

Physiology, Ecological Niches and Species Distribution

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ABSTRACT

Although many studies have debated the theoretical links between physiology, ecological niches and species distribution, few studies have provided evidence for a tight empirical coupling between these concepts at a macroecological scale. We used an ecophysiological model to assess the fundamental niche of a key-structural marine species. We found a close relationship between its fundamental and realized niche. The relationship remains constant at both biogeographical and decadal scales, showing that changes in environmental forcing propagate from the physiological to the macroecological level. A substantial shift in the spatial distribution is

detected in the North Atlantic and projections of range shift using IPCC scenarios suggest a poleward movement of the species of one degree of latitude per decade for the 21st century. The shift in the spatial distribution of this species reveals a pronounced alteration of polar pelagic ecosystems with likely implications for lower and upper trophic levels and some biogeochemical cycles.

Key words: fundamental niche; realized niche; physiology; spatial distribution; north Atlantic ocean; pelagic realm; *Calanus finmarchicus*.

INTRODUCTION

Biogeographical studies necessitate having a reasonable knowledge of the ecological niche, defined here as the range of tolerance of a species when several environmental factors are taken simultaneously (Hutchinson 1957). Hutchinson (1957) conceptualized this notion with the so-called **n**-dimensional hypervolume, in which **n** ideally corresponds to all the environmental factors. This concept is a powerful tool against which researchers can better assess potential effects of global change on species distribution (Beaugrand and Helaouët 2008). Indeed, the concept of ecological

niche has been extensively used to understand and model anthropogenic impacts such as the introduction of exotic species and pollution on species distribution (Peterson 2003). Determining the contribution of different environmental factors is achieved from knowledge of the distribution of species with field observations that can be related to environmental predictor variables (Guisan and Thuiller 2005). Different techniques exist, depending on species data, which can simply be presence data (for example, ecological niche factor analysis (Hirzel and others 2002)), presence–absence data (for example, generalized additive models (Hirzel and others 2006)) or abundance data based on field sampling (for example, all regression analyses (Legendre and Legendre 1998)). However, these techniques can only estimate the realized niche because they are based on observational data. Pulliam (2000) proposed a new type of model to explain and assess differences between fundamental

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and realized niches. As stated by Hutchinson (1957), his study indicates that the realized niche is smaller when factors reducing survival such as competition predominate. However, Pulliam (2000) also provided evidence that the realized niche can be greater than the fundamental one when dispersal is high.

The fundamental niche represents the response of all physiological processes of a species to the synergistic effects of environmental factors (Figure 1). Only optimal conditions generate high abundances and allow for successful reproduction. When the environment becomes less favorable, this affects consecutively the reproduction, growth and feeding (Figure 1). Extreme conditions become critical and may eventually affect survival (Schmidt-Nielsen 1990). Ideally, any study that attempts to predict the habitat of a species based on the knowledge of the environment should use both fundamental and realized niches. Past studies have largely focussed on the realized niche (for example, Hirzel and others 2002; Helaouët and Beaugrand 2007) whereas estimation of the fundamental niche has been neglected. However, comparison of both niches can provide important insights on biological mechanisms (for example, competition or predation) that structure a population.

Climate change affects the structure, the dynamics and the functioning of marine ecosystems through many physical and biological processes (Reid and Beaugrand 2002). Changes in the state of the climate system may also unbalance the location of boundaries between major biogeographical systems (Lomolino and others 2006). Key-structural species are useful for tracking such changes in ecosystem state and location. Understanding the spatial distribution of key-structural species has become an important issue in marine ecology (Helaouët and Beaugrand 2007). *Calanus finmarchicus* is a key-structural marine zooplankton copepod species in the North Atlantic Ocean and is among the most studied copepods in this area (for example, Heath and others 2000). This mainly herbivorous species plays an important role in transferring primary production to higher trophic levels in the food web (Mauchline 1998). Indeed, it has been suggested that the species is a key element for the larval survival of some commercially important fish species such as the Atlantic cod (Beaugrand and others 2003). The species also modulates the abundance of phytoplankton through changing grazing pressure (Carlotti and Radach 1996). Assessing future changes in the spatial distribution of the species is a prerequisite to anticipate ecosystem changes but should be based

on the joint assessment of the fundamental and the realized niches.

In this study, we assess both the fundamental and realized niches of *C. finmarchicus* and provide evidence for a close correspondence of the two niches at a macroecological level. The concomitant spatial changes seen in physiology and biogeography are constant at a decadal scale which makes it possible to propose projections of the spatial distribution of the copepod as a function of different scenarios of changes in temperature established by the Intergovernmental Panel on Climate Change W.G.I (2007). Our study shows that the temperature rise observed and projected by atmosphere-ocean general circulation models over the North Atlantic sector propagates from the physiological to macroecological level. Implications of the result for ecological niche modelling are discussed and potential consequences of the change in this key-structural species for ecosystem structure and functioning outlined.

MATERIALS AND METHODS

The area covered by this study extended from 99.5°W to 19.5°E of longitude and from 29.5°N to 69.5°N of latitude thereby covering all the North Atlantic Ocean and adjacent seas.

Biological and Environmental Data

Calanus finmarchicus

Data on the abundance of adult *Calanus finmarchicus* (copepodite CV and CVI) were provided by the Continuous Plankton Recorder (CPR) survey. The CPR survey is a large-scale plankton-monitoring program managed and maintained by the English laboratory of the Sir Alister Hardy Foundation for Ocean Science (SAHFOS) since 1990. The sampler is towed at a constant depth of 7 m (Reid and others 2003). Despite the near-surface sampling, the sampling gives a satisfactory picture of the epipelagic zone (Batten and others 2003). Water enters through an inlet aperture of 1.61 cm² and passes through a 270-µm silk filtering mesh (Batten and others 2003). Individuals greater than 2 mm such as adult copepodite stages CV and CVI of *C. finmarchicus* are then removed from both the filtering and covering silk. In general, all individuals are counted, however, in particularly dense samples, a sub-sample can be realized (Batten and others 2003). We created gridded data (from 99.5°W to 19.5°E of longitude and from 29.5°N to 69.5°N of latitude with a spatial resolution of 1° latitude × 1° longitude) averaging the abundance

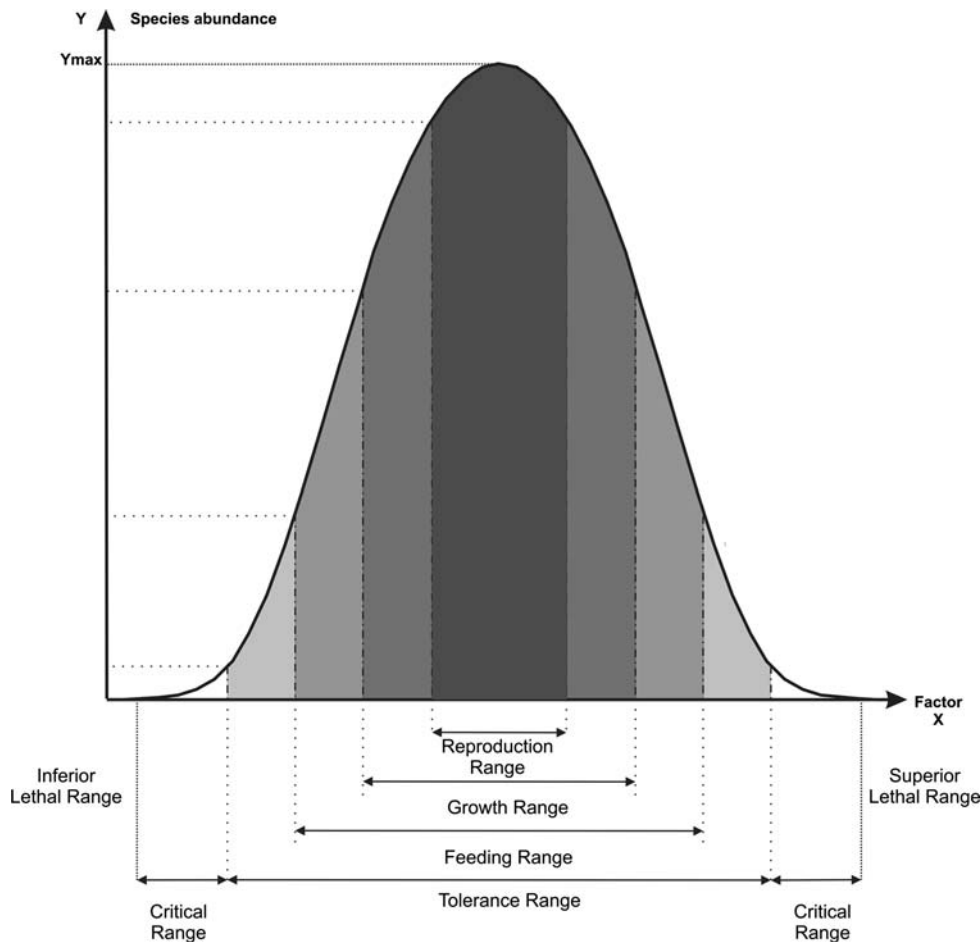


Figure 1. Response curve illustrating the effects of an environmental factor (X) on the species abundance (Y). Extremes values of X are lethal; less extreme values prevent feeding and then growth; only optimal conditions allow reproduction.

of *C. finmarchicus* for the whole sampling period 1960–2005. The climatology of the abundance of *C. finmarchicus* for each decade of the period 1960–2005 (1960s, 1970s, 1980s, 1990s) and for the most recent period 2000–2005 was based on interpolated data. Interpolation was made to maximize the number of values and thereby increase the quality of model comparison. Interpolation was realized using the inverse squared distance method (Lam 1983) with a search radius of 250 km (about 135 miles) using a technique adopted by Beaugrand and others (2001).

Sea Surface Temperature

Temperature (as Sea Surface Temperature) was selected as this parameter strongly influences the abundance and spatial distribution of marine ectotherms (Schmidt-Nielsen 1990; Mauchline 1998). Sea Surface Temperature (SST) data come from the Comprehensive Ocean-Atmosphere Data Set (COADS) and were downloaded from the internet site of the National Oceanographic Data Center (NODC), which manages acquisition, con-

trols quality and ensures the long-term safeguarding of the data (Woodruff and others 1987). To perform all the analyses, we created two different kinds of SST climatology with a spatial resolution of 1° of latitude and 1° of longitude. The first climatology was based on the averaging of 45 years (1960–2005), the second one was the result of the average of each decade for the period 1960–1999 (1960s, 1970s, 1980s, 1990s), and the most recent period 2000–2005.

In order to evaluate the potential impact of changes in SST on spatial distribution, data (1990–2100) from the ECHAM 4 (EC for European Centre and HAM for Hamburg) model were utilized. This Atmosphere-Ocean General Circulation Model (AO-GCM) has a horizontal resolution of 2.8° latitude and 2.8° of longitude (Roeckner and others 1996). The data in this study were selected by the Intergovernmental Panel on Climate Change W.G.I (2007) based on criteria among which are physical plausibility and consistency with global projections. Data are projections of monthly skin temperature equivalent above the sea to SST (<http://ipcc-ddc.cru.uea.ac.uk>). Data used here are modelled

data based on scenario A2 (concentration of carbon dioxide of 856 ppm by 2100) and B2 (concentration of carbon dioxide of 621 ppm by 2100) (Intergovernmental Panel on Climate Change W.G.I 2007). In scenario A2, the increase of CO₂ has a rate similar to current observed data (Intergovernmental Panel on Climate Change W.G.I 2007). The scenarios A2 and B2 are based on a world population of 15.1 and 10.4 billion people by 2100, respectively. A decadal mean was calculated for the 2050s and 2090s.

Chlorophyll a

Phytoplankton concentration is also an important parameter to explain changes in the spatial distribution and abundance of *C. finmarchicus*. Therefore chlorophyll a data were selected. These data originated from the program and satellite Sea-viewing Wide Field-of-view Sensor (SeaWiFS) from the National Aeronautics and Space Administration (NASA). Chlorophyll a data were converted into food concentrations (F) using equation (1) (Hirche and Kwasniewski 1997):

$$F_{t,s} = r \times C_{t,s} \quad (1)$$

with $F_{t,s}$ the food concentrations (in $\mu\text{g l}^{-1}$) at time t and location s and $C_{t,s}$ the quantity of chlorophyll a (in $\mu\text{g l}^{-1}$) at time t and location s using a carbon:chlorophyll ratio r of 40 (Hirche and Kwasniewski 1997). A climatology of food concentration was calculated, based on the period 1997–2005. This implicitly assumes that the period is representative of 1960–2005, which is, for the selected spatial scale, a reasonable assumption.

Bathymetry

The spatial distribution of *C. finmarchicus* in the area is influenced by bathymetry, the species being rarely detected when the water column becomes shallow (Helaouët and Beaugrand 2007). We used bathymetry data to restrict our calculations in areas deeper than 50 m. This threshold was fixed after examination of the spatial distribution of *C. finmarchicus* (Beaugrand 2004; Helaouët and Beaugrand 2007). Bathymetry data originated from the database General Bathymetric Chart of the Oceans (GEBCO).

Estimation of the Realized Niche

The realized niche was inferred from the calculation of the spatial distribution of adult *C. finmarchicus* (CV and CVI) for the whole sampling period, that is 1960–2005. As already mentioned in the

introduction, the realized niche represents the fundamental niche modified by factors, such as dispersal, which increase the width of the niche or factors, such as competition, which, on the contrary, tighten it.

Estimation of the Optimal Part of the Fundamental Niche

Many studies have revealed that reproduction is maximal when the species is at its optimal part of the fundamental niche (Hirche 1990). We used this physiological property as a proxy to determine the central part of the fundamental niche of *C. finmarchicus* (see Figure 1). When the optimal part of the fundamental niche is reached, the species must have its maximum abundance. Potential egg production rate (EPR) at time t and location s ($E_{t,s}$, in Eggs · female⁻¹ d⁻¹) was therefore calculated based on information on temperature and food concentration (Heath and others 2000):

$$E_{t,s} = p_1 (F_{t,s} - F_h)^{p_2} p_3 10^{\frac{p_4 - ((T_{t,s} - T_{opt}) p_5)^2}{100}} \quad (2)$$

with $T_{t,s}$ the sea surface temperature (in °C) at time t and location s and T_{opt} , the temperature optimum. The latter, which determines the maximum value of egg production, was taken from Heath and others (2000), which fixed its value at 6°C. $F_{t,s}$ is food concentration (in $\mu\text{g l}^{-1}$) at time t and location s (see equation (1)). Parameter F_h is the food concentration below which no egg production is expected. This parameter was fixed at 8 $\mu\text{g l}^{-1}$ by Richardson and others (1999). Other parameters from p_1 to p_5 were estimated by non-linear least square regression and were taken from Hirche and others (1997) ($p_1 = 6.2$; $p_2 = 0.48$; $p_3 = 0.14$; $p_4 = 60$; $p_5 = 1.9$). It is clear from equation (2) that this model is only valid in situations when $F_{t,s} \geq F_h$. Therefore, when food concentration was below 8 $\mu\text{g l}^{-1}$, the value of EPR was set to 0.

The possibility to use or forecast egg production of *C. finmarchicus* is limited by the difficulty in obtaining chlorophyll a data. Therefore, we simplified equation (2) by fixing food concentration ($F_{t,s}$) to its optimal value. The optimal value of the food concentration was fixed to 21.79 $\mu\text{g l}^{-1}$ which corresponds to 0.55 $\mu\text{g l}^{-1}$ of chlorophyll a. Over the time period, 62% of the geographical cells in which *C. finmarchicus* was detected (mean abundance > 1 individual) had values above 0.55 $\mu\text{g l}^{-1}$ of chlorophyll a. This percentage varies between 51.23% and 85.51% during the period from April to September which corresponds to the reproductive season of the species. The optimal value

($21.79 \mu\text{g l}^{-1}$) was determined by fitting equation (2) to potential EPR versus temperature (climatology based on the period 1960–2005). When $F_{t,s} = 21.79 \mu\text{g l}^{-1}$, equation (2) becomes:

$$E_{t,s} = 3.06 \times 10^{\frac{p_4 - ((T_{t,s} - T_{opt})/p_5)^2}{100}} \quad (3)$$

It should be noted that when EPR is used alone, it means more accurately potential EPR per female and per day. The use of this indicator is based on the fact that only optimal ecological conditions allow for optimal reproduction. High potential EPR can only occur in favorable ecological conditions (see Figure 1; Schmidt-Nielsen 1990). Less suitable conditions will rapidly affect reproduction rates and more specifically egg production rate.

Correlations

The Pearson coefficient of correlation was calculated to examine the relationship between the realized (spatial distribution of *C. finmarchicus*) and the optimal part of the fundamental niche (EPR) for different time periods (Figure 2). To evaluate the impact of spatial autocorrelation when correlation was calculated between maps, the minimum degree of freedom (called *nf*) needed to have a significant correlation ($P = 0.01$) and corresponding to the observed correlation value was assessed.

Procedures and Analyses

Figure 2 summarizes the different analyses performed in this study.

RESULTS

Analyses confirm that *C. finmarchicus* is a subarctic species, mostly abundant in the north of the Oceanic Polar Front (Dietrich 1964) (Figure 3A). Its realized niche shows an optimum range around 6°C but abundance remains high between 2.5 and 9.5°C . This optimum corresponds to the temperature where egg production rate, determined in laboratory experiments, is maximal (Hirche and others 1997). Spatial distribution of EPR closely matches the spatial distribution of the abundance ($r = 0.71$ for all marine regions and $r = 0.81$ for regions deeper than 50 m, Figure 3A and B, Table 1), confirming that the abundance of the species is proportional to its potential EPR. These results suggest a strong correspondence between physiology and the spatial distribution of the species.

The central part of the fundamental niche is narrower than the realized niche as it is inferred

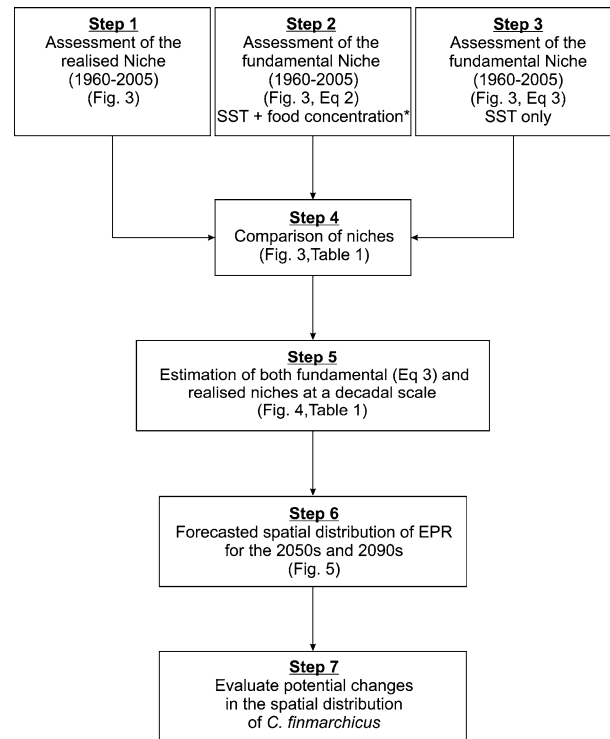


Figure 2. Sketch diagram summarizing the different steps and analyses performed in this study. * The climatology of food concentration is based on chlorophyll a data, only available for the period 1997–2005.

from EPR (Figure 3C and D). The adjustment of the model by non-linear least square fitting is best when food concentration ($F_{t,s}$ in equation (2)) is fixed to $21.79 \mu\text{g l}^{-1}$. This value allowed us to simplify equation (2) (see equation (3) in Materials and Methods). Correlation between the two ways of assessing EPR (from equation (2) and (3)) is high and ranges from $r = 0.89$ ($P < 0.001$, Table 1) when all marine regions are considered to $r = 0.93$ ($P < 0.001$) when only regions deeper than 50 m are included in the analysis. This result suggests that food concentration is not so limiting in the regions of interest, probably because chlorophyll covaries well with temperature ($r = -0.71$; $P < 0.001$; $n = 3148$; $nf = 19$). Such a simplified model, depending only upon temperature, is an advantage because good quality data on chlorophyll are restricted to years after 1997 and also because chlorophyll data assessed from biogeochemical models have large uncertainties.

At a decadal scale, the spatial distribution of the abundance of *C. finmarchicus* also closely corresponds to EPR (Figure 4). Correlations ranged from 0.62 in the 1960s to 0.82 in the 1980s (Table 1). It is interesting to note that correlations are fairly

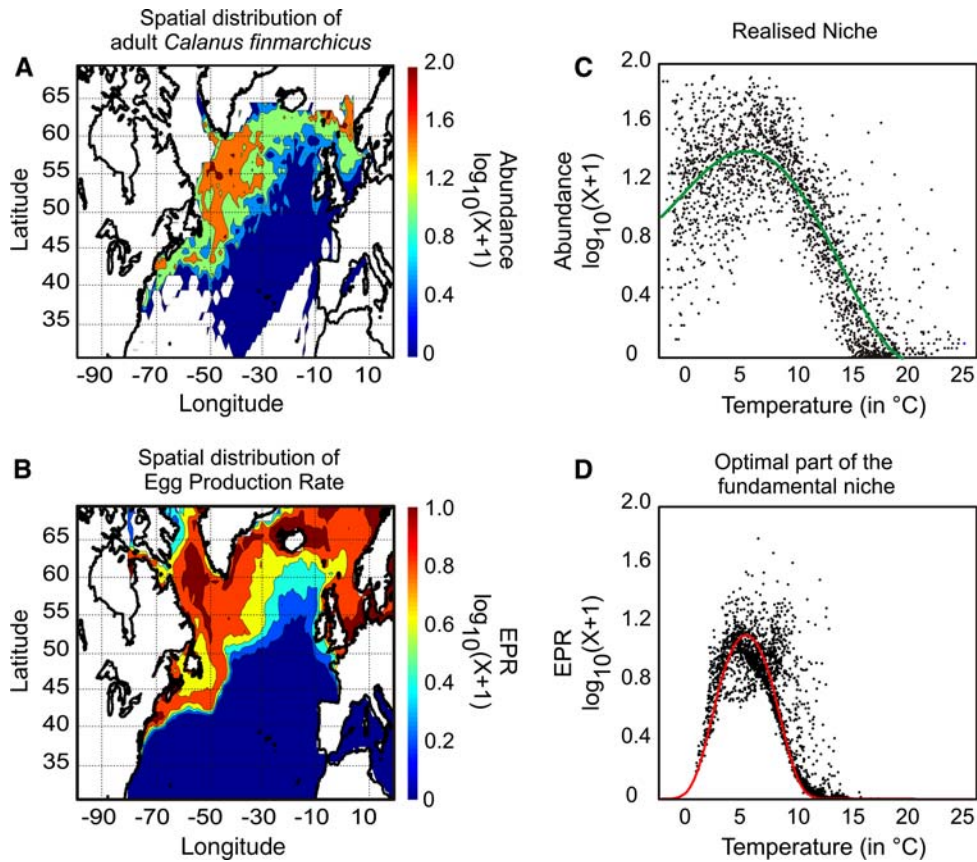


Figure 3. **A** Spatial distribution of *C. finmarchicus* for the period 1960–2005. **B** Spatial distribution of EPR calculated from equation (2) and using temperature data for the period 1960–2005 and a climatology of food concentration based on chlorophyll a data for the period 1997–2005. The reproduction potential is high in the whole North Sea although the species rarely occurs in the shallow part of this sea. **C** Abundance as a function of temperature (mean SST regime). Data are from Figure 3A. The **bold green line**, reflecting the realized niche was calculated from a polynomial regression of order 5. **D** Egg production rate (EPR) as a function of temperature. Data are from Figure 3b. The **bold red line** was calculated by adjusting $F_{t,s}$ in equation (2) as a function of data, using least square fitting.

Table 1. Relationships Between Fundamental and Realized Niches

| All regions | Correlation | Probability | Degree of freedom (n) | Degree of freedom (nf) |
|-------------------|-------------|-------------|-----------------------|------------------------|
| E/E* | 0.89 | <0.001 | 3144 | 10 |
| E/Ab | 0.71 | <0.001 | 1697 | 18 |
| E*/Ab | 0.79 | <0.001 | 1698 | 14 |
| Regions > 50 m | | | | |
| E/E* | 0.93 | <0.001 | 2757 | 8 |
| E/Ab | 0.81 | <0.001 | 1618 | 13 |
| E*/Ab | 0.82 | <0.001 | 1618 | 13 |
| Decadal analysis | | | | |
| E*/Ab (1960–1969) | 0.62 | <0.001 | 1567 | 25 |
| E*/Ab (1970–1979) | 0.74 | <0.001 | 1528 | 17 |
| E*/Ab (1980–1989) | 0.82 | <0.001 | 1227 | 13 |
| E*/Ab (1990–1999) | 0.79 | <0.001 | 1189 | 14 |
| E*/Ab (2000–2005) | 0.79 | <0.001 | 1358 | 14 |

Pearson correlation coefficients calculated between maps of EPR estimated from equation (2) (E) and equation (3) (E*), abundance (Ab) for the period 1960–2005 (see Figure 3) and at a decadal scale (see Figure 4). Abundance data were transformed ($\log_{10}(Ab + 1)$) prior to the calculation of correlation. ‘nf’ denotes the degree of freedom needed to have a significant correlation at $P = 0.01$. This was calculated to evaluate the strength of the correlation and to take into account that data are spatially autocorrelated. For example, when $nf = 10$ and $n = 3000$, this indicates that the correlation remains significant even when 10/3000 geographical pixels are kept (0.33% of the 3000 pixels).

constant (with no observed trend) and that EPR explains between 38.44% and 67.24% of the variation in the abundance of *C. finmarchicus*. A concomitant northwards movement of the species and EPR is observed in the north-eastern part of the North Atlantic Ocean after the 1980s (Figure 4). The reduction in the abundance of the species detected in the North Sea after 1990 is clearly explained by EPR. A reduction is also detected over the eastern Scotian Shelf.

The close correspondence in the spatial distribution of both abundance and EPR and thereby both fundamental and realized niches as well as the constancy of the correlation at the decadal scales together make it reasonable to use EPR as a proxy to forecast the spatial distribution of *C. finmarchicus*, utilizing a scenario of temperature changes from AO-GCMs (here ECHAM 4 data using the moderate scenarios A2 and B2). This way of forecasting the spatial distribution of the species is currently neglected and more emphasis is needed on the estimation of the likely distribution from the realized niche. Mapping of forecasted EPR for the 2050s and the 2090s shows a pronounced biogeographical change in the north-eastern part of the North Atlantic Ocean (Figure 5B and C). In the North Sea, the species could disappear at the end of the 21st century (Figure 5C). Changes are observed on the western side of the Atlantic. Although our analysis is limited in spatial resolution, a reduction in the abundance of *C. finmarchicus* is predicted over George Bank and Newfoundland.

DISCUSSION

This study provides compelling evidence, at a macroecological scale, that the spatial distribution of a species (here a marine pelagic species) is constrained by the influence of temperature on its physiology (for example, Huggett 2004). A close relationship has been found between the fundamental and the realized niche (that is, its optimal part) of *C. finmarchicus* which was evident when egg production rates and spatial distributions were mapped together at both bioclimatological and decadal scales (Figure 3 and 4, Table 1). Our results demonstrate that the species is generally present in regions where it can reproduce and that a high level of abundance is detected in places where reproduction is maximal. This correspondence between physiology and spatial distribution was expected from the ecological niche theory (for example, Leibold 1995; Guisan and Thuiller 2005; Begon and others 2006) illustrated in Figure 1 and some authors also stressed this relationship from

laboratory experiments (Parmesan 2005 and references therein).

The concept of the niche (sensu Hutchinson) is multidimensional. However, in this study, the emphasis was made on temperature, and the niche we assessed was mainly a thermal niche. The first reason for this is that Helaouet and Beaugrand (2007) showed that temperature was the main driver of the spatial distribution of *C. finmarchicus*. The parameter correlated well with other factors such as oxygen and nutrient concentration and to a lesser extent chlorophyll concentration. Therefore, temperature can be considered as a good proxy for other factors. The second reason is that temperature appears to be the most accessible parameter from Atmosphere-Ocean general circulation models. Our analysis showed that removing chlorophyll from the ecophysiological model did not alter the results (see Figure 4 and 5). A second parameter, the bathymetry, was identified but its impact was much less important than temperature. Bathymetry correlated well with mixed layer depth and wind-induced turbulence. Bathymetry was considered, although indirectly, by removing data at a depth below 50 m.

An ecophysiological model, originally built upon data on *C. finmarchicus* in the northeastern part of the North Atlantic Ocean, was applied in this study. Its applicability at the scale of the North Atlantic Ocean appeared to be a valid assumption (see Figure 4). There is an ongoing debate on whether or not genetic differentiation exists among the population of *C. finmarchicus* (Bucklin and others 2000; Provan and others 2008). Recent results suggest that there is no genetic difference at the scale of the North Atlantic basin, which might allow the species to track changes in available habitat in the context of global warming.

Foundations of niche modelling are intimately linked to Hutchinson's fundamental and realized niche concepts, and most modellers subscribe to this framework (Guisan and Thuiller 2005; Araújo and Guisan 2006 and references therein). Despite this general agreement, some authors argue that ecological niche models based on observed data provide an approximation of the fundamental niche (for example, Soberon and Peterson 2005). Many others workers consider that niche models provide a spatial representation of the realized niche (for example, Guisan and Zimmermann 2000; Pearson and Dawson 2003). Chase and Leibold (2003) suggest dropping Hutchinson's concept and provided a major revision of the niche theory. They defined the niche as the environmental conditions that allow a species to keep the population

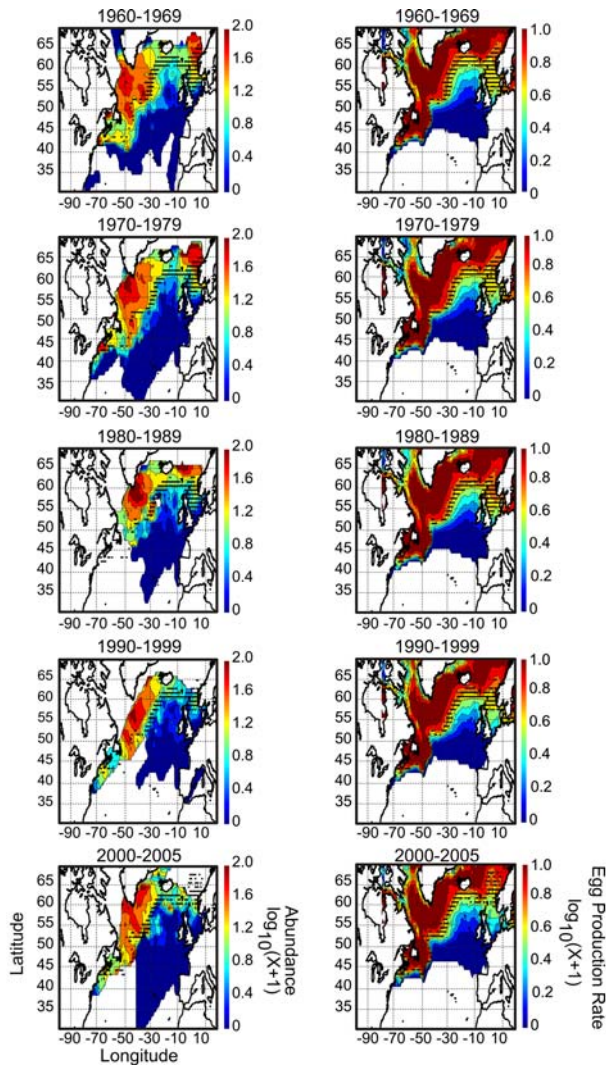


Figure 4. Decadal changes in the spatial distribution in the abundance of *C. finmarchicus* (in left) and egg production rate (in right). Abundances are extrapolated to improve the number of values and thus increase the quality of model comparison. The isotherm 9–10°C is represented by asterisks (Beaugrand and others 2008).

growth rate positive or null (besides both immigration and emigration). Our results suggest, however, that the combined use of both fundamental and realized niches enables a better understanding of the environmental conditions that allows the growth of the population (Chase and Leibold 2003).

Two hypotheses can be proposed to explain the tight coupling between egg production and abundance observed in this study. First, although dispersal is generally considered to be high in the pelagic realm (Longhurst 1998), hydrodynamical features might behave as a barrier and prevent

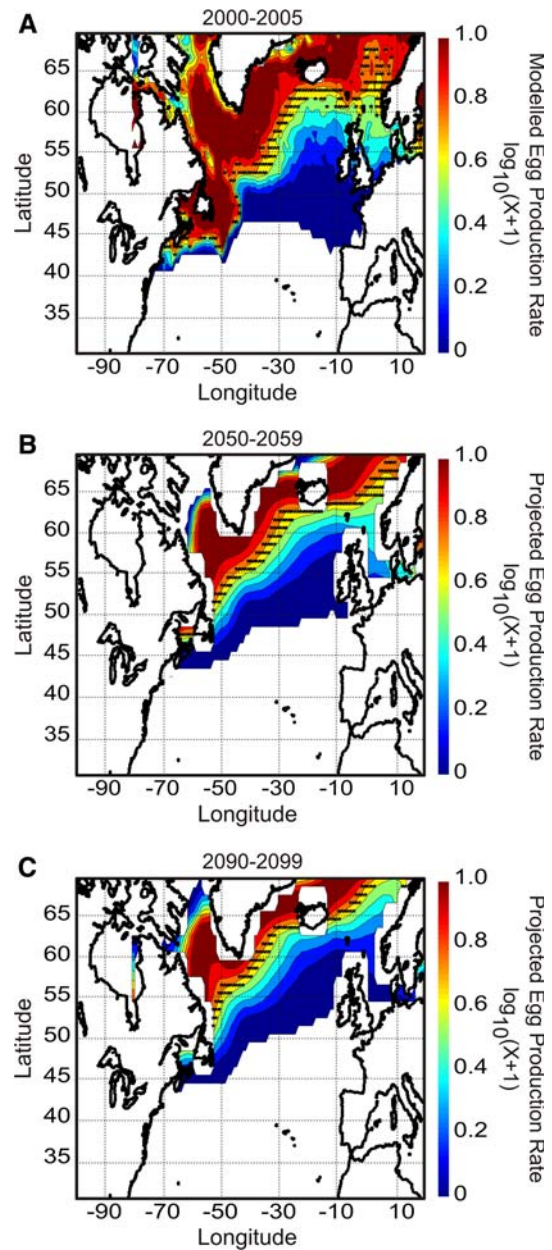


Figure 5. **A** Spatial distribution of EPR of *C. finmarchicus* based on observed SST data for the period 2000–2005. **B** Projected spatial distribution of EPR based on scenario A2 of SST change for the period 2050–2059. The EPR is used here as a proxy to evaluate future changes in spatial distribution of the abundance of *C. finmarchicus* with global climate change. **C** Projected spatial distribution of EPR based on scenario A2 of SST change for the period 2090–2099. Scenario B2, which gives very similar results, is not presented. The isotherm 9–10°C is represented by asterisks (Beaugrand and others 2008).

migration. Indeed, the spatial distribution of *C. finmarchicus* clearly matches the subpolar gyre and is limited by the Oceanic Polar Front (Dietrich

1964) and associated oceanic currents (Krauss 1986; Helaouët and Beaugrand 2007). Second, the link between egg production and spatial distribution may be explained by the fact that an expatriated population is unlikely to persist and therefore to be detectable at the scale of our study. Pulliam (2000) stressed that a population may persist as long as the immigration rate from source regions nearby is sufficient. Dispersion from source habitats (region where local reproduction exceeds mortality; Pulliam 1988) seems to be rapidly counteracted by mortality related to physiological stress, which might in turn be worsened by interspecific competition, parasitism and predation in sink habitats (regions where mortality exceeds local reproduction; Pulliam 1988).

Our results show that *C. finmarchicus* could be abundant in the North Sea as the model forecasts high reproductive potential. This paradox has already been noted by Heath and others (1999). The species is not observed throughout the year because it typically requires bathymetry greater than 500 m to overwinter in diapause (Hirche 1996). The North Sea is thought to be invaded each spring by adults from deeper oceanic regions (Heath and others 1999). Not only the magnitude of the spring invasion has been reduced due to a warming of the Norwegian Sea Deep Water (Heath and others 1999), but our results also suggest that the potential for this remaining population to reproduce and grow during the season has been considerably reduced. Year-to-year changes between the abundance of *C. finmarchicus* and the modelled egg production rate in this region are highly correlated ($r = 0.66$, $P < 0.001$, 45 years). The parallelism between decadal changes in both egg production and abundance (see Figure 4) indicates that a reduction of offspring quickly propagates to the level of species population. The concomitant changes between level of abundance and egg production rate suggests that an approach based on physiological rule combined with biogeographical information enables better projections of change in spatial distribution to be made (Parmesan 2005). Overall, we found a very close link between abundance and potential EPR. However, at a regional scale, local hydrodynamics such as the volume of Norwegian Sea Deep Water and its influence on spring invasion (Heath and others 2000) on the eastern side of the North Atlantic or the state of the NAO, and its impact on the Labrador Sea Water may have a strong influence (Greene and others 2003).

Modelled sea surface temperature (SST) data from the ocean-atmosphere general circulation model (ECHAM4 scenarios A2 and B2) and ob-

served sea surface temperature (COADS) data are highly positively correlated in the area covered by this study, showing that we can be confident in the use of the two scenarios of changes in SST for our projection of spatial patterns in egg production rate (Beaugrand and others 2008). Modelled changes in the egg production rate for the period 2050–2059 and 2090–2099 show a substantial poleward movement of the species of about one degree of latitude per decade (Figure 5). Regions characterized by high abundance and high reproduction rates, observed (Figure 4) or modelled (Figure 5), are just below the isotherm 9–10°C. This isotherm represents a biogeographical boundary between the Atlantic Arctic and Atlantic Westerly Winds Biome (*sensu* Longhurst 1998) (Beaugrand and others 2008). Beaugrand and others (2008) linked a change in the location of this boundary to an abrupt ecosystem shift affecting the food web from phytoplankton to zooplankton to fish. As a key structural species (Planque and Batten 2000; Speirs and others 2004), *C. finmarchicus* is one of the most abundant copepods in subarctic waters of the North Atlantic Ocean (Conover 1988). This species transfers energy from phytoplankton to upper trophic levels (Mauchline 1998) and represents a key-prey for at least some stages of exploited fish (for example, cod (Sundby 2000)). Its biogeographical movement might therefore reveal major ecosystem changes that will propagate northwards if climate warming continues (Intergovernmental Panel on Climate Change W.G.I 2007). The expected changes in the abundance of the species might impact the trophodynamics of pelagic ecosystems, altering predator–prey relationships (Cushing 1997) and some biogeochemical cycles (Beaugrand 2009).

The current knowledge of the spatial distribution of species up to now is limited in the pelagic realm, which covers 71% of the earth surface. With the establishment of a link between physiology, ecological niches and species distribution, our study opens a new avenue for predicting the potential response of species and ecosystems to global climate change. Further investigations of regions and species, for which information on physiology and distributional patterns are known, would make it possible to generalize this link to other realms. Such a validation might bring new empirical evidence to the ongoing debate on the redefinition of the fundamental and realized niches (Araújo and Guisan 2006).

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