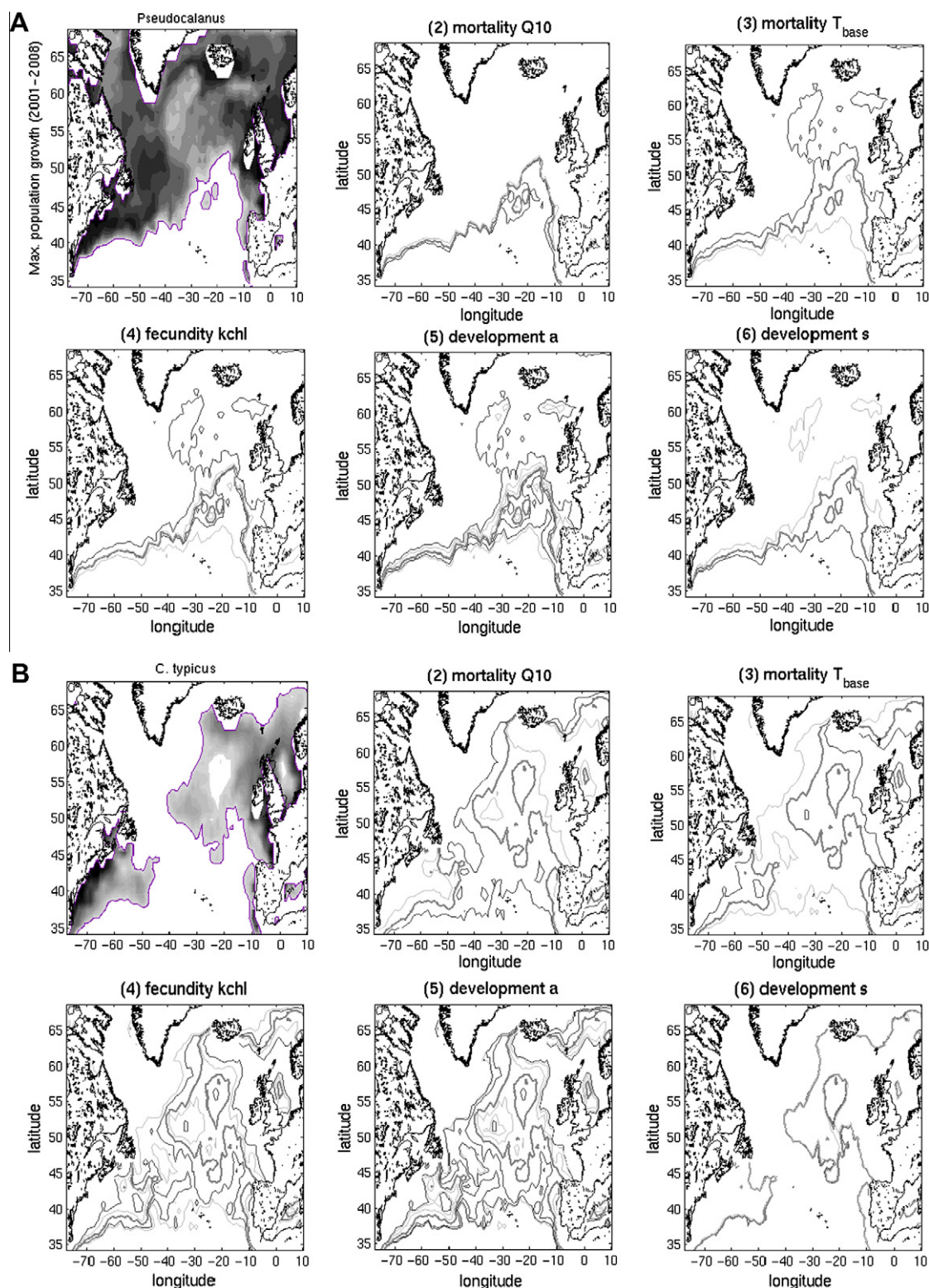
Population growth at an increase (thin black line) and decrease (thin grey line) of that parameter by 20% is given together with the base-line parameter values listed in Table 1 (thick line) as a reference. This analysis reveals that *Pseudocalanus* is not sensitive to the mortality Q10 or to the half-saturation constant for food-dependent fecundity, but it is affected by developmental parameters and the reference temperature in the mortality term. *Centropages typicus* is more sensitive to both mortality parameters but much less sensitive to the variation of food-dependent developments (Fig. 5, B6). This analysis shows the generally strong influence of temperature on various life cycle characteristics and thus on the growth potential in these species. Such a dependence on temperature was shown in other studies: For example, Beaugrand et al. (2007) found a strong correlation between the first principal component of *C. typicus* distribution and sea surface temperature. Similarly, Molinero et al. (2009) showed a latitudinal trend during seasonal maxima of *C. typicus* in the Mediterranean Sea corresponding to a temperature trend during the same season (their Fig. 7). The reference temperature – which increases the overall mortality – has the highest influence on seasonal extent. This result is in agreement with a study by Kiørboe (1997), who found that the demography of copepods is more influenced by variation in post-hatching mortality rather than fecundity. Generally, the warm water *C. typicus* is more sensitive to the parameter values than is *Pseudocalanus*. We found a similar result in tests with other warm and cold water related copepod species.

#### 3.2. Seasonal variation

A study on *C. typicus* abundance based on the CPR survey data was published by Beaugrand et al. (2007), who analyzed macroecological patterns of phenological parameters. The monthly distribution pattern shown there generally agrees with the annual cycle estimated by potential population growth in this study (Fig. 6).

In February *C. typicus* is hardly found in the North Atlantic Ocean in either study. The first increase appears in the Bay of Biscay in spring followed by an increase in the Celtic Sea and the North Sea. On the US Continental Shelf higher values of abundance and population growth appears later than in the eastern Atlantic Ocean, increasing in the southern part in summer, while the maximum in the Gulf of Maine region is found in fall, followed by a decrease until December. The maximum extent is not further than Newfoundland in both studies, and no population appears in the Labrador Sea.

However, some differences were found between the two studies: The increase in abundance in April/May in the Bay of Biscay is larger in the CPR data. This is probably due to differences in

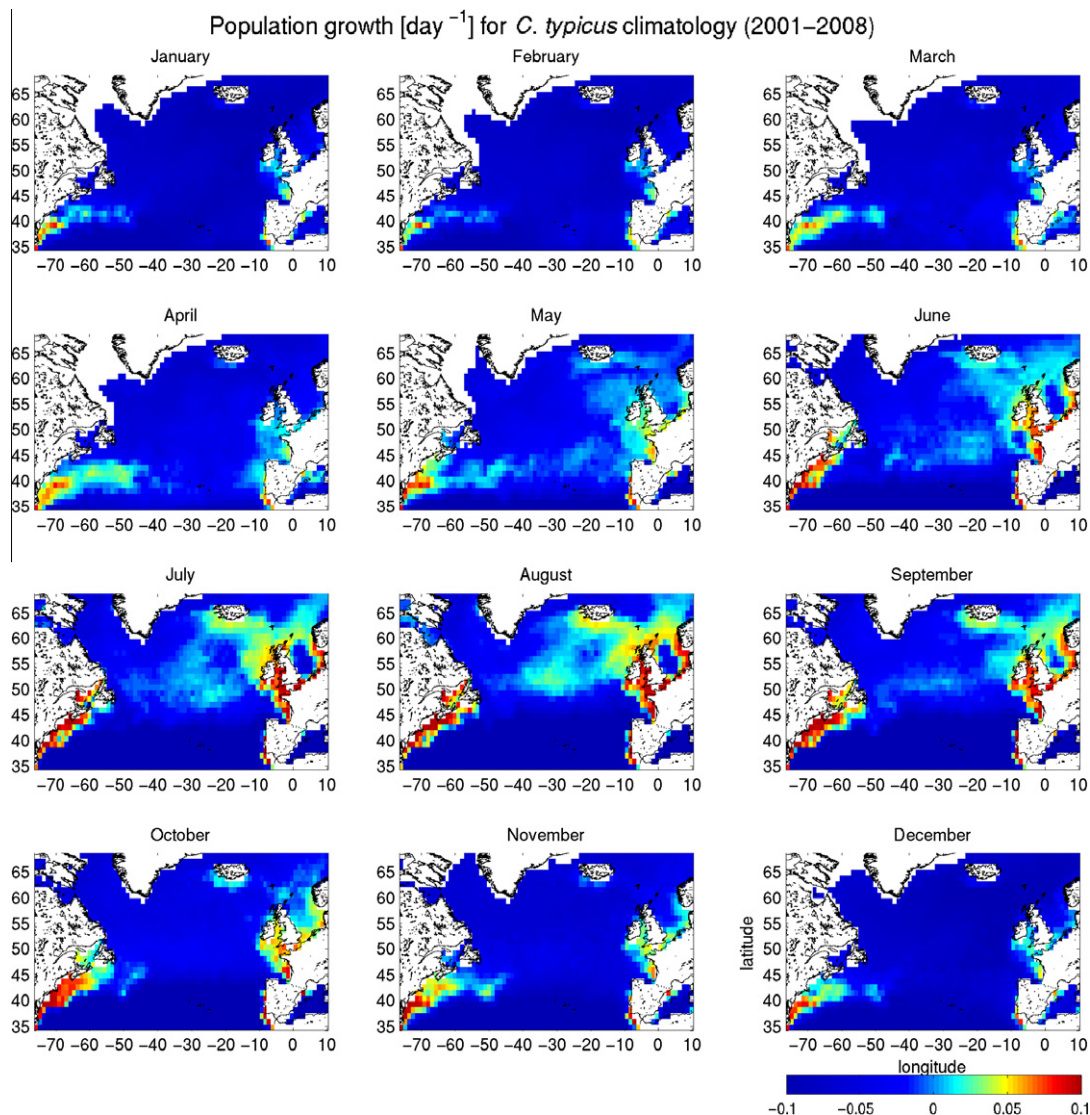


**Fig. 5.** The region where annual maximum population growth is greater than zero for *Pseudocalanus* (A) and *C. typicus* (B) using baseline parameter values (panel 1 in A and B). In other panels (2–6), the thick line is the distribution generated by the baseline values of the parameters, while the thin black and grey lines are distributions generated by parameter values 20% higher and lower than baseline, respectively.

the SeaWiFS chlorophyll (Fig. 2), which is lower in the open ocean than the Phytoplankton Color Index (PCI) from CPR surveys (cf. Fig. 8 in Beaugrand et al., 2007). On the northern US Continental Shelf, however, population growth starts to increase in April/May, while CPR data shows an abundance increase not until July.

In August abundances and population growth are high in the US and European Continental Shelf area, though this study shows an extent up to Iceland not present in CPR data. In November both studies shows reduced estimates on the European shelf, while values remain high in the Gulf of Maine region.





**Fig. 6.** Monthly distribution of population growth potential for *Centropages typicus* using climatological temperature (monthly mean values of 2001–2008 from the MIROC3.2 model).

There are possible reasons for the differences found especially in the Iceland region. One suggestion is that the mortality pressure on *Centropages* at lower temperatures is higher than in the present parameterization. Halsband-Lenk et al. (2002) presented mortality observations from two different ecosystems with a significant mortality increase below 5 °C in the North Sea and the Mediterranean Sea, which was not respected in the present study. A mortality increase in *Centropages* for temperatures below 10 °C would reduce population growth south of Iceland, but would not cause extinction in this regions, as conditions are favorable with high chlorophyll and 16 °C (close to estimated optimum temperature of 17 °C for *C. typicus*, after Beaugrand et al. (2007)). Another reason for the missing abundance can stem from increased predation pressure. Furthermore, the CPR data they used is for 1958–2002. Gislason et al. (2009) reported a temperature increase south of Iceland of ~1 °C from 1990 to 2007. Although no appearance of *C. typicus* is reported in this area in recent years, as shown below, it might be a suitable future habitat for this species.

### 3.3. Inter-species differences

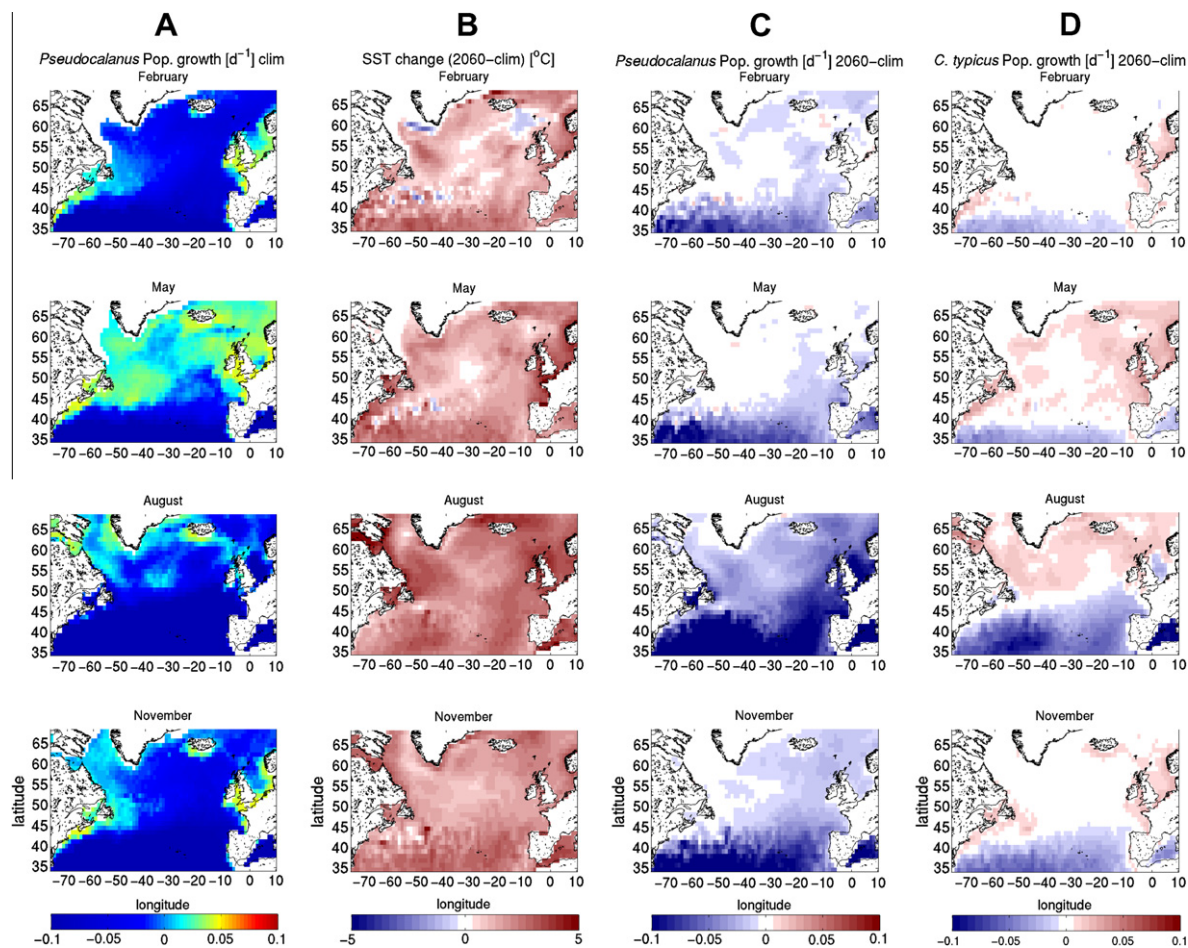
The difference in seasonality between the two species is reflected in their population growth. Opposed to the described summer/fall

increase of *C. typicus*, *Pseudocalanus* increases in February in the shallow shelf areas and has maximum growth and distribution in May (Fig. 7A). In the warm summer months, population growth declines in the European and US Continental Shelf areas and is restricted to latitudes >55°N, before a further fall increase on the shelves is found, which generally agrees with observed abundances.

The simulated spatial distribution of population growth varies with the predicted change in temperature until 2060 of about 1–2 °C in the open ocean and up to 4 °C in some shelf areas (Fig. 7B). The overall warming reduces the potential population growth of *Pseudocalanus* in most of the North Atlantic Ocean (Fig. 7C). The population growth is reduced in winter and spring by 0.01–0.05 d<sup>-1</sup> in large areas, particularly south of 45°N and west of the British Islands. For the warm water *Centropages* species, the increase in temperature can cause an increase in potential population growth at latitudes above 40°N in spring and fall, especially on the NW Atlantic shelf (Fig. 7D). Here, the temperatures increase from ca. 14 °C to 16–18 °C at which population growth is much higher. In summer the temperature south of 45°N and the southern North Sea increases to >24 °C, where population growth decreases at lower food levels (cf. Fig. 4).

The potential population growth of *Pseudocalanus* decreases compared to that of *C. typicus* in both areas with a remarkable





**Fig. 7.** (A) Population growth potential for *Pseudocalanus* for climatology (2001–2008). (B) Absolute change of SST (2060 – climatology). (C and D) Absolute difference of population growth potential ( $r_{2060} - r_{mean}$ ) between 2060 and the simulated climatology of 2001–2008.

decrease in the second half of the 21st century (Fig. 8). Furthermore, with the difference increasing towards *C. typicus*, the period of seasonal *C. typicus* dominance (in terms of population growth) extends in the Gulf of Maine from June–November in 2001 to nearly year-round by 2080. A similar change was found in the North Sea, where in October a shift was found around 2040 and in May by 2020. On the Nova Scotian Shelf and the English Channel, a shift was found for May (in 2075 and 2055) and November (by 2065 and 2045). The prediction for the Middle Atlantic Bight shows year-round higher population growth of *C. typicus* first in 2013 and mostly after 2058.

Spatially, the region with the same potential population growth for *Pseudocalanus* and *C. typicus* shifted northward during the 21st century (Fig. 9). In shelf areas, the increase in 2009 of *Pseudocalanus* is higher in May, coinciding with the spring bloom, while *C. typicus* had higher rates in summer. The transition area was along the 43°N latitude in May and 47°N as well as with the 45°W in August. With predicted increasing temperature until 2060, the May transition area was found at 45°N and ~42°W in November.

## 4. Discussion

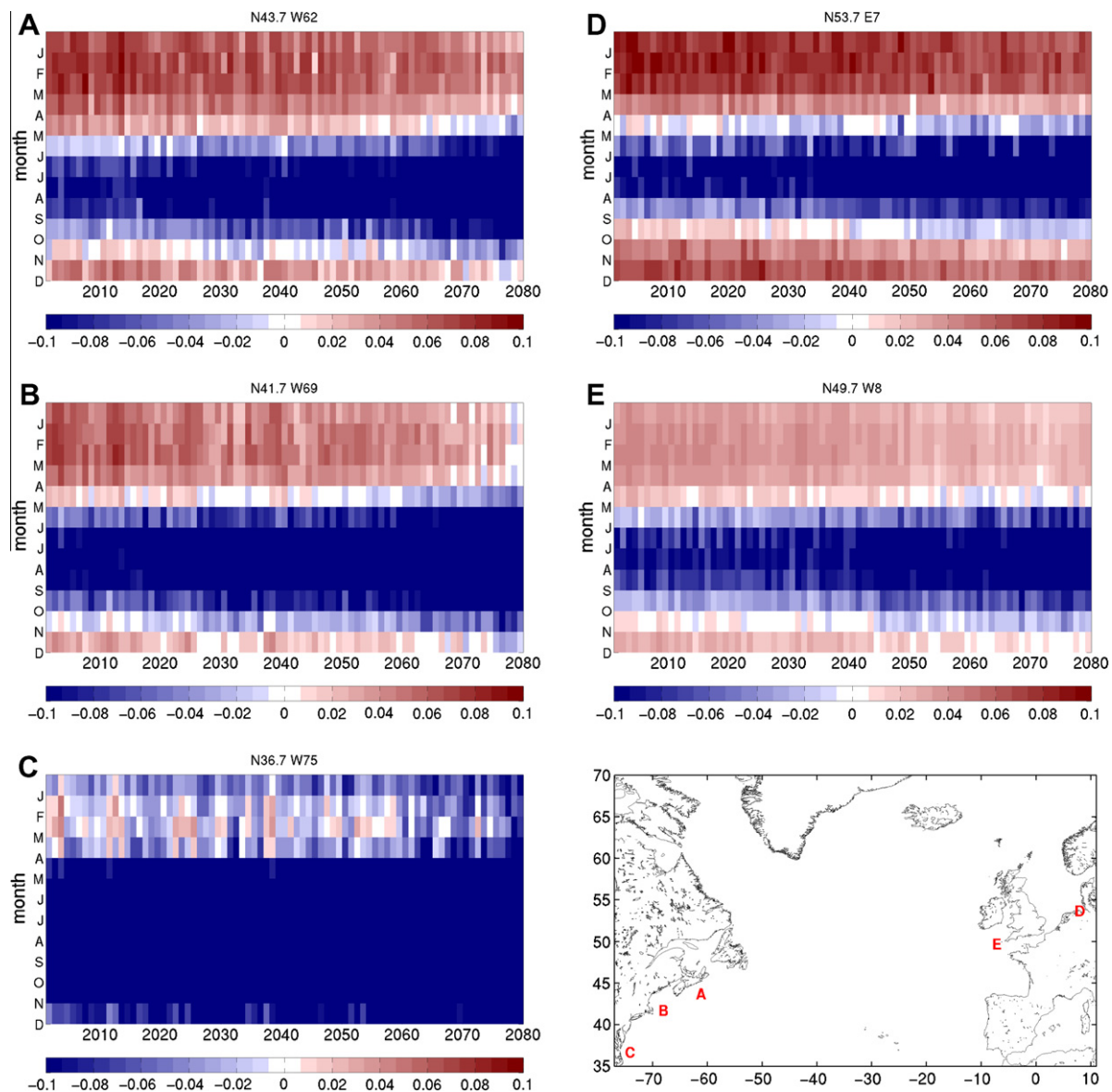
### 4.1. Ecological impact

In this study, the highest population growth potential was found in the continental shelf areas, whereas it is limited in the open ocean by food supply. A biogeographical boundary of a northern *Pseudocalanus* dominated area is distinguished from a *C.*

*typicus* dominated area in the southern part of the North Atlantic. Based on the climatology for 2001–2008 (present state) the transition zone is located in the south of the Gulf of Maine and the North Sea in May. With the increase in temperature, this boundary is predicted to shift northwards, so that population growth of *C. typicus* prevails in both ecosystems. This northward shift is driven by different physiological processes, which are influenced by the environmental change.

For *Pseudocalanus* the mortality was found to be the key process causing the population growth to decrease significantly for temperatures above 18 °C. For *C. typicus* mortality also increases with increasing temperatures, but not as much as for *Pseudocalanus* (cf. Fig. 3). Furthermore, *C. typicus* reproduction rate increases significantly until its critical value is reached at a temperature of 18 °C. The mean temperature in the Gulf of Maine in May is predicted to increase from ca. 14 °C to about 17 °C by 2060. The temperature range of 12–18 °C was found to be the most critical as population growth strongly changes in both species. In areas with this temperature regime, which is also found in the North Sea, an increase of 1–2 °C has a significant impact on the population growth potential and the shift towards *C. typicus* is strongest (Fig. 8). In colder (<7 °C) or warmer (>20 °C in summer) areas, the temperature increase has less impact on the difference in the species population growth potential.

These major changes especially taking place in the mid-latitude shelf areas as the Gulf of Maine and the North Sea are critical for the population dynamics of local fish populations, for which copepods are a major food source. It is reported, that *Pseudocalanus*



**Fig. 8.** Absolute difference of potential population growth of *Pseudocalanus* and *C. typicus* for five ecosystems (rPs-rCt, i.e. red indicates higher *Pseudocalanus* growth). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

is a preferred food item for juvenile fish like cod (Munk, 1997) and that it is a main prey item for North Sea herring, while only a small amount of *Centropages* was found in gut content observations (Voss et al., 2009). Examining the onset and seasonal extent of both species (as the first month and the number of months, when population growth is positive) in these shelf areas, we found that the onset of *Centropages* growth shifted from July towards May. The estimated seasonal extent of potential population growth in the North Sea is reduced for *Pseudocalanus* by 2–3 months, whereas the time of positive population growth increases for *Centropages*. This finding implies that the time of favorable food conditions for larval and juvenile fish will be shortened and the timing will become more critical.

In a study of impacts of climate change Drinkwater (2005) examined the response of North Atlantic cod on predicted future warming, as the fishes themselves are influenced by temperature. He predicted a stock increase around Newfoundland assuming a temperature increase of 2–3 °C. However, from the present study, *Pseudocalanus* will have reduced population growth in this area during summer and fall. This implies that, though the temperature

regime became physiologically more favorable for cod, the food availability will be reduced and supports the reported shift in spawning time at higher temperatures. For the North Sea and in the Gulf of Maine, Drinkwater (2005) further predicted a decrease and a potential collapse at a temperature increase of  $\geq 3$  °C. With the reduced prey concentration such a collapse is even more likely. As a response to the climatic induced shift in copepod distribution, a change in feeding behavior or in biogeographical boundaries of pelagic fishes is expected.

#### 4.2. Influence of food supply

The present study focused on the direct effect of ocean warming on copepod population growth potential through temperature related physiological processes. However, the temperature will also change other ecosystem variables like phytoplankton, which has a secondary influence on the food conditions of copepods. The potential influence of climate variables on primary production and on the chlorophyll concentration has been investigated recently. Henson et al. (2009) found that the spring bloom magnitude is

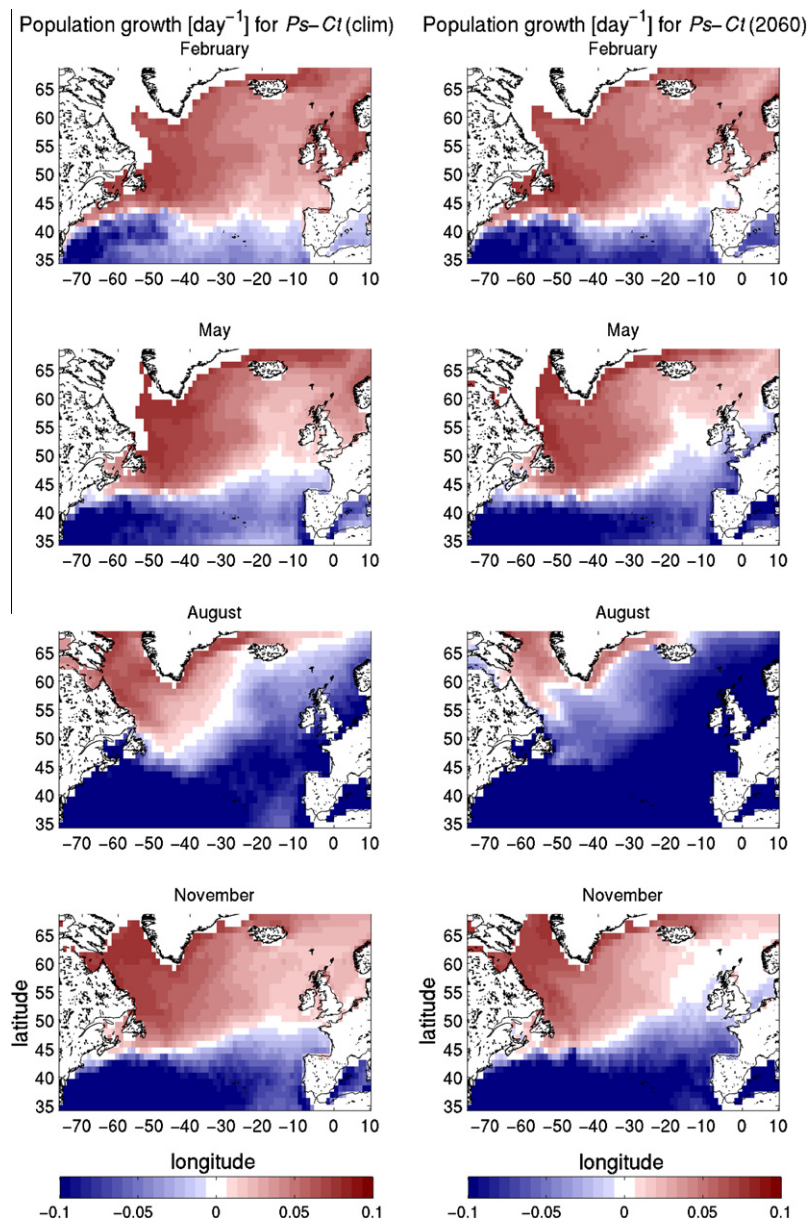
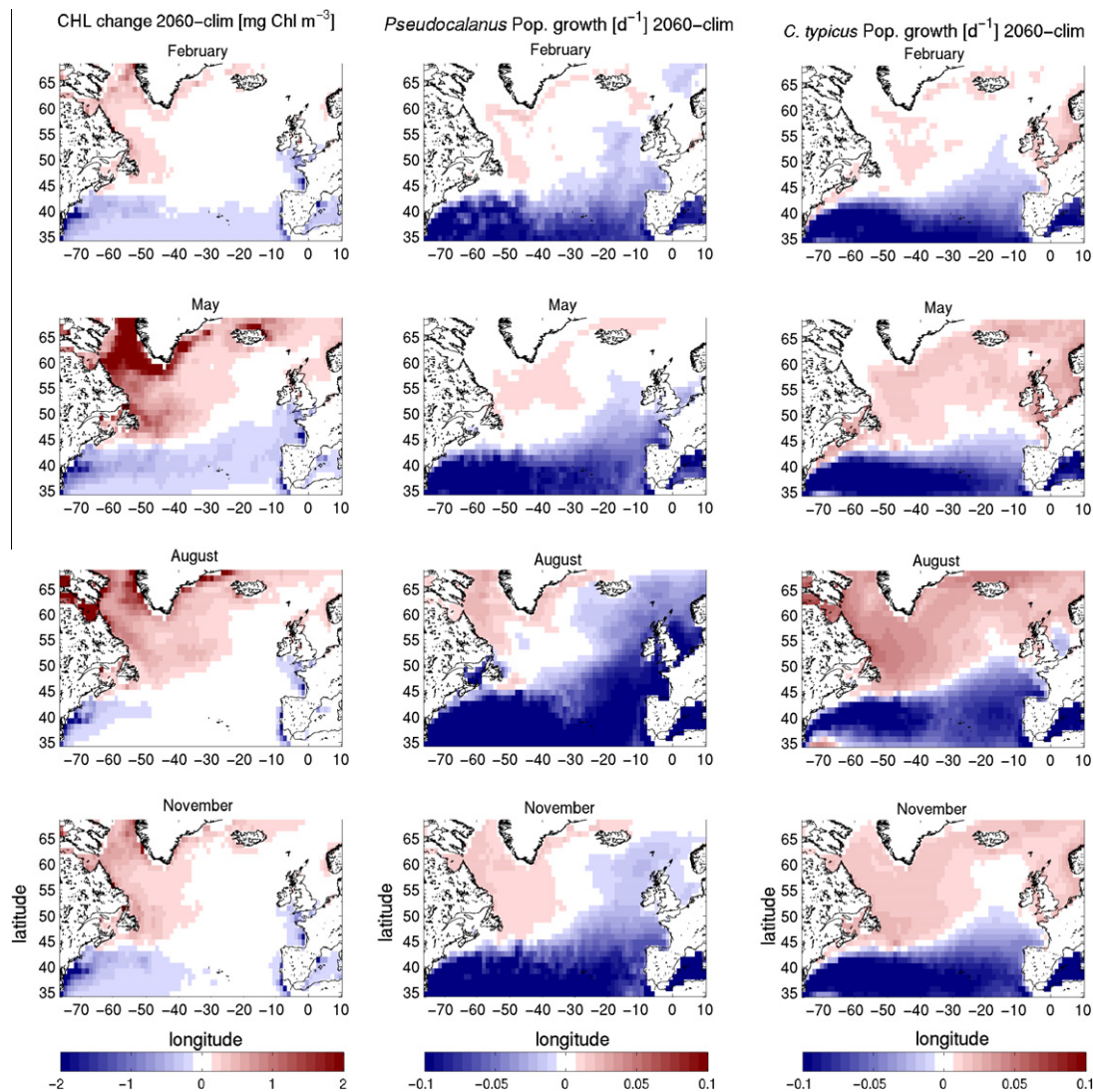


Fig. 9. Absolute difference of potential population growth of *Pseudocalanus* (Ps) to that of *Centropages typicus* (Ct) for 2009 and 2060.

related to the mixed layer depth (MLD), which in turn is correlated to the NAO (Hurrell and Deser, 2009). Gregg et al. (2005) reported an increase of global chlorophyll of 4% corresponding to an increase in SST since the early 1980s, which corresponds to  $\sim 1^\circ\text{C}$  following NCEP data from Fig. 2. Sarmiento et al. (2004) investigated the response of ocean ecosystems on climate warming using an empirical model. They found different responses in the world oceans. For the North Atlantic Ocean they predicted a general increase in chlorophyll. Behrenfeld et al. (2006) found an inverse relationship of SST and chlorophyll changes from satellite observations in the past decade for large areas of the world ocean. A more detailed relationship was observed by Richardson and Schoeman (2004) in their study in the northeastern Atlantic Ocean, where they found a positive relationship of SST and chlorophyll in cooler waters and a negative relationship in warmer regions, but no correlation at regions with annual mean SST of ca.  $12.5^\circ\text{C}$ . Stratification has a main influence, as it supports longer phytoplankton growth season in the upper nutrient-rich layer, while separating phytoplankton and nutrients in warmer already stratified areas.

To investigate the influence of temperature related changes in chlorophyll we used the findings of Richardson and Schoeman (2004) for a modified chlorophyll distribution. Depending on the annual mean of the 2001–2008 climatology we changed the chlorophyll concentration by 10% for each  $1^\circ\text{C}$  difference compared to  $13^\circ\text{C}$  with increase at lower temperatures and decrease in warmer waters (Fig. 10). As a result on potential population growth we found an increase in the Labrador Sea and the Irminger Sea for *Pseudocalanus*. As *C. typicus* is more affected by low food concentrations (Fig. 4) the change has a higher impact compared to *Pseudocalanus*. Population growth potential in the Bay of Biscay is now decreased opposed to the scenario without food change. Generally, the gradient of higher population growth in the north-western and lower in the south increased. This will support a stronger convergence of *Centropages* populations. For the US coastal ecosystems a decrease in food in summer/fall up to the Gulf of Maine will boost the competition among remaining species. The advantage towards *Centropages* in this ecosystem (Fig. 8) is more likely to be translated into trends in abundances. For the North





**Fig. 10.** (A) Assumed change in chlorophyll concentration (see text for detail). (B and C) Absolute difference in population growth potential of *Pseudocalanus* and *C. typicus* between 2060 and climatology of 2001–2008 ( $r_{2060} - r_{mean}$ ) at assumed change in chlorophyll concentration in 2060.

Sea the chlorophyll is not predicted to change. However, regional effects can have further influence on this forcing. In the Wadden Sea a decrease by up to 45% in summer chlorophyll concentration has been observed within a 25 year period as a response to reduced river nutrient influxes (van Beusekom, 2005).

An increased resolution can support a better representation of regional effects, like the influence of freshening, which has further influence on phytoplankton growth (Ji et al., 2007). Furthermore, including biological processes into models for ocean ecosystem predictions could help to get a better representation of the lower trophic dynamics and would enable a prediction for the food forcing of this study.

#### 4.3. A note on the material and methods

Generally, an increase in potential population growth results in higher abundances with the rate of change depending on the growth rate. This study was based on static forcing data and does not directly reflect advective processes, though advection of populations can be neglected on larger scales (Aksnes et al., 1997). It therefore shows an instantaneous response to the environmental conditions. In reality, there is a certain response time

towards environmental changes. Kiørboe (1997) determined the potential growth rates of phytoplankton depending on predation pressure and the time lag between the peaks of both groups. He reported a phase of one month or more between the abundance peaks of phytoplankton and copepods, which implies that the effect of high population growth may be visible in abundance the following month.

While simulations within the IPCC AR4 are in good agreement with respect to atmospheric variables (e.g. air temperature anomaly, IPCC, 2007), the results differ in terms of oceanic parameters, e.g. in sea ice transport (Sen Gupta et al., 2009), SST (Hollowed et al., 2009) and other hydrographic parameters (de Jong et al., 2009). With an predicted change in SST of 3–4 °C in 2060 (Fig. 7) and up to 6 °C in 2080 (Fig. 11) from the MIRO model a difference to observations of ~3 °C (Fig. 2) questions the validity of these findings. However, the model evaluations showed that all GCMs give similar results in terms of general trends, which include an increase in SST for the North Atlantic Ocean from all but one model at each location and a generally stronger warming in summer compared to winter (Fig. 11). Given the uncertainty, the present study cannot provide precise estimates but present the trends under predicted conditions. Given this, the shift from *Pseudocalanus* to

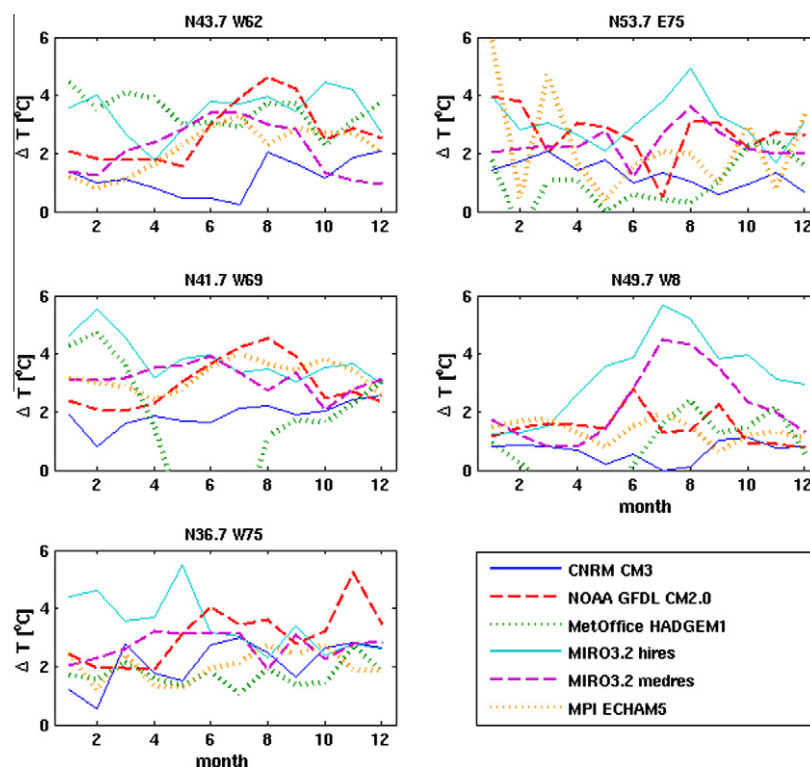


Fig. 11. Predicted change of SST at five locations (see Fig. 8 for a map) in the North Atlantic Ocean from six different coupled climate-ocean models.

*C. typicus* in mid-latitude shelf areas as the Gulf of Maine and the North Sea is supposed to happen, whereas more precise estimation of the forcing will help in better prediction of the timing.

## 5. Summary

This study of potential population growth shows a basin-scale distribution and temporal development of biogeographical boundaries in two copepod species with different seasonal cycles and life strategies. As the climate model predictions are updated, this empirical method can be used to obtain improved estimates of potential population shifts in copepod species.

We used climatological chlorophyll data from SeaWiFS and SST predictions from a global climate model simulation within the 4th Assessment Report of the IPCC for the 21st century. The simulation predicts a general increase in SST of about 3 °C in this time. This predicted warming of the North Atlantic Ocean causes shifts in the biogeographical boundaries in the copepod species. *Pseudocalanus* abundances are expected to decrease in temperate shelf areas like the Gulf of Maine and the North Sea while warmer water species like *Centropages* have the potential to increase in these shelf areas in growth and in the seasonal extent. Such a shift in species composition especially influences the food supply and recruitment success of local fish stocks.

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