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Applying the concept of the ecological niche and a macroecological approach to understand how climate influences zooplankton: Advantages, assumptions, limitations and requirements

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ABSTRACT

Ecosystem effects of climate change have been detected in all components of the Earth System. In the marine biosphere, climate-change responses have caused large and well-documented biogeographical and phenological shifts, which have in turn altered local dominance hierarchies, and also the structure, diversity and functional linkages within regional marine ecosystems. There is an urgent need to improve both our knowledge of the global-scale effects of climate change on marine biodiversity and our capacity to project future impacts. But extrapolation of previously estimated changes to additional places and to future conditions is complicated by non-linear responses to environmental variables, and also by complexities of multivariate interaction that can lead to tipping-points. In this paper, we show how observations from widely-spaced locations can be combined to characterise the ecological niche of a species, and how the concept of the niche can be used to understand and project how climate-induced changes in temperatures will alter marine zooplankton both locally and globally. As an example to illustrate our view, we apply this framework to the relatively well-known copepod *Calanus finmarchicus*. Our results suggest that climate change will strongly affect the local abundance of this species in the North Atlantic Ocean by the end of this century. Predicted changes are large (e.g. increase by ±6–10-fold of the temporal changes in the abundance of *C. finmarchicus*) and vary as a function of the magnitude of warming and the local sign and steepness of the thermal niche. Substantial rates of change hold even under optimistic climatic scenarii. After reviewing the main limitations of the niche concept in bioclimatological research, we argue that the application of this concept in ecology and bioclimatology might nevertheless represent the best tool currently available to scientists to discern and anticipate the effect of global climate change on species and ecosystems. The framework we proposed forces us however to think globally and to develop a worldwide coordinated macroecological approach, that includes global monitoring, new mathematical tools of detection and new types of modeling.

1. Introduction

Multiple environmental parameters influence the productivity and distributions of individual marine species, and their grouping together as biocoenoses and ecosystems. Nutrients and light limit phytoplankton production (Behrenfeld, 2010). Both bathymetry and local spatial variability in bathymetry are key determinant of the marine pelagic biodiversity (Helaouët and Beaugrand, 2007). Dissolved oxygen must remain high enough to support respiration (Goberville et al., 2010; Pörtner, 2001). Mixed Layer Depth (MLD) is an important parameter for phytoplankton production and controls the spatial distribution of many plankton species (Longhurst, 2007; Sverdrup, 1953). Oceanic pH influences calcifying organisms such as coccolithophorids, foraminifers, corals and pteropods (Kroeker et al., 2010; Orr et al., 2005). Wind intensity, affects prey-predator encounter rates (Rothschild and Osborn, 1988) by its effects on oceanic turbulence, and nutrient supply rates by its effects on vertical mixing (Longhurst, 2007). Wind direction, by its control of the distribution of some meroplankton species might strongly affect recruitment of some benthic

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organisms (Jolly et al., 2009). The above list is far from exhaustive, but shows the complexity of pathways and types of control that the environment might exert on organisms and biocoenoses.

However, temperature is perhaps the most broadly influential environmental factor because it controls all biological processes from the molecular to the cell and the organism levels (Brown et al., 2004). Temperature alters growth, reproduction, mortality, the behaviour of organisms at the species level and species interaction at the community level (Chapperon and Seuront, 2011; Kirby and Beaugrand, 2009; Schmidt-Nielsen, 1990). It also controls the effects of other environmental parameters on marine species (Pörtner and Knust, 2007; Rutherford et al., 1999). At a global scale, temperature patterns largely determine the location of biogeographic provinces and biomes and modulate the ecological services such as food production and carbon sequestration that marine ecosystems provide to humanity (Beaugrand et al., 2010; Sarmiento et al., 2004). It is therefore not surprising that many biogeographical studies have revealed a cardinal influence of temperature on marine biodiversity (Rombouts et al., 2009, 2010; Rutherford et al., 1999; Tittensor et al., 2010).

Ocean surface temperature, controlled by the climatic state of the atmosphere and the ocean, has varied greatly over the history of the planet. Global temperature decreased by about 60 °C over the full 4.5 Ba history of the Earth (Lineweaver and Schwartzman, 2004). Over the 540 Ma time scale of the Phanerozoic, global temperatures have fluctuated by about 10 °C (Royer et al., 2004). During the Pleistocene, and especially the last 800,000 years, temperatures varied between glacial maxima and interglacials by 13 °C over Antarctica, and by 4–5 °C for global mean temperature (Jouzel et al., 2007; Petit et al., 1999). In the last 2000 years, Northern Hemisphere temperatures varied in the range of 1 °C due to a combination of solar and volcanic forcing (Mann et al., 2009; Moberg et al., 2005). On a shorter time scales, temperature is also influenced by the meteo-oceanic oscillations (e.g. Pacific Decadal Oscillation, the El Niño Southern Oscillation), which might interact with global warming in nonlinear ways (Overland et al., 2010). Global temperatures have warmed by about 0.7 °C since the beginning of the instrumental record (Intergovernmental Panel on Climate Change, 2007). Marine organisms have therefore tolerated previous changes in temperature. However, projections indicate that global temperatures might increase very rapidly in the near future: between 1.1 and 6.4 °C by the end of this century. How might such a large and rapid climate change influence marine zooplankton populations? How can we realistically anticipate the effects of climate-induced changes in temperatures on species abundance both locally and globally?

In this paper, we propose to use the theoretical concept of the ecological niche (Hutchinson, 1957: 'the range of tolerance of species when several factors are taken simultaneously') in bioclimatological research, to anticipate how climate change affects marine organisms. After reviewing the limitations of the niche concept, we argue that it is probably nevertheless the best tool currently available to appraise the future effects of climate-induced temperature changes on zooplankton. We use the key-structural species *Calanus finmarchicus* as an example to establish these generalizations. Although some variability occurred in the past 100 years, our framework based on the concept of the ecological niche shows a 6–10-fold increase in the variability of populations of *C. finmarchicus* in the North Atlantic by the end of this century, the exact magnitude of this being dependent on the intensity of warming. We demonstrate how local studies can lead to misinterpretations by only examining part of the niche, and propose development and application of the macroecological approach in marine ecology to investigate the impact of climate on marine organisms and ecosystems and place the marine biosphere under the "macroscope" (Belgrano and Brown, 2002; de Rosnay, 1979).

2. Materials and methods

2.1. Environmental data

2.1.1. Annual sea surface temperature (1900–2010)

We obtain global surface temperature patterns for the past century from the ERSST_V3 dataset, which is a reanalysis on a 2° × 2° spatial grid of the most recently available International Comprehensive Ocean-Atmosphere Data Set (ICOADS) SST data. ERSST_V3 has used improved statistical methods to produce a stable monthly reconstruction from sparse data (Smith et al., 2008).

2.1.2. Annual sea surface salinity (climatology)

Annual Sea Surface Salinity (SSS, average values between 0 and 10 m) data was obtained from the Levitus's climatology (Levitus, 1982).

2.1.3. Bathymetry

Bathymetry data originated from a global ocean bathymetry map (1 degree longitude × 1 degree latitude) (Smith and Sandwell, 1997). The dataset originated from data obtained from ships with detailed gravity anomaly information provided by the satellite GEOSAT and ERS-1 (Smith and Sandwell, 1997).

2.1.4. Climatic scenarii for the end of this century

To estimate future ocean temperature patterns, we used model outputs corresponding to different global warming scenarii considered by the IPCC. These scenarii are based on socio-economic, technological and environmental projections for emissions of greenhouse gases and aerosols (described in detail in the Special Report on Emissions Scenarii (SRES)) and were used by IPCC to predict a potential range of global climate outcomes (Intergovernmental Panel on Climate Change, 2007). The scenarii are frequently classified as 'optimistic', 'most likely', and 'pessimistic'. The best estimates of outcome from 'optimistic' scenarii are for an end-of-21st-century increase of about 2 °C, the likely range being between 1 and ~4 °C (Intergovernmental Panel on Climate Change, 2007). For most 'pessimistic' scenarii, the best estimates ranged from ~3 to 4 °C and the likely range is between ~2 and 6.4 °C. A worst-case scenario ($\Delta T = 6.4$ °C) places the Earth System in a state resembling the start of the Paleocene–Eocene Thermal Maximum (PETM; 55 million year ago; $[CO_2] = 1000$ ppm) (Zeebe et al., 2009). During the PETM, a CO_2 increase from 1000 to 1700 ppm over a few millennia was accompanied by an increase in SST ranging from 4–5 °C in the tropics to 8–10 °C in high latitudes (Zachos et al., 2003).

Under scenario A1B (thought to be the most likely emissions scenario), the most probable global temperature increase will be 2.8 °C, but the increase might be as large as 4.4 °C. The level of CO_2 concentration in Mauna Loa was 396.78 ppm in May 2012, a value estimated at the peak warming of the early Pliocene 4–5 million year ago when global temperature were about 4 °C warmer at equilibrium than preindustrial conditions (Pagani et al., 2009). Using planktonic foraminifera, these authors assessed the climatic sensitivity of climate system (i.e. the average global temperature response to a doubling of atmospheric CO_2 concentrations through radiative forcing and associated feedbacks) during this period and estimated it was 9.6 ± 1.4 °C per CO_2 doubling at equilibrium. It is therefore not unlikely that the magnitude of the warming during the 21st century might reach 4 °C or more. This is close to the total warming experienced by the planet between the LGM (Last Glacial Maximum, 20,000 years ago) and today. However, an important difference is the rate of warming: 4 °C in the next century, *versus* the LGM and the Holocene warming trend that was spread over more than 5000 years.

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For both SRES (Special Report on Emissions Scenarii) scenarii A1B and B1, we used the first run of the Hadley Centre Coupled Model, version 3 model (HadCM3; Hadley Centre Coupled Model, version 3) (Gordon et al., 2000). For the non-SRES scenario 1PTO4x (1% to quadruple), we used the first run of the Hadley Centre Global Environmental Model, version 1 (HadGEM1) (Johns et al., 2006).

2.1.5. Data on *Calanus finmarchicus*

Data on *Calanus finmarchicus*, originating from the Continuous Plankton Recorder (CPR) survey (Reid et al., 2003a), were utilised to test the theoretical ecological niche of the copepod. We did not base the assessment of the niche on CPR data but on expert knowledge. The CPR data was used to test the spatial distribution of the species assessed from the knowledge of its ecological niche.

2.2. The ecological niche sensu Hutchinson

2.2.1. The concept of the niche

All zooplankton species could have a pandemic distribution if they were not limited by the constraints of the environment affecting their physiology. This ecological fact is summarised by the Bejerinck's law, which posits that "*everything is everywhere, but the environment selects*" (Lomolino et al., 2006). This law is especially true for plankton and probably explains why they adjust very quickly their spatial distribution to changing climatic and environmental conditions (Helaouët and Beaugrand, 2009). Species with high dispersal capabilities is rapidly constrained by the effect of the environment on its physiology. When and where stress from the thermal environment is large, it is likely that a species' ability to overcome limitations on fitness from biotic components of the niche (e.g. predation and competition) is also impaired. Therefore, the species in average occurs in a region where environmental conditions are suitable for their existence and the sum of all (biotic and abiotic) conditions where the species occurs define its ecological niche (Hutchinson, 1957).

Different definitions of the ecological niche have been proposed (Chase and Leibold, 2003; Elton, 1927; Grinnell, 1917) and a full review of the concept is out of the scope of the present paper. However, the concept of the niche of Hutchinson (1957, 1978) is probably the definition of the niche that has been the most widely applied by ecologists. The Huchinsonian niche represents the combination of environmental tolerances and resources required by an organism. Hutchinson (1957) conceptualised this notion with the so-called n-dimensional hypervolume, in which n ideally corresponds to all environmental (biotic and abiotic) factors. This way to define the niche was considered to be revolutionary because it was operational, enabling a straightforward quantification of the niche of a species.

Subsequently, Hutchinson (1978) made the distinction between the fundamental and the realised niche. The fundamental niche represents the response of all physiological processes of a species to the synergistic effects of environmental factors in the absence of negative biotic interaction (e.g. competition, parasitism or predation) or dispersal. Although Hutchinson stated that the fundamental niche was larger than the realised niche, it is not true in all situations (Bruno et al., 2003; Pulliam, 1988). The realised niche, more frequently estimated in practice than the fundamental niche, integrates the effect of species interaction and dispersal. Plankton can be advected into regions where environmental conditions are not favourable (Pulliam, 2000), making it more difficult the determination of their niche. In this paper, we also use the term thermal niche, which is the part of the realised niche only represented by temperature (here SST).

2.2.2. Assumptions of the ecological niche when applied to zooplankton

Our assumption is that upper ocean temperature is a primary niche dimension for pelagic zooplankton. This assumption is particularly true for *C. finmarchicus*. Although the calanoid spends about half of the year in deep waters in diapause (Heath et al., 2004; Hirche, 1996), upper ocean temperature has been shown empirically to be a key proxy of the spatial distribution of the species (Helaouët and Beaugrand, 2009; Helaouët et al., 2011; Reygondeau and Beaugrand, 2011). Helaouët et al. (2011) found that annual SST explained the greatest proportion of the variance related to the annual spatial distribution of the copepod. Annual SST was negatively related to dissolved oxygen, nutrients and chlorophyll a, suggesting that annual SST is also a good proxy at this scale for these important factors. Helaouët et al. (2011) also identified other more secondary parameters such as bathymetry and sea surface salinity. Bathymetry is an explanatory variable important to model correctly the annual spatial distribution of species in some regions such as in the southern part of the North Sea (Reygondeau and Beaugrand, 2011). As a result, we estimated the ecological niche of *C. finmarchicus* as a function of annual SST, bathymetry and sea surface salinity.

Both food quality and quantity are obviously a key parameter for *C. finmarchicus*, as for most species living in the oceans (Frost, 1972; Helaouët and Beaugrand, 2009; Kleppel, 1993). However, indices of food quality or quantity mask the fact that copepod selects both the size of food particles and the type of species (Cowles et al., 1988; Frost, 1972; Wilson, 1973). The other problem is that, in general, such indices cannot be known with relative accuracy to establish future projections, because it is a composite index and therefore the product of many biotic and abiotic factors that interact and exhibit nonlinear dynamics. This level of complexity cannot be modeled with our current state of knowledge of the trophodynamics of pelagic ecosystems. Some authors argue that biotic interactions represent the stochastic component of the response of species to climate change whereas the use of the concept of niche *sensu* Hutchinson has a strong deterministic component (Beaugrand, 2012). Therefore, any attempt to include food concentration in the establishment of future projections may reduce the explanative power of the model and be counterproductive. In practice for *C. finmarchicus* at the scale of its spatial distribution, indices of food quality or quantity have a weak explanatory power on the species because food is rarely limiting during the period when the copepod is in the epipelagic zone (Reygondeau and Beaugrand, 2011). Indices often considered are chlorophyll a concentration estimated by satellite (Helaouët and Beaugrand, 2007), chlorophyll a estimated *in situ* (Heath et al., 2000) and other composite index of food quality and quantity such as the CPR-derived Phytoplankton Color Index (Helaouët and Beaugrand, 2009). The latter authors characterised the ecological niche of both *C. finmarchicus* and its congeneric species *Calanus helgolandicus* using annual SST and CPR-derived Phytoplankton Color Index. However, most of the variance was explained by annual SST.

The structure of the water column influences many biogeochemical processes and the spatial distribution of species (Bopp et al., 2005; Rutherford et al., 1999; Sarmiento and Gruber, 2006). It has an effect on the spatial distribution of plankton and on the life cycle of many pelagic organisms (Boyd, 1973). Reygondeau and Beaugrand (2010) found that the thermal stratification of the water column influence the spatial distribution of *C. finmarchicus*. The frequency of occurrence of this species tends to diminish when stratification augments, this effect being more pronounced for young copepodite stages. However, this parameter is unlikely to be more important than SST. Helaouët et al. (2011) found that mixed layer depth had a much lower effect than SST on the spatial distribution of adult *C. finmarchicus* in the North Atlantic Ocean.

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The ecological niche was based on bathymetry, mean salinity and annual SST. It did not incorporate any dimension reflecting oceanic transport. Advection can have a strong effect on zooplankton (Heath et al., 1999). The phenomenon could explain the underestimation that has been observed between modeled and observed abundance of *C. finmarchicus* in the North Sea (Reygondeau and Beaugrand, 2011) where populations of *C. finmarchicus* are seasonally transported from the Norwegian Sea Deep Water to the northern part of the North Sea (Bucklin et al., 2000; Heath et al., 1999). Despite the underestimation detected by Reygondeau and Beaugrand (2011) in the North Sea, the model explained well the pronounced decline in the abundance of *C. finmarchicus* observed in the North Sea during the 1980s (Reid et al., 2003b). The ecological niche concept has already been applied to *C. finmarchicus* and explained a large part of the variance of observed abundance of *C. finmarchicus* (Helaouët and Beaugrand, 2009; Helaouët et al., 2011), based on CPR data and more conventional sampling protocols (Reygondeau and Beaugrand, 2011). To conclude on this point, advection is likely to have a strong influence at a local scale but is not expected to substantially influence our estimations at a macroscale.

2.2.3. Estimation of the ecological niche of *C. finmarchicus*

As we said above, we took the example of the subarctic species *Calanus finmarchicus* for illustrating the usefulness of the approach of the ecological niche in bioclimatological research. We chose this copepod because the effect of the environment is relatively well-known (Heath et al., 2000; Helaouët and Beaugrand, 2007; Hirche and Kwasniewski, 1997; Reygondeau and Beaugrand, 2011). The ecological niche of the species was assessed using the Non-Parametric Probabilistic Ecological Niche (NPPEN) model (Beaugrand et al., 2011). The technique is based on the Generalised Mahalanobis distance and a simplified version of a non-parametric test called Multiple Response Permutation Procedure (MRPP). This numerical tool, not correlative, tests the potential of a given spatial environment to accommodate a species by comparison to a niche-space reference matrix (i.e. n-dimensional environmental matrix within which the species is present). The model NPPEN has been used on benthic organisms, zooplankton and fish (Beaugrand et al., 2011; Lenoir et al., 2011; Reygondeau and Beaugrand, 2011; Rombouts et al., 2012) and to characterise the state and the variability of coastal systems (Goberville et al., 2011a, 2011b).

In this study, the model NPPEN was applied on three physical variables: bathymetry, annual Sea Surface Salinity (SSS; as a proxy for the ecological effects of salinity stratification and impact on osmotic tolerance) and annual SST. However, only annual SST varied on a year-to-year basis. Annual SSS was mainly used as a controlling factor for the spatial distribution of species (Reygondeau and Beaugrand, 2011). It was therefore assumed that the probability of occurrence of *C. finmarchicus* was mainly determined by the effects of annual SST. Note however that many physical and chemical parameters covary with annual SST (Helaouët and Beaugrand, 2007). Both the lower and upper limits of bathymetry (8000–0 m), annual SSS (30–36 psu) and annual SST (0–12 °C) were fixed by the expert knowledge of the species (Helaouët and Beaugrand, 2007; Reygondeau and Beaugrand, 2011). These thresholds were used to model the ecological niche of *C. finmarchicus*. No CPR data were utilised to create the ecological niche of the copepod.

The CPR data were used to examine how closely the NPPEN model estimated the observed abundance of *C. finmarchicus* in the North Atlantic Ocean. The niche was represented by the probability of occurrence of the copepod as a function of the three parameters. The probability of occurrence was assumed to reflect the abundance of the calanoid copepod. This assumption was verified in the study thereafter.

2.3. Estimation of a baseline spatial distribution in the probability of occurrence of Calanus finmarchicus

Once the ecological niche is described in environmental variate space, we projected it onto geographical space (latitude and longitude) using observed spatial patterns of annual SST (1960–2010), annual SSS and bathymetry. The result provides a spatial map of the probability of occurrence of *C. finmarchicus* during the period 1960–2010. To test consistency with sparser field observations of *C. finmarchicus* distribution, we calculated the correlation between NPPEN-derived probability of occurrence and CPR estimates of average abundance calculated for the same period. The annual spatial distribution of *C. finmarchicus* was mapped using the procedure proposed by Beaugrand et al. (2000).

2.4. Estimation of long-term changes in the probability of occurrence of Calanus finmarchicus

From our knowledge of the 1960–2010 ecological niche of *C. finmarchicus*, we also estimated annual changes in the probability of occurrence of the species for the years 1960–2010. We then showed the theoretical relationships between expected changes in the probability of occurrence (1960–2010) and annual SST in six regions of the North Atlantic Ocean ranging from the southern edge (the Celtic Sea) to centre (the Subarctic Gyre) to northern edge (the Labrador Sea) of the spatial distribution of the species (Fig. 1): (1) western part of the English Channel; (2) southern part of the North Sea; (3) the northern part of the North Sea; (4) the centre of the Subarctic Gyre; (5) the north-western part of the Subarctic Gyre; (6) the northern edge of the Subarctic Gyre. This analysis illustrates how the local examination of the relationship between a zooplankton species and temperature (annual SST) can lead to misinterpretation when this local relationship is generalised in space or assumed to be constant in time.

2.5. Effect of climate-induced changes in annual SSTs on *C. finmarchicus*

In these analyses, the niche of *C. finmarchicus* was estimated using annual SSTs from the period 1960–1969, mean SSS and bathymetry. We then used the niche assessed from NPPEN (1960–1969) to explore the consequences of long-term changes in annual SSTs on the species based on the knowledge of past temperatures (Fig. 2) and the employment of climatic projections (Figs. 3–5). The niche was assumed to be constant for the whole period, an assumption that is based on the constancy of the niche of *C. finmarchicus* found for the period 1960–2002 in Helaouët and Beaugrand (2007). Throughout the paper, we assume that a climate-induced change in annual SSTs has an effect on the probability of species occurrence that is inferred from the knowledge of the species niche.

2.6. Past climate-induced changes in annual SSTs

We looked for geographical cells (0.1° longitude × 0.1°latitude) of a lattice (35.5°N–80.5°N and 80.5°W–70.5°E) that corresponded to each thermal category (−2 °C to 24 °C by step of 0.5 °C) and the corresponding interval of probability of occurrence along the niche of *C. finmarchicus* (niche based on the decade 1960–1969; Fig. 2A). For all geographical cells that had a given thermal (i.e. SST) regime corresponding to the reference period (1960–1969) and each temperature category, we divided the distribution of values of annual SSTs into 10 groups with equal frequencies and calculated the first, the fifth (median) and ninth deciles. The first and ninth deciles are the values below which 10% and 90% of all values of annual SSTs lie, respectively. The median corresponds to the value below which

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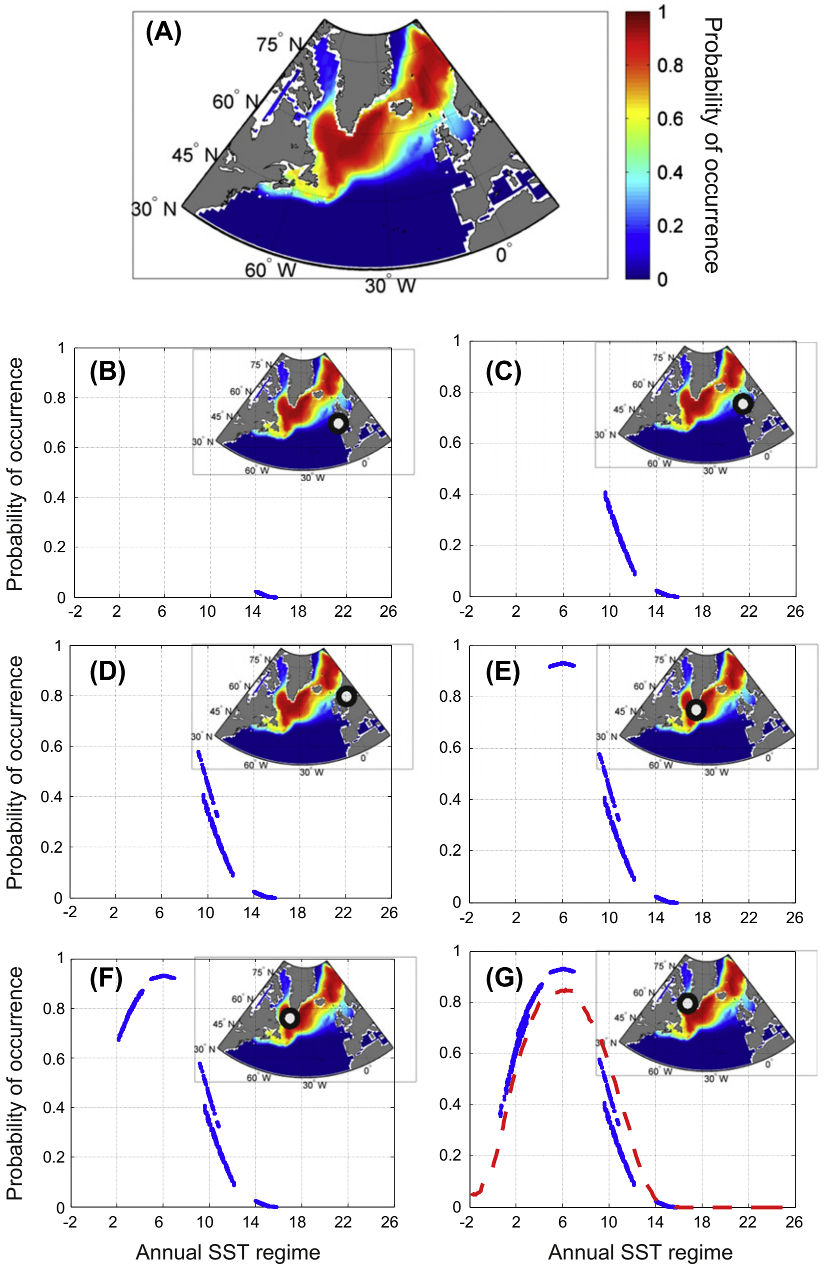

Fig. 1. Spatial distribution in the probability of occurrence of *Calanus finmarchicus* and potential influence of the climatic variability (1960–2010) on the species in different regions of the North Atlantic using the model NPPEN. (A) Modelled spatial distribution in the probability of occurrence of *C. finmarchicus* in the North Atlantic Ocean based on the period 1960–2010. (B–G) Potential long-term changes (1960–2010) in the probability of occurrence of *C. finmarchicus* as a function of annual SST in the western part of the English Channel (B). Data on long-term changes (1960–2010) in the probability of occurrence of *C. finmarchicus* are then progressively added for the southern part of the North Sea (C), the northern part of the North Sea (D), the centre of the Subarctic Gyre (E), the north-western part (F) and the edge (G) of the Subarctic Gyre. Each blue dot represents a probability of occurrence for a specific area and year (1960–2010). The circle on the maps indicates the area taken to calculate the average of the probability of occurrence of *C. finmarchicus*. The dashed red line shows the thermal niche of *C. finmarchicus* as assessed from the NPPEN model.

50% of all values of annual SSTs lie. The implications of climate-induced changes in annual SSTs for the probability of occurrence of the calanoid were assessed by reporting each decile (first and ninth deciles, median) of every category of annual SSTs on the ecological niche of *C. finmarchicus* (Fig. 2; see grey dashed arrows as an example). This analysis gives an estimation of the temporal and spatial variability in annual SSTs around the niche of *C. finmarchicus* and its effects on the probability of occurrence of *C. finmarchicus* using as a reference period the decade 1960–1969.

First, we performed this analysis for all years of the period 1960–1969 based on the decade 1960–1969. This analysis was conducted to provide a baseline (i.e. an estimation of the intra-decadal changes) against which the potential implications of changes in annual SSTs on the probability of occurrence of *C. finmarchicus* can be better interpreted for other decades (estimated and projected annual SSTs). We repeated the analysis for all years of the decades 1900–1909 (not shown but see Fig. 5B) and 2000–2009 (Fig. 3B) to evaluate the changes in annual SSTs and its potential effects on the probability of occurrence of *C. finmarchicus* for the decades 1900–1909 and 2000–2009 by using as a reference period the decade 1960–1969.

2.7. Projected future climate-induced changes in annual SSTs

We then compared the modeled description of the niche of *C. finmarchicus* (also based on annual SSTs for the decade

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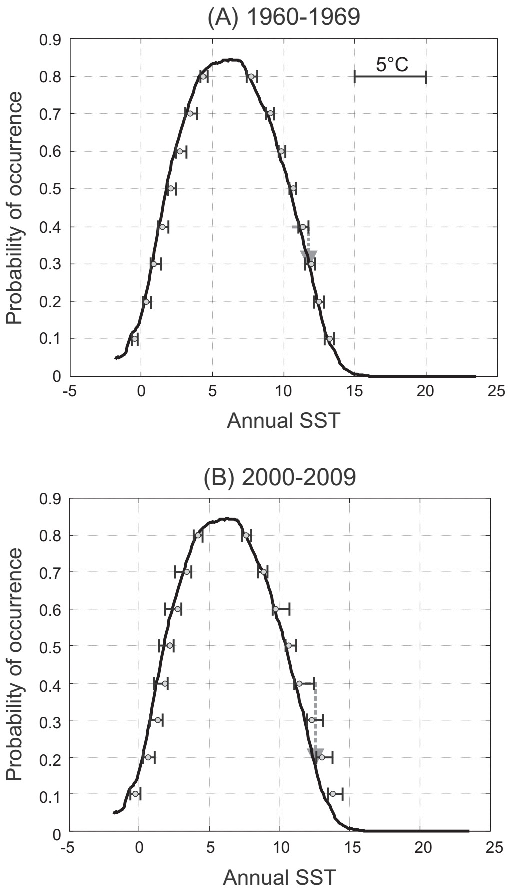

Fig. 2. Potential effect of climate change on the probability of occurrence of *C. finmarchicus*. (A) First (left vertical black bar), 5th (grey dot) and 9th (right vertical black bar) deciles showing the spatial variability in annual SSTs (1960–1969) along the niche of *C. finmarchicus*. The horizontal bar gives an estimation of the variability between the first and ninth decile. (B) First, 5th and 9th deciles showing the effect of climate-induce changes in annual SSTs (2000–2009) on *C. finmarchicus*. The dashed grey arrows show the implication of variability (A) or climate-induced changes in annual SSTs (B) on the probability of occurrence of *C. finmarchicus*. Probability of occurrence was determined theoretically by the model NPPEN (1960–1969).

1960–1969), with various scenarii/components of total temperature change to investigate the potential effects of climate change (decade 2090–2099) on this species, using a moderate scenario (SRES Scenario A1B) (Fig. 3) and both optimistic (B1) and pessimistic ($[CO_2] \times 4$) scenarii (Fig. 4). We repeated the procedure described in the previous paragraph, calculating the first, fifth (median) and ninth deciles of the annual SST changes expected in the area covered by the species for the period 2090–2099 (Figs. 3 and 4). As in the previous analyses, when the values of each decile are reported on the ecological niche of *C. finmarchicus* for every category of temperature, it enables us to evaluate the potential implications of climate change for the probability of occurrence of *C. finmarchicus*.

2.8. Quantification of long-term observed or expected changes in the probability of occurrence of C. finmarchicus

The preceding steps produced estimations of climate-induced changes in annual SSTs for the probability of occurrence of *C. finmarchicus* for the decades 1900–1909, 1960–1969, 2000–2009 and 2090–2099 (Scenarii A1B, B1, $[CO_2] \times 4$) along the 1960–1969 thermal niche of the copepod. We then calculated the implications of climate-induced changes in annual SSTs for the probability of occurrence of the calanoid for the four decades (observed and expected changes in annual SSTs) by calculating the difference between the probability corresponding to the median (1900–1909; 1960–1969; 2000–2009; 2090–2099; Sections 2.6 and 2.7) and the probability estimated from NPPEN (1960–1969). By performing this analysis, we show the implications of climate-induced changes in annual SSTs for the probability of occurrence of *C. finmarchicus* at the scale of the North Atlantic, taking as a reference for its niche the decade 1960–1969. We produced histograms that ranged from −0.6 to 0.6, which allowed us to assess the potential effects of climate change from the knowledge of the species niche (Fig. 5).

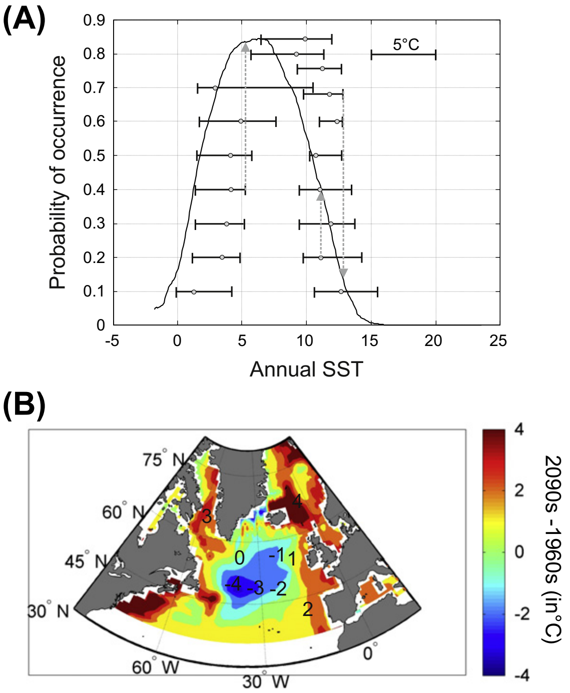

Fig. 3. Potential influence of global climate change and variability for the end of this century (2090–2099) under a moderate scenario (SRES Scenario A1B). (A) Thermal niche of *C. finmarchicus* based on annual SST (1960–1969) and temperature range observed at the end of this century (2090–2099) under a SRES scenario A1B for each category of annual SST (black horizontal lines). On each horizontal line, the point denotes the median, the left vertical line the first decile and the right vertical line the ninth decile. (B) Difference in annual SST between the 2090s (SRES Scenario A1B) and the 1960s (observed ERSST annual SST). The negative anomalies in the centre of the North Atlantic Ocean result from the slow-down of the Meridional Overturning Circulation (MOC). The dashed grey arrows show the implication of climate change on the probability of occurrence of *C. finmarchicus*.

3. Results

3.1. Assessment of the ecological niche of C. finmarchicus

How will climate-induced changes in temperature alter both local abundance and the spatial distribution of zooplankton? We use the concept of the niche (Hutchinson, 1957, 1978) and take the example of *C. finmarchicus* to answer to this question. Fig. 2A shows the present theoretical spatial distribution of *C. finmarchicus* in the North Atlantic Ocean, as modeled by NPPEN and based on expert knowledge (see Section 2). As expected, the probability of occurrence of *C. finmarchicus* is high north of the Oceanic Polar Front (OPF) (Dietrich, 1964) in the Subarctic Gyre, the Labrador Sea and in Nordic Seas. The probability of occurrence is intermediate south of Newfoundland and in Georges Bank. In the Celtic Sea and the southern part of the North Sea, the probability of occurrence is very low. The spatial pattern in the probability of

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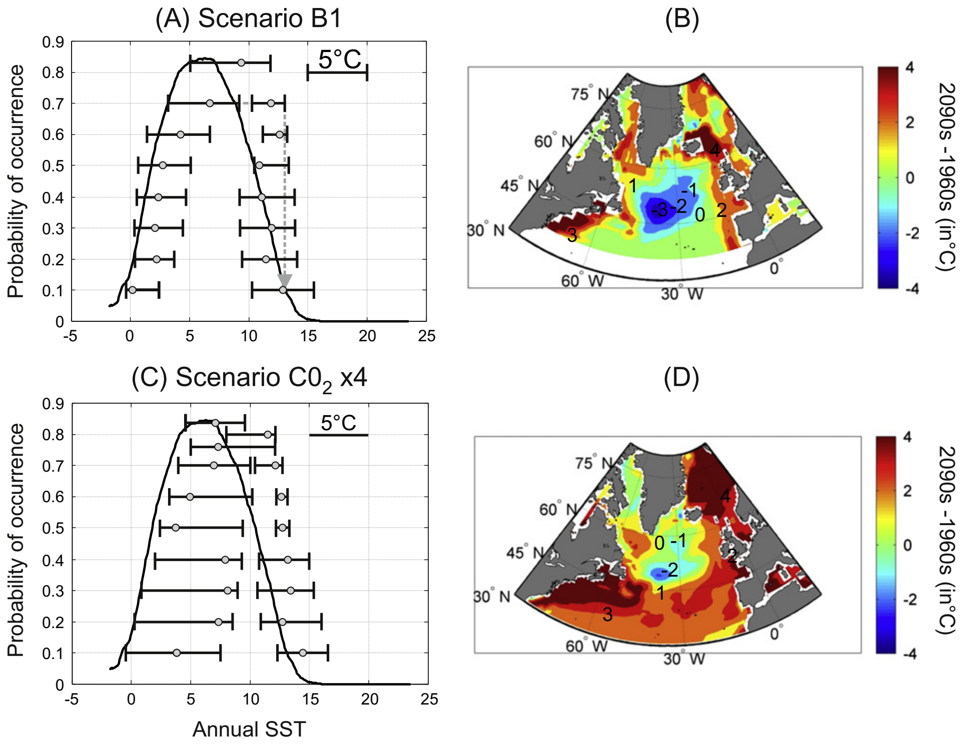

Fig. 4. Potential influence of global climate change and variability for the end of this century (2090–2099) under an optimistic scenario (SRES Scenario B1) and a pessimistic scenario ($CO_2 \times 4$). A. Thermal niche of *C. finmarchicus* based on annual SST (1960–1969) and temperature range observed at the end of this century (2090–2099) under a SRES scenario B1 (black horizontal lines). On each horizontal line, the point denotes the median, the left vertical line the first decile and the right vertical line the ninth decile. (B) Difference in annual SST between the 2090s (SRES Scenario B1) and the 1960s (observed ERSST annual SST). (C) Thermal niche of *C. finmarchicus* based on annual SST (1960–1969) and temperature range observed at the end of this century (2090–2099) under a scenario $CO_2 \times 4$ (black horizontal lines). On each horizontal line, the point denotes the median, the left vertical line the first decile and the right vertical line the ninth decile. (D) Difference in annual SST between the 2090s (Scenario $CO_2 \times 4$) and the 1960s (observed ERSST annual SST). The dashed grey line indicates that the probability of occurrence between the 1960s and the 2090s might experience a rapid reduction from 0.8 to 0.1 if changes in annual SST follows Scenario B1. The dashed grey arrows show the implication of climate change on the probability of occurrence of *C. finmarchicus*.

occurrence (1960–2010) was highly correlated positively with the mean abundance of the calanoid estimated from the CPR survey ($r = 0.82$, $p < 0.001$, $n = 1568$). To evaluate the risk of over-fitting due to spatial autocorrelation, the degrees of freedom were recalculated (n^*) to indicate the minimum number of samples needed to maintain a relationship significant at $p \leqslant 0.05$ (Beaugrand et al., 2008; Helaouët et al., 2011; Rombouts et al., 2009). The smaller n^*, the less likely the effect of spatial autocorrelation on the probability of significance. The correlation remained significant with $n^* = 4$ at a probability threshold $p \leqslant 0.05$, therefore when only six observations were kept. It is therefore unlikely that the significance of the correlation was exclusively due to the effect of spatial autocorrelation.

We used the ecological niche assessed from annual SST, annual SSS and bathymetry and projected the 3-dimensional niche into one dimension to obtain the thermal niche. We estimated from the knowledge of the thermal niche the year-to-year changes in the probability of occurrence of *C. finmarchicus* in different regions of the North Atlantic Ocean and its adjacent seas during the period 1960–2010. The thermal niche allows us to explore between-location differences in how a species may react to climate-induced changes in temperatures. For example in the Celtic Sea (Fig. 1B), any examination of the relationship between annual SST and abundance or biomass (here, the probability of occurrence; 1960–2010) of *C. finmarchicus* might conclude that the relationship is slightly negative, and well-approximated by a linear statistical analysis (although a nonlinear fit might be slightly better). However, neither the linear nor the nonlinear Celtic Sea equation assessed at this regional scale would describe correctly the response of *C. finmarchicus* in the southern part of the North Sea (Fig. 1C), where the negative relationships between the probability of occurrence of *C. finmarchicus* and annual SST becomes much stronger. In the northern part of the North Sea, the negative correlation remains elevated (Fig. 1D). In the core of the subarctic gyre however, annual temperature is near the optimum for *C. finmarchicus*, and the local correlation between probability of occurrence and temperature cancels off (Fig. 1E). Towards the northern part of the distributional range of the species, the relationship becomes positive (Fig. 1F and G). Only when all regions are considered together (the red dashed line), can we fully describe the thermal niche of the species and therefore the relationships between temperature and the probability of occurrence of the copepod (Fig. 1G). This analysis demonstrates both the usefulness of the niche concept and the necessity to adopt a macroecological approach to investigate the implications of global climate change on species in time and space. This macroscale relationship between the probability of occurrence of *C. finmarchicus* and SST has also been observed between the abundance of the copepod and SST and between modeled egg production rates and SST (Helaouët and Beaugrand, 2009), suggesting that our theoretical framework reflects actual patterns of changes .

3.2. Influence of climate change on C. finmarchicus

3.2.1. Past climate-induced changes in annual SSTs

Climate-induced changes in annual SSTs observed for all years of the decade 1960–1969 in the North Atlantic (black lines and grey circles) were superimposed on the niche of *C. finmarchicus* (Fig. 2A). The vertical line on the left side of each horizontal bar

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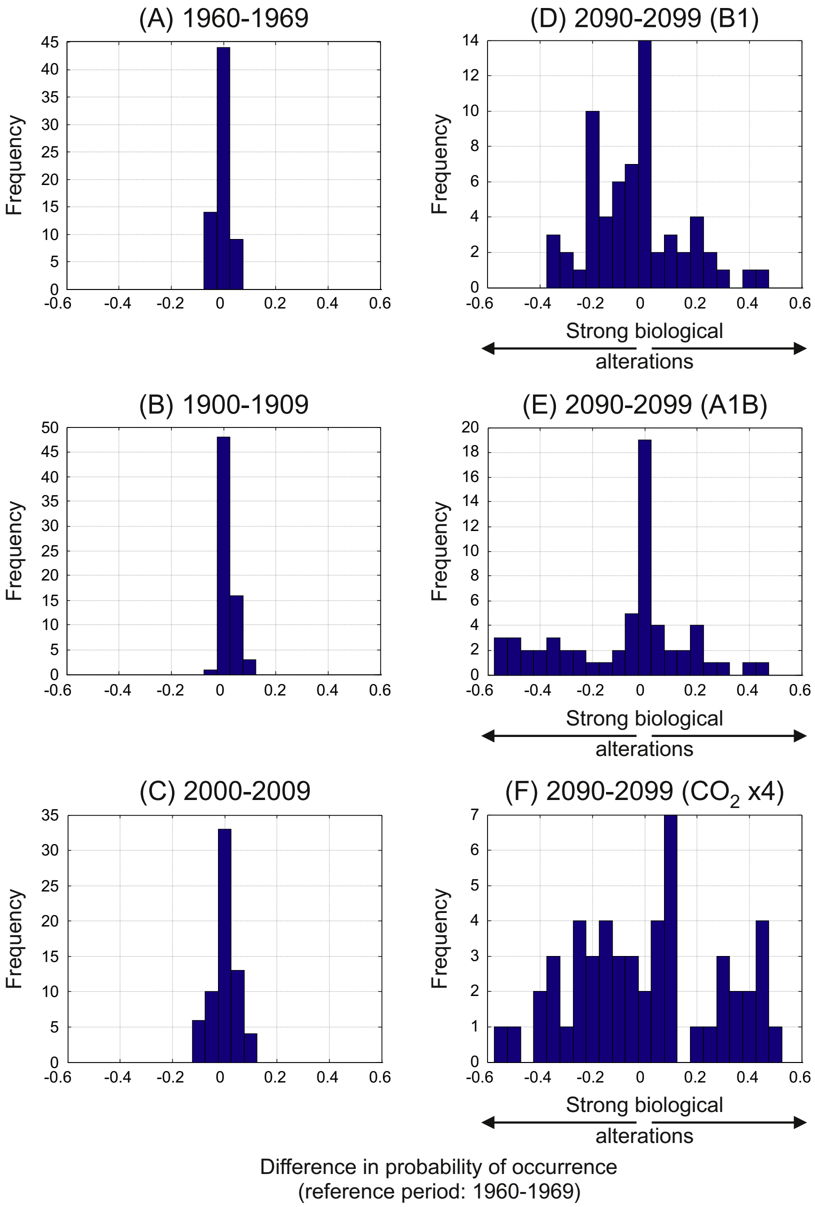

Fig. 5. Implications of climate-induced changes in annual SSTs for the probability of occurrence of *C. finmarchicus*. The niche of the calanoid was determined by NPPEN for the period 1960–1969 and by expert knowledge. The implications of climate-induced changes in annual SSTs for the probability of occurrence of the calanoid were assessed for the four decades (observed and expected changes in annual SSTs) by calculating the difference between the probability corresponding to the median (1900–1909; 1960–1969; 2000–2009; 2090–2099) and the probability estimated from NPPEN (1960–1969). (A) Histogram showing the effect of the spatial variability in annual SSTs for the probability of occurrence of *C. finmarchicus* during the period 1960–1969 (reference histogram). (B) Histogram showing the effect of climate-induced changes in annual SSTs for the probability of occurrence of *C. finmarchicus* during the period 1900–1909. (C) Period 2000–2009. (D) Period 2090–2099 (scenario B1). (E) Period 2090–2099 (scenario A1B). (F) Period 2090–2099 (scenario $CO_2 \times 4$). The median was chosen to calculate the difference in the probability of occurrence (see Section 2).

represents the first decile of the distribution of temperature values for all years of the decade under investigation (here 1960–1969) and all geographical cells having a thermal (i.e. SST) regime that corresponded to the interval of annual SST and corresponding probabilities of occurrence of a given section of the niche of *C. finmarchicus* estimated from the reference decade 1960–1969; the circle represents the median and the vertical line on the right the 9th decile; the length of the horizontal line represents an estimation of the amplitude of changes in annual SSTs for the corresponding years (here 1960–1969) and geographical cells that used to have a thermal (i.e. SST) regime corresponding to the period of reference (1960–1969). The median of the differences in mean annual SSTs between the first (left vertical lines in Fig. 2A) and the ninth decile (right vertical lines in Fig. 2A) along the niche are equal to 0.55 °C with a range between 0.38 °C and 0.76 °C (first and ninth decile of the absolute differences in mean annual SSTs, respectively). Reporting the first, the fifth or the ninth decile on the thermal niche allows the expected climate-induced alterations in the probability of occurrence of *C. finmarchicus* to be estimated (see the dashed grey arrows as examples in Fig. 2). Changes in the probability of occurrence corresponding to the difference in temperatures between the first and ninth decile are 0.02 (median) with a range between 0.006 (first decile) and 0.05 (ninth decile). This variability in both annual SSTs and probability of occurrence during the period 1960–1969 is considered hereafter as a reference to better evaluate the increase in the alteration of the probability associated with climate change.

Climate-induced changes in mean annual SSTs increase during the decade 2000–2009 (Fig. 2B; the horizontal lines are larger in general in comparison to Fig. 2A). The median of the differences

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in mean annual SSTs between the first and the ninth decile (all horizontal lines along the niche in Fig. 2B) are equal to 0.89 °C with a range between 0.55 °C and 1.17 °C (first and ninth decile of the differences in annual SST, respectively). Changes in the probability of occurrence corresponding to such differences in annual SST are 0.03 (median) with a range between 0.02 (first decile) and 0.07 (ninth decile). On the right side of the niche at a probability level of 0.4 (Fig. 2B; see the dashed grey arrow), the ninth decile (the right vertical bar) of mean annual SSTs indicates that at least 10% of the values show an increase in mean annual SSTs during 2000–2009 accompanied by a reduction of 0.2 or more in the probability of occurrence of *C. finmarchicus*, the double of what is observed for 1960–1969 (Fig. 2A *versus* Fig. 2B; dashed grey arrow).

3.2.2. Niche response to projected climate-induced changes in annual SSTs

The alterations in the probability of occurrence of *Calanus finmarchicus* that are likely to result from changes in annual SSTs that would be reached by 2090–2099 under Scenario A1B are much larger than the shifts that took place between 1960–1969 and 2000–2009 (Fig. 3A *versus* Fig. 2A–B). The median of the differences in annual SSTs between the first and the ninth decile (the length of the horizontal line in Fig. 3A) are equal to 4.17 °C with a range between 2.26 °C and 6.20 °C (first and ninth decile of the differences in mean annual SSTs, respectively). Changes in the probability of occurrence corresponding to the difference in temperatures between the first and ninth decile are 0.12 (median) with a range between 0.06 (first decile) and 0.26 (ninth decile). This analysis indicates that an average 6-fold increase in the amplitude of changes in the probability of species occurrence is likely when the decade 1960–1969 is taken as a reference (0.02 *versus* 0.12) and an increase of 4-fold in comparison to the decade 2000–2009 (0.03 *versus* 0.12). The comparison of Fig. 3B with Fig. 2 is patent (see the horizontal lines) and in some cases, the changes in probability associated to climate-induced changes in mean annual SSTs can reach as much as 0.5.

On a large part of the species thermal niche (section of the niche <10 °C), the range of thermal changes is as expected asymmetrical, indicating that a warmer thermal (i.e. SST) regime will affect most populations of *C. finmarchicus* with both positive (left side of the niche) and negative (right side of the niche) responses to higher annual SST. However, this analysis also reveals more complex changes in response in areas where 1960–1969 mean annual SSTs were above 10 °C. Indeed, some mid-Atlantic populations might experience a cooling that will mitigate the strong impact that global-average warming would have at other locations on the high temperature side of the niche. Further examination indicates that the mid-Atlantic (45°W–10°W and 45°N–58°N; Fig. 3B; negative values in blue) differences are related to the slow-down of the Meridional Overturning Circulation (MOC) because of the accumulation of surface less-saline waters in the Nordic Seas, which originates from both the melting of the high-latitude cryosphere and increasing precipitation (Rahmstorf, 2002). The modeled difference between the thermal (i.e. SST) regime of the 2090s and the 1960s suggests that the middle part (i.e. ~45°W–10°W and 45°N–58°N) of the North Atlantic Ocean indicated by the areas in blue on the map might undergo a reduction in annual SSTs of 4 °C at the same time all other areas warm. This result also indicates that outcome will depend on geographical location, as well as on present-day annual SSTs. Populations in the middle part of the North Atlantic Ocean will increase and a slight southward migration of the range might be expected whereas populations of the north-eastern part of the North Atlantic Ocean (including the North Sea) are expected to decrease, perhaps to the verge of extirpation.

Both Fig. 3B and the outcomes described above represent the "most likely" IPCC scenario A1B. We also examined niche responses under two other scenarii (Fig. 4): one said to be optimistic (SRES Scenario B1; Fig. 4A and B) and one pessimistic (Scenario $[CO_2] \times 4$; Fig. 4C and D). In Scenario B1, the cooling of the central part of the North Atlantic Ocean and warming of the north-eastern part are less intense (Fig. 4B). Nevertheless, at many locations, the consequences are almost as strong as for Scenario A1B (Fig. 4A). Some populations, currently characterised by a probability of occurrence of 0.8, might be close to extirpation by the end of this century. For a very pessimistic scenario ($[CO_2] \times 4$), the warming is so intense that populations of *C. finmarchicus* disappear throughout the North Sea (Fig. 4C). The cooling in the central part of the North Atlantic is also less pronounced (Fig. 4D; area in blue on the map).

For Scenario B1, the median temporal change in mean annual SSTs between the first and the ninth decile is 4.63 °C with a range between 2.59 °C and 6.35 °C (first and ninth decile of the differences in annual SSTs, respectively). Changes in the probability of occurrence corresponding to the difference in temperatures between the first and ninth decile are 0.12 (median) with a range between 0.04 (first decile) and 0.29 (ninth decile); an increase of 6-fold in comparison to the decade 1960–1969 (0.02 *versus* 0.12). For Scenario $[CO_2] \times 4$, the median change in annual SSTs between the first and the 9th decile is 4.75 °C with a range between 1.06 °C and 7.86 °C (first and ninth decile of the differences in annual SSTs, respectively). Changes in the probability of occurrence corresponding to the difference in temperatures between the first and ninth decile are 0.20 (median) with a range between 0.04 (first decile) and 0.38 (ninth decile); an increase of 10-fold in comparison to the decade 1960–1969 (0.02 *versus* 0.20).

3.2.3. Quantification of long-term observed or expected changes in the probability of occurrence of C. finmarchicus

Fig. 5 shows the histogram of the differences in the probability of occurrence of *C. finmarchicus* between the median of changes for different decades (1900–1909, 1960–1969, 2000–2009, 2090–2099) and values of probability of occurrence corresponding to the niche for the reference period 1960–1969 (see Section 2). In the decade 1960–1969, climate-induced changes in the probability of occurrence were small as the niche was calculated for this same decade (Fig. 5A). This analysis was conducted to provide an estimation of the intra-decadal changes. In a colder decade 1900–1909 (Intergovernmental Panel on Climate Change, 2007), climate-induced changes in the probability of occurrence were also small but most changes were positive (19 positive changes *versus* 1 negative shift), indicating a potential increase in *C. finmarchicus* over the studied region (Fig. 5B). In the warmest decade since the start of the instrumental record (2000–2009, Hansen et al., 2010), a 2-fold increase in climate-induced changes of the probability of occurrence is detected (Fig. 5C). Both positive and negative changes are observed, with negative changes occurring in the southern part of distributional range of *C. finmarchicus* and positive changes occurring in the northern part of its distributional range. All projected climate-induced changes in the probability of occurrence for the last decade of this century increased considerably by a factor 6 for scenarii A1B and B1 and 10 for scenario $[CO_2] \times 4$ (Fig. 5D–F). Over the whole species spatial distribution, there are a few places where the abundance of *C. finmarchicus* is expected to increase; e.g. northern part of its distributional range and in the centre (i.e. ~45°W–10°W and 45°N–58°N depending on scenarii) of the North Atlantic cooling as a result of the shutdown of MOC, but overall the species is likely to experience important reduction in their abundance (up to 0.55 in terms of probability of occurrence) for both A1B and $[CO_2] \times 4$. Reductions of the occurrence probability are more common than increases: 33 negative

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changes *versus* 16 positive shifts for Scenario B1, 26 *versus* 16 for Scenario A1B and 30 *versus* 16 for Scenario $[CO_2] \times 4$ (Fig. 5D–F).

4. Discussion

4.1. Influence of climate change on *C. finmarchicus*

The modeled spatial distribution of *C. finmarchicus* closely corresponds to (1) the observed spatial distribution inferred from the CPR survey (Helaouët and Beaugrand, 2007), to more conventional sampling datasets (Heath et al., 2004; Reygondeau and Beaugrand, 2011), to the distribution inferred from models (Speirs et al., 2005) and to the macrophysiological knowledge of the species (Helaouët and Beaugrand, 2009). The optimum of 6 °C we determined corresponds to the thermal optimum of egg production rate (Heath et al., 2000; Hirche et al., 1998) and the realised niche of the species (Helaouët and Beaugrand, 2009). This result is also close to the optimum based on the examination of its spatial distribution in surface from CPR data (Helaouët and Beaugrand, 2007). This result suggests that the niche inferred from NPPEN was close to the actual niche of the species.

Future projections suggest ongoing and more substantial increases in sea temperatures, which appear to be a function of the accumulation of greenhouse gases in the atmosphere and its interaction with natural climatic variability (Intergovernmental Panel on Climate Change, 2007). Our spatial examination of the effect of climate-induced changes in mean annual SSTs in the North Atlantic (Figs. 3–5) revealed marked regional disparities in the effect of climate change. For example, the centre (i.e. ~45°W–10°W and 45°N–58°N depending on scenarii) of the North Atlantic is expected to cool by the end of this century due to the reduction in MOC (Rahmstorf, 1999) whereas in some regions (e.g. Nordic seas) warming is likely to be very substantial (i.e. up to 4 °C increase in annual SST). Regional climate-induced changes in annual SSTs will thereby have strong effects on populations of *C. finmarchicus*; an increase is expected in the central part (i.e. ~45°W–10°W and 45°N–58°N depending on scenarii) of the North Atlantic where cooling takes place whereas a reduction is anticipated in the warming regions located in the southern part of the current distribution of the species. In the North Sea, the species might decline substantially, perhaps to the verge of extirpation. It is likely that other more thermophile species such as *Calanus helgolandicus* will replace the subarctic species if climate continues to warm in the decades to come (Helaouët et al., 2011; Reygondeau and Beaugrand, 2011). Reid et al. (2003b) already observed a substantial changes in the dominance of both *Calanus* in the North Sea. In the 1960s, the subarctic species represented 80% of the total *Calanus* in the North Sea. In 2000, its congeneric species *C. helgolandicus* represented 80% of the genus.

The application of the concept of the ecological niche (Hutchinson, 1957) to bioclimatological research suggests that the effect of climate-induced changes in annual SSTs on marine zooplankton depends not only on the thermal (i.e. SST) regime of an area but also on the (thermal) niche of a species. Because the thermal niche is a non-linear function of temperature (typically an optimum flanked by zones of declining abundance or probability of occurrence) prediction of the local implications of climatic variability and climate change on zooplankton populations is difficult to understand when examined at a local scale, and populations separated in space or time are likely to experience different outcomes (Drinkwater, 2005). This has been observed for fish such as the Atlantic cod *Gadus morhua* (Beaugrand and Kirby, 2010; Planque and Fredou, 1999). Beaugrand and Kirby (2010) showed that at the warmer edge of the thermal niche of cod in the North Sea, there is a prominent influence of climate on cod stock that was mediated through temperature effects on the plankton. In contrast, in the present optimal part of the Atlantic cod niche around Iceland, the influence of climate through its effects on plankton was much less important. It thereby appears that a similar change in the thermal (i.e. SST) regime of a region or an identical climatic anomalies cannot be extrapolated in space because it will not have the same effect on a given marine species (Drinkwater, 2005). Local interpretations of the global influence of climate on zooplankton populations therefore need to be made with caution. This is also emphasised by the fact that at a local scale, more environmental parameters or anthropogenic forcing might interfere and obscure the relationships between a climatic variable and the state of a zooplankton population (Pearson and Dawson, 2003).

A much less known effect forecasted by the niche concept is that in a given area, the relationship between temperature and a zooplankton species (or more generally an ectotherm) may vary in time because it depends upon the thermal (i.e. SST) regime of an area and its implications for the abundance of a species. With no rapid climate change, a statistical model might be applied locally to forecast the abundance of a species as a function of temperature, providing that the signal is sufficiently strong in comparison to the noise associated to sampling. However, if the temperature regime changes too substantially, this is likely to affect the type of relationships between temperature and a biological variable. For example, the temperature (i.e. SST) regime of the southern part of the North Sea might become rapidly similar to the thermal (i.e. SST) regime of the western part of the English Channel if temperatures continue to rise (Fig. 1B and C). In such a hypothetical case, this change would be accompanied by a modification in the relationships between temperature and the abundance of *C. finmarchicus*. Such an effect has probably been observed in the North Sea. In this region, the abundance of *C. finmarchicus* was negatively correlated with the state of the North Atlantic Oscillation (NAO) (Fromentin and Planque, 1996). We assumed hereafter that the influence of the NAO on *C. finmarchicus* operated preferentially through its effects on SSTs (Beaugrand, 2012). Planque and Reid (1998) used a linear regression analysis to forecast the abundance of *C. finmarchicus* in 1996 as a function of the state of the NAO. However, the forecasted abundance proved to be far from observed abundance in 1996, which led the authors to suggest that the correlation between the state of the NAO and the calanoid broke down in 1996. However, subsequent analyses have provided evidence that the relationship stopped at the time of the 1980s ecosystem shift and that the correlation NAO-*C. finmarchicus* was modulated by the thermal (i.e. SST) regime of the North Sea (Beaugrand, 2012; Kimmel and Hameed, 2008). A pronounced increase in sea temperatures occurred at the end of the 1980s, which altered the relationship between the state of the NAO and the abundance of the calanoid. These results suggest that in a world of rapid climate change, empirical relationships between temperature (or a climatic process influencing temperatures) and a species might break down because global warming might rapidly and substantially alter the temperature (i.e. SST) regime of a region. This effect is especially important as many authors have attempted in the past to forecast the abundance of a key species as a function of a climatic variable or temperature (Brander, 2005). If such an attempt is made at a local scale, without considering the thermal niche of a species, the niche concept suggests this can lead to strong discrepancies. This phenomenon is well explained by referring to the niche concept (Beaugrand, 2012).

The concept of the niche shows how climate change might alter marine zooplankton populations. Applied to *C. finmarchicus*, the niche concept shows that time-integrated changes in the probability of occurrence increased with global warming (Figs. 3–5). A twofold increase in the changes in the probability of occurrence of the species was detected for the decade 2000–2009 in comparison to

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1960–1969 (Fig. 5) and the time-integrated changes are expected to increase by a factor 6 or 10 by the end of this century, the extent of increase depending upon the magnitude of warming (Fig. 5). The variance is an important parameter to monitor because it informs on the rapidity of changes and might anticipate severe ecological transitions (Beaugrand et al., 2008; Carpenter and Brock, 2006). Furthermore, it shows that the consequences of climate change on marine populations might inevitably lead to unanticipated changes. Unanticipated changes, called surprises in climatic research, might make projections of future biological trajectories more difficult to achieve in a warmer world (Beaugrand, 2012). Our study suggests that global climate change will increase the amplitude of the changes in species populations, the magnitude depending on the intensity of global climate change and its local interactions with sea temperatures. When we used a moderate climatic scenario (A1B), we found that the climate-induced amplitude in temperatures was likely to increase from 1 °C (Fig. 3A) to 5 °C in comparison to the period 1960–1969, involving a 6-fold increase in the average amplitude of changes (i.e. the extent of the changes seen on the histogram from negative to positive values) in populations of *C. finmarchicus* in the North Atlantic Ocean at the end of this century (Fig. 2A *versus* Fig. 3A). Interestingly in the case of the optimistic scenario (B1), climatic change increased with the same magnitude for the end of this century (Fig. 2A *versus* Fig. 4A) and a corresponding 6-fold increase in climate-induced changes in the probability of occurrence was detected. The magnitude increased to up to 8 °C in some regions in the case of the pessimistic scenario (Fig. 2A *versus* Fig. 4B), leading to a 10-fold increase in the probability of occurrence.

4.2. Potential shortcomings of the approach of thermal niche

The number of studies including the keyword 'niche' has strongly increased in the scientific literature (Robinson et al., 2011). An increasing number of statistical tools have been developed to determine the potential response of species to global warming (Beaugrand et al., 2011; Cheung et al., 2008; Hirzel et al., 2006; Kaschner et al., 2006; Philips et al., 2006). Based on the Hutchinsonian concept and the relation between species niche and distribution, these models project the multidimensional distribution of species into an environmental variate space or into a geographical space (Colwell and Rangel, 2009). Some models can also be used with outputs of atmospheric-ocean general circulation models to establish scenarii of changes in the spatial distribution of species or in the long-term changes of the probability of species occurrence at a local scale (Lenoir et al., 2011).

However as for any technique or procedure, the concept of the ecological niche includes assumptions and limitations that users must be aware of. The first point is related to the potential rate and extent of genetic adaptation of a given species to climate change. How much can a species alter its niche? Some authors suggest the possibility of rapid genetic responses to natural selection rather than direct reaction of species according to their ecological niche (Lee, 2002). This might be effective for small and spatially-isolated zooplankton population, especially of neritic species such as *Acartia* spp. or *Eurytemora affinis*. Niche conservatism (i.e. a tendency of a species to preserve ancestral ecological traits and environmental distribution) is an hypothesis that has been often invoked and used by paleoclimatologists to reconstruct past climates and paleoecologists to estimate the past spatial distribution of some species (Crisp et al., 2009). This hypothesis has been often tested and the usual conclusion is that species rarely changed biome. However, the species might have the potential to alter slightly the shape of their niche, which might influence significantly the niche or ecological niche models. To our best knowledge however, no study has examined this issue in the marine realm for zooplankton. In the terrestrial realm, some translocation experiments indicate the possibility for a species to adapt quickly to changes in environmental conditions. For example, Woodward (1990) provided evidence for rapid adaptation to low temperature of navelwort (*Umbilicus rupestris*). When placed artificially beyond (north of) its geographical limit, 50% of the surviving population tolerated low temperatures in 1987 that were lethal in 1979. Zooplankton have rapid generation time, which in theory might promote more rapid evolutionary change. Some works suggest that evolutionary rates in marine plankton and fish can be rapid during period of transient isolation (Dawson and Hamner, 2005; Palumbi, 1992). This has been found for reef goby fish in the Caribbean Sea (Palumbi and Warner, 2003). However, for most marine zooplankton species, the potential for rapid evolutionary change will be limited by their great dispersal and resulting strong mixing within a large gene pool (Dawson and Hamner, 2005). Like many other zooplankton species, *C. finmarchicus* has a large capacity for zoogeographic displacement because of its large dispersal capacity and reproductive strategy (*r* strategy) (Mauchline, 1998). This might have reduced pressure for genetic adaptation. Helaouët and Beaugrand (2007) did not find any alteration of the thermal niche during the period 1958–2002 in the North Sea. The species only needs to occur close to oceanic regions sufficiently deep to overwinter (Heath et al., 2004). Furthermore, the spatial distribution of *C. finmarchicus* (as many other zooplankton species) is limited by hydroclimatic features. It does not occur south of the Oceanic Polar Front (OPF). One might therefore question why a species that had plenty of opportunities to alter genetically its thermal niche does not have at present a larger thermal niche after hundreds of thousand years of evolution, and does not occur south of the OPF. Bucklin and colleagues showed in four Norwegian fjords (Lurefjorden, Masfjorden, Sognefjorden and Sorfjorden) that most *Calanus finmarchicus* populations were not genetically distinct whereas populations of *Acartia clausi* exhibited significantly distinct genetic structures (Bucklin et al., 2000). Some estuarine species such as *Eurytemora affinis*, more constrained by geographic factors might be more likely candidates for genetic adaptation (Lee, 1999).

A second limitation is that the species distribution reflects the species niche and both are in equilibrium with present-day climate. This point has been heavily discussed in the terrestrial realm (Pearson and Dawson, 2003). The assessment of the niche from the spatial distribution (i.e. realised niche) is only valid if the current distribution of a species is in equilibrium with climate. In the terrestrial realm, this assumption can be easily violated because of the great age at maturity of some plants and their lower dispersal capacity. The violation of this assumption would result in an underestimation of the magnitude of the change. This limitation is however much less relevant for zooplankton because the combined effects of mobility and rapid demographic turnover allow species distributions to track climate quickly. This makes this taxon a unique group to understand and evaluate the potential current implications of climate change for organisms and ecosystems. Assessment of the fundamental niche represents an alternative and robust way to evaluate or overcome any potential lack of equilibrium, but requires a thorough knowledge of the species physiology.

A third point is related to biotic interactions. The realised niche, more often assessed than the fundamental niche, is the niche assessed when dispersal and biotic interactions are accounted for (Hutchinson, 1978). As the biocoenoses will reorganize, many biotic interactions (e.g. predation, competition, facilitation) will be altered. This is likely to modify the realised niche of the species. Changes in species interaction such as those recently shown for pelagic ecosystems of the North Sea (Kirby and Beaugrand, 2009) might strongly affect the ability of a species to inhabit a region. This effect is however likely to be stronger at local scales and less

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significant at a macroecological scale (Pearson and Dawson, 2003). For example, Helaouët and Beaugrand (2009) used a macrophysiological model that estimated the optimal part of the fundamental niche (i.e. niche without the influence of biotic interaction and dispersal) and the realised niche (i.e. niche with effect of biotic interaction and dispersal) of *C. finmarchicus* from CPR data and concluded that the species occurred where it was able to reproduce successfully (i.e. where it was able to maximise the evolutionary fitness). The projection of the two (realised and fundamental) niches in the geographical space gave similar patterns, which indicate that spatial differences in biotic interactions do not alter substantially the spatial distribution of *C. finmarchicus* at a macroecological scale. The spatial distribution at that scale was mainly controlled by temperature, although other factors played a role (bathymetry, stratification of the water column and food). Future development is likely to use realised and fundamental niches jointly to increase the robustness of projections of the potential effect of climate change on organisms. However, as said earlier, it requires information on the physiology of the organism (e.g. Egg Reproduction Rate as a function of SST).

Other complications have been recently discussed in some reviews on the subject (Colwell and Rangel, 2009; Robinson et al., 2011). One important example is the ontogenic variability of the niche. Reygondeau and Beaugrand (2010) found clear evidence for variation in the breadth of the ecological niche during ontogeny. They found that young stages of *C. finmarchicus* (e.g. copepodite stage 1) were more sensitive to water stratification and that this sensitivity decreased up to copepodite stage 5 (C5). Adults were more sensitive than C5, probably because they need to place their eggs in optimal conditions for maximising survival. The ontogenic shift observed for many organisms is not easy to consider for plants or benthic organisms. However, for zooplankton it might be easier to overcome as the developmental time of these organisms is generally short and less complex. Developmental time lasts generally a few weeks although this also depends on temperature. Depending on temperature, a population can be composed of multi- or univoltine organisms. In polar biomes, some organisms might need several years to reach maturity (i.e. semivoltine species). If temperature increases enough to allow the species to complete its life cycle within a year, this might have strong consequences for the population. Another complication arises from the existence in some zooplankton species of dormancy stage. This enables the species to overcome a period when environmental conditions are outside its niche. A study on *C. finmarchicus* showed that dormancy can strongly vary spatially in the Northwest Atlantic (Johnson et al., 2008). Dormancy onset and emergence dates differed by nearly 150 days among sites and varied interannually by ~50–100 days within 787 sites (Mackas et al., 2012). Clearly the concept of the niche does not incorporate these levels of complexity. However, the niche concept works on emergent properties. The concept of emergence in ecology stipulates that an ecological entity or unit cannot be predicted from the study of its elements. This is also called nonreducible property, indicating that the property of an organism 'is not reducible to the sum of the properties of the parts' (Odum, 1971). If this principle is correct, and many examples in ecology suggest it is, this limits the capacity of Individual Based Models (IBMs) to forecast the potential response of a species to global climate change.

The last point, but not the least, is methodological. It is crucial to have data that are sufficient to define correctly the ecological niche. Assessment of the niche of a species from only a part of its global distribution might lead to a truncated niche, while too scarce sampling may deform the realised niche and bias projection (Lenoir et al., 2011). Unfortunately, the cost and difficulty of large-scale sampling of the marine realm often leads to incomplete coverage. The problem increases when the number of explanatory variables or ecological dimensions increases because variables require more sampling effort. Incomplete sampling is undoubtedly more important than the impact of spatial autocorrelation (Dormann et al., 2007) because it may strongly distort the shape of the niche.

As other concepts, the ecological niche of Hutchinson should be applied with a clear knowledge of these potential risks and limitations. Nevertheless, a simplified but robust (thermal) niche model might represent the best tool currently available to bioclimatologists to assess and predict the potential responses of zooplankton to climate change. Once the niche is assessed with high confidence, it represents the deterministic effect of climate change on species. The alternative approach (detailed mechanistic simulation models) requires a thorough understanding of the physiology and life history traits that is at best presently available for only a very few species. The concept of the ecological niche combines a macroecological view with a concept that has a long history originating from the law of minimum of Justus von Liebig (1840), the law of tolerance of Shelford (1913) and the first concept of the niche envisioned by Joseph Grinnell in 1917 (Colwell and Rangel, 2009).

4.3. Potential benefits of placing zooplankton populations under the macroscope

Many studies have documented the influence of climatic variability and global climate change on organisms (Cloern et al., 2010; Mackas et al., 2007; Richardson and Schoeman, 2004). It is very likely that current and future climate change will unbalance biomes and provinces and will greatly alter the biological and ecological systems of the oceans and the seas (Lenoir et al., 2011; Sarmiento et al., 2004). The regional consequences will be considerable. At the species level, abundance will change, which will in turn modify the communities (Parmesan and Matthews, 2006). Biotic interactions will be altered in sign and strength (Kirby and Beaugrand, 2009). There is however a potential to forecast at least some of the biological and ecological changes by using the concept of the ecological niche and adopting a macroscopic comparative approach. The macroscope is a theoretical concept, coined by de Rosnay (1979), that looks for properties of a system at a macroscopic level. In the same way a microscope is needed to observe the infinite small or a telescope is needed to observe the infinite big, the macroscope is a theoretical concept to investigate complex systems (de Rosnay, 1979). Applied in ecology, it enables to better apprehend spatial and temporal changes in the ecosystems. This concept is often implicitly assumed in the new emerging science of macroecology (Blackburn and Gaston, 2003; Brown, 1995). By utilising such an approach, we have shown how climate can interact with the thermal niche of a species to trigger changes in abundance, and cause both phenological and biogeographical shifts (Beaugrand, 2009; Edwards and Richardson, 2004; Mackas et al., 2007). Zooplankton have the capacity to track quickly climate change (Hatun et al., 2009; Taylor et al., 2002). They are among the best taxonomic groups to evaluate the fingerprint of climate warming on ecosystems because of their short generation time, their great dispersal capacity and the absence of absolute geographical barrier in the pelagic realm.

The ecological niche (*sensu* Hutchinson) of a species can only be determined from large-scale datasets. For some zooplankton species, this can currently be achieved with the CPR survey (Fig. 6A). Even for large-scale monitoring programmes such as the CPR or CalCOFI (California Cooperative Oceanic Fisheries Investigations), many species niches might remain incomplete (e.g. truncated), limiting their relevance for understanding and forecasting the effect of climate on marine organisms. Alternatively, we can build new datasets by combining data from a large number of widely-distributed different regional sampling programmes (Fig. 6B). This

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effort has already been done by some authors (Heath et al., 2004; Speirs et al., 2005). Recently, Reygondeau and Beaugrand (2011) did a similar work to investigate the macroecology of *C. finmarchicus* in the North Atlantic Ocean. This effort was made it possible because data were kindly provided by researchers such as Pr Mike Heath, Dr Erika Head, Dr Xabier Irigoien and available as part of international programmes such as TASC and GLOBEC (Fig. 6C). In the same way, a global-scale information on the species richness of foraminifers and copepods has been proposed and has allowed a better understanding of global-scale patterns in the diversity of these organisms (Fig. 6D and E) (Rombouts et al., 2009; Rutherford et al., 1999). When different datasets are used, it may often be sufficient to use presence-only data, and thereby avoid some of the quantitative intercalibration issues associated multiple sampling methods and survey designs. Several techniques exist to deal with presence-only data: ENFA (Ecological Niche Factor Analysis) (Hirzel et al., 2002), MAXENT (*MAX*imum *ENT*ropy approach to species distribution modeling) (Philips et al., 2006) and NPPEN (Non-Parametric Probabilistic Ecological Niche model) (Beaugrand et al., 2011), and should be applied to characterising the ecological niches (or more specifically the thermal niche) of additional species.

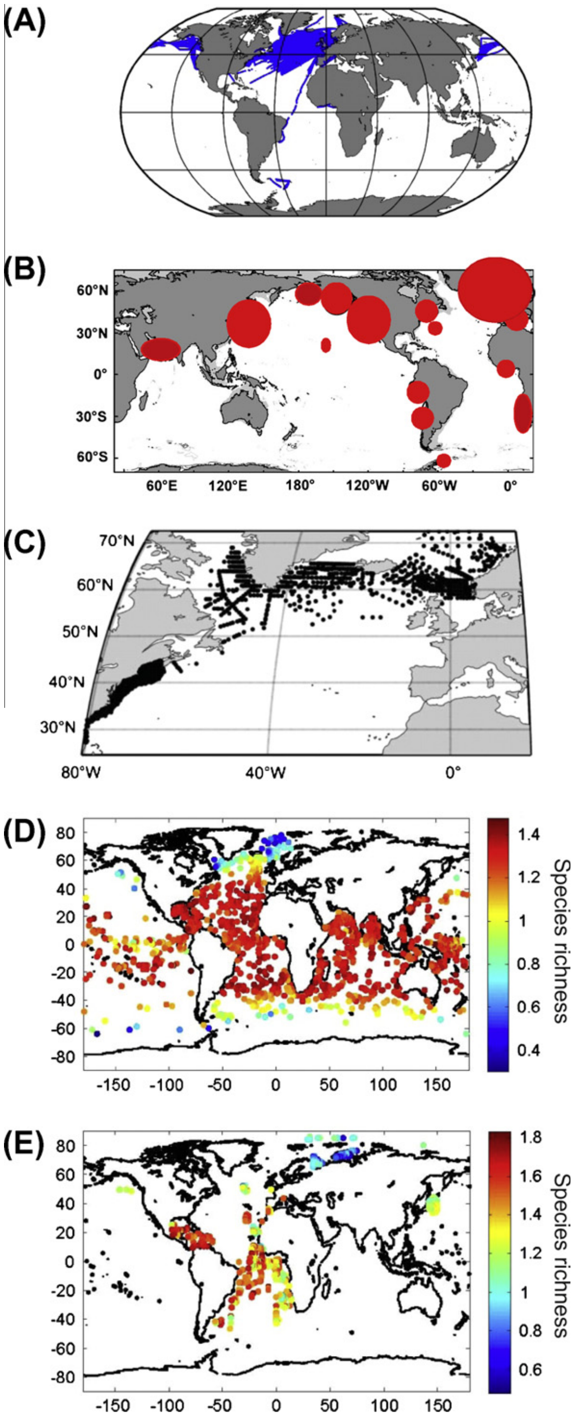

Fig. 6. Some examples of zooplankton global datasets. (A) Sampling coverage by the CPR survey. (B) Long-term datasets available in different area of the world (Mackas and Beaugrand, 2010). (C) Data on *C. finmarchicus* gathered from TASC and GLOBEC programmes (Dr Erika Head; Pr Mike Heath; Dr Xabier Irigoien) (Reygondeau and Beaugrand, 2011). (D) Species richness (in logarithm) of foraminifers (Rutherford et al., 1999). (E) Species richness (in logarithm) of copepods (Rombouts et al., 2009).

At a time when a lot of effort is devoted to better understand how ecosystems work at a microscale (high-frequency but localised monitoring), we think it is as crucial to build global datasets and to design new joint (global-scale) monitoring strategies to tackle the issue of not only global climate change but global ecosystem change. It is obvious that neither a single sampling programme nor a single laboratory can do that alone. This effort should be done as part of a consortium in which sampling strategies and protocols are designed to be used in every biome and province of the oceans (Longhurst, 2007; Sherman, 1995) and new numerical techniques elaborated. We might create a new observatory based on modern techniques: a Global Observatory for plankton (or better a Global Observatory of the Marine Biosphere) that might help us to better study issues such as ocean acidification, biodiversity response to climate change by using an ecosystem approach and the alteration of the biological pump in a warming world. We caution however that rough measurement of total zooplankton biomass are not sufficient to allow us to understand the system and provide poor predictive capabilities (Beaugrand, 2005). Lavaniegos and Ohman (2003) indeed said that '*bulk zooplankton biomass is comprised of organisms representing as many as four trophic levels as well as widely different morphologies, body sizes, ratios of carbon: wet biomass, life histories, growth rates, and biogeographic distributions. Such diverse organisms are unlikely to respond in a uniform manner to environmental forcing, and thus the aggregated biomass of such disparate taxa is unlikely to be a sensitive indicator of environmental change*'. We need to identify zooplankton at the species level, just as an atmospheric chemist identifies the chemical composition of the atmosphere or a botanist identifies all plants occurring in her/his sampling site. The taxonomic information is essential to understand the full complexity of marine ecosystems, evaluate their current states and detect and predict ongoing and future changes.

A global effort would allow us to have direct coordinated measurements, that would not only provide better quality data for calibrating all types of models, but this would also represent an alternative to modeled data. We are currently perhaps too dependent on ecosystem models. Ecosystems models, and models such as Ecopath-Ecosim contain too many assumptions to be considered as able to determine parameters to inform on good ecological status. Except for some exploited fishes, there is not enough knowledge of biological/physiological properties of common species. Global observation networks have long been recognised as essential by meteorologists and physical oceanographers. Especially in meteorology, global-scale monitoring is done on a routine basis and has proved its relevance to (1) determine weather, (2) the state of climate and (3) serve as a baseline for both meteorological and climatic models. Although local studies still tend to dominate our scientific efforts in biological oceanography, the issue of global change is compelling us to plan and implement broader (joint) scientific strategies.

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5. Conclusions

Biogeographical works showed that the location and extent of major biomes and provinces are mainly controlled by climate in both the oceanic and the terrestrial realms (Lomolino et al., 2006; Longhurst, 2007). This core principle is substantiated by evidence gained from both fossil records and contemporaneous changes (Hughes, 2000; Walther et al., 2002). The spatial distribution of individual marine species is also primarily driven by climate. The need for better comprehension of the impact of climate on marine organisms therefore forces us to think and observe at the scale of the spatial distribution of species and at the scale of the entire thermal niche of a species. At more regional and local scales, it becomes obvious however that we also need to consider additional abiotic parameters (e.g. nutrients) and biotic factors to approximate better the ecological niche of the species (thermal niche + main environmental parameters + biotic interactions) (Pearson and Dawson, 2003).

In this rapidly changing world, zooplankton will help us to understand the instantaneous influence of global climate change on ecosystems because this group can track rapidly environmental changes (Beaugrand et al., 2009). This is not the case in the terrestrial realm for many taxonomic groups (e.g. plants and insects), for which changes in spatial distributions in response to climate change are limited to a rate of 2 km decade^{-1} or less (e.g. beetles). The average rate of 6 km per decade determined by Parmesan and Yohe (2003) and based on 1700 both terrestrial and marine species might therefore underestimate the rate needed for the biocoenoses to track current climate change. Beaugrand et al. (2009) found that biodiversity of calanoid copepods have been responding quickly to SST rise in the Northeast Atlantic by moving geographically northwards at a rapid rate up to 23.16 km yr^{-1} during the period 1958–2007.

To evaluate the current effect of global climate change on the marine biosphere, we need to implement jointly new types of global-scale monitoring programmes, selecting a representative set of key and indicator species from different trophic levels. The data should be quickly available and used in conjunction with new statistical procedures or analyses (Goberville et al., 2011b) specifically designed to work on large-scale ecological data. Biological and ecological systems are complex and there are undoubtedly limits to our predictive capability. We will be able to forecast global trajectories but local changes are unlikely to be forecasted with a high level of confidence. More works on this aspect is urgently needed especially in this period of preparation of the fifth IPPC assessment report on the impacts of climate changes on natural systems.

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