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Are *Calanus* spp. shifting poleward in the North Atlantic? A habitat modelling approach

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Abstract:

In the last decade, the analysis based on Continuous Plankton Recorder survey in the eastern North Atlantic Ocean detected one of the most striking examples of marine poleward migration related to sea warming. The main objective of this study is to verify the poleward shift of zooplankton species (*Calanus finmarchicus*, *C. glacialis*, *C. helgolandicus*, *C. hyperboreus*) for which distributional changes have been recorded in the North Atlantic Ocean and to assess how much of this shift was triggered by sea warming, using Generalized Additive Models. To this end, the population gravity centre of observed data was compared with that of a series of simulation experiments: (i) a model using only climate factors (i.e. niche-based model) to simulate species habitat suitability, (ii) a model using only temporal and spatial terms to reconstruct the population distribution, and (iii) a model using both factors combined, using a subset of observations as independent dataset for validation. Our findings show that only *C. finmarchicus* had a consistent poleward shift, triggered by sea warming, estimated in 8.1 km per decade in the North Atlantic (16.5 per decade for the northeast), which is substantially lower than previous works at the assemblage level and restricted to the Northeast Atlantic. On the contrary, *C. helgolandicus* is expanding in all directions, although its northern distribution limit in the North Sea has shifted northward. *Calanus glacialis* and *C. hyperboreus*, which have the geographic centres of populations mainly in the NW Atlantic, showed a slight southward shift, probably responding to cool water penetrating southward in the Labrador Current. Our approach, supported by high model accuracy, shows its power in detecting species latitudinal shifts and identifying its causes, since the trend of occurrence observed data is influenced by the sampling frequency, which has progressively concentrated to lower latitudes with time.

Keywords: *Calanus* ; climate change ; habitat model

1. Introduction

Data from Continuous Plankton Recorder (CPR) survey in the Northeast Atlantic Ocean indicate that zooplankton exhibit distribution range shifts in response to global warming that are among the fastest and largest of any marine or terrestrial group (Beaugrand *et al*., 2002; Lindley and Daykin, 2005; reviewed by Richardson, 2008). Habitat models based on CPR data have also been developed to provide projections of future climate-driven shifts (Helaouet and Beaugrand, 2007, 2009; Beaugrand *et al*., 2008; Helaouet *et al*., 2011; Reygondeau and Beaugrand, 2011). Factors that control the spatial distribution of populations can be grouped into two main categories, external and internal (Planque *et al*., 2011). External controls, which are often referred to as environmental controls, are independent of population state, and they are the basis of the ecological niche theory (Hutchinson, 1957). Different statistical and mathematical techniques have been developed to model the spatial distribution of species, also termed species distribution models (Elith and Leathwick, 2009), climate envelope models (Pearson and Dawson, 2003), habitat distribution models (Guisan and Zimmermann, 2000), or habitat suitability models (Hirzel et al., 2002). A climate envelope model generally characterizes a set of suitable habitats for a species derived from their present geographic location. As, in general, habitat models are constructed from the associations between the extant geographic position of a species' occurrence and its climate, there is difficulty in testing these models under different climates (Lawing and Polly, 2011).

The second type of factors affecting the spatial distribution of populations is the internal control, which are directly linked to the population prospects (reproduction, mortality and migration rate, that in the case of copepods is mainly based on advection). These include density-dependent processes, the effect of demographic structure and biogeographical processes (Ohman et al., 2001; Planque et al., 2011). These two factor types have traditionally differentiated both the conceptual view of species control (niche theory vs. population dynamics) and the modelling approaches (habitat models vs. individual based models (IBMs, see Runge et al., 2005)). When modelling the pelagic habitat of plankton, dispersal limitation is often neglected although it can play an important role on community structure (Irigoien et al., 2011; Chust et al., 2013). Research efforts need to focus on integrating the two mechanisms in the modelling approach for zooplankton species, as attempted for fish and invertebrates (Cheung et al., 2009).

Time series of spatially-explicit biological data such as zooplankton occurrence are challenging to analyse because of non-uniform sampling across time and space. Very few predictive models have been validated using independent data (but see Lewis et al., 2006; and Llope et al., 2012). Past works showed shift of populations (zooplankton assemblages) based on northward/southward limits of a restricted region (Northeast Atlantic) and did not encompass the overall distribution range of species (e.g. Beaugrand et al., 2002). Therefore, data reconstruction methods and models encompassing all North Atlantic and including both niche and population factors are needed to avoid bias in trend analysis and to explore possible causes of population shifts. The application of habitat models to case species also requires key steps to be accurately undertaken to avoid model over-fitting (Burnham and Anderson, 2002), such as the selection of the explanatory variables and model validation. Model validation is one of the critical steps in order to extrapolate models to conditions outside of those used to generate the model, such as to other regions (Valle et al., 2011) and to future climate (Lawing and Polly, 2011).

Our objective is to develop models of habitat suitability (at species level) and data reconstruction for analysing past changes in zooplankton species (e.g. *Calanus* spp.) due to prominent climate drivers, particularly sea warming within the North Atlantic (Fig. 1), using Generalized Additive Models (GAMs, Hastie & Tibshirani, 1990). Zooplankton are good indicators of climate change for several reasons (Richardson, 2008): highly sensitive to temperature, most species are short-lived so there can be tight coupling of climate and population dynamics, copepods are usually not commercially exploited avoiding confusion with trends in exploitation, and the distribution of zooplankton can accurately reflect temperature and ocean currents because plankton are free floating. In this work, habitat suitability models were built for each one of the four copepod species (*Calanus finmarchicus*, *C. glacialis*, *C. helgolandicus*, and *C. hyperboreus*) within the temperate to subarctic North Atlantic from 1959 to 2004. These species, especially *C. finmarchicus,* dominate zooplankton biomass in N. Atlantic; as the one of the main grazers they transfer energy from phytoplankton to higher trophic levels such as commercially exploited fish (Planque and Batten, 2000; Richardson, 2008). The aim of this paper is to test whether population gravity centres of key taxa such as *Calanus* spp. shift poleward, and if so to explore whether this movement could be associated with sea warming. To this end, we compare time series of observed data with a series of GAM models as numerical experiments: 1) a model using only temporal and spatial terms, as a data reconstruction method, to simulate population movement, 2) a model using only climate factors (i.e. niche-based model) to simulate the habitat suitability, and 3) a model using both climate and spatio-temporal factors combined. Subsequently, for all the models the distribution of the species was predicted over the whole spatio-temporal domain. Thus, the rate of change of the geographic gravity centre of the modelled occurrence probability allowed us studying the shifts of the species population and habitat suitability along time.

MATERIAL AND METHODS

Biological data and sampling frequency

Data on the abundance (mean density (ind./m^3) of four species (*C. finmarchicus, C. glacialis, C. helgolandicus, C.hyperboreus*), total diatoms and dinoflagellates and the phytoplankton colour index (PCI) were obtained from the CPR data base. The CPR survey is an upper layer plankton monitoring program that has regularly collected samples, at monthly intervals, in the North Atlantic and adjacent seas since 1946 (Warner and Hays, 1994). Water enters the CPR through a small aperture at the front of the sampler and travels down a tunnel where it passes through a silk filtering mesh of 270 µm before exiting at the back of the CPR. The plankton filtered on the silk is fixed to a final concentration of 4% formalin into a tank within the CPR body. On return to the laboratory, the silk roll is unwound and cut into sections corresponding to 10 nautical miles (approx. 3 m^3 of seawater filtered), the greenness of the silk is assessed and the plankton microscopically identified (Jonas et al., 2004). The CPR data used in the present study represent monthly data collected between 1959 and 2004 within 35º to 65ºN and 75ºW to 9ºE. Data were gridded using the inverse-distance interpolation method (Isaaks and Srivastava, 1989), in which the interpolated values were the nodes of a 1 degree by 1 degree grid. Total diatoms and dinoflagellates represent an aggregation of data from 66 and 39 genera, respectively. *C. glacialis* and *C. hyperboreus* are artic species, while *C. finmarchicus* is a subarctic species and *C. helgolandicus* dwells on temperate regions (Beaugrand et al., 2002). *C. finmarchicus* overlaps in size range with *C. helgolandicus* and *C. glacialis* which is the largest among them. The *C. finmarchicus, C. helgolandicus, C. glacialis* and *C. hyperboreus* data here used is represented by the 5th copepodite and adult stages (i.e. CV-CVI). We use the Phytoplankton Colour Index (PCI), which is a visual assessment of the greenness of the silk, as an indicator of the distribution of total phytoplankton biomass across the Atlantic basin (Batten et al., 2003; Richardson et al., 2006). This index covaries positively with both fluorimeter and satellite measures of chlorophyll (Batten et al., 2003; Raitsos et al., 2005).

A non-uniform distribution of sampling in space and time might influence the subsequent analysis of the poleward shift of species population gravity centres. Therefore, sampling frequency have been analysed as a function of year, latitude and longitude, in order to test the uniformity of sampling effort over the time period.

Environmental data and climate variability

Environmental data compiled had a spatial resolution of 1º longitude and 1º latitude and cover the entire domain defined. Sea surface temperature (SST), salinity, vertical velocity, and sea level anomaly were extracted from reanalysis OS3 ECMWF (European Centre for Medium-Range Weather Forecasts) model and downloaded from CliSAP-Integrated Climate Data Center (ICDC). Bathymetry was extracted from ETOPO1 global model (NOAA).

The time series trends of sea surface temperature was analysed over the period 1959-2004 to test whether isothermals increased at all latitudes. In addition, overall mean SST was analysed over the period and map differences between cold and warm periods were calculated.

Habitat modelling and occurrence reconstruction

The approach consisted in modelling the species occurrence as a function of environmental factors (SST and salinity, vertical velocity), surrogates of environmental factors and population features (latitude and longitude, month), temporal trend (year), and potential food resources (PCI, total abundance of diatoms and of dinoflagellates), using Generalized Additive Models (GAMs, Hastie & Tibshirani, 1990). GAMs enable the fit of non-linear models for a wide family of statistical distributions. The presence / absence of each *Calanus* spp. was assumed to follow a binomial error distribution and the logit was considered as the link function.. Overfitting was prevented by restricting the degrees of smoothness as explained below and by visualizing the response for each variable. The CPR dataset encompasses 178,910 samples across the spatial domain and irregularly distributed at year and monthly basis (see 2004 data as an example in Fig. 1).

SST and salinity were used because of their recognised influence, either direct or indirect, on the spatial distribution of *Calanus* spp. (e.g. Helaouët and Beaugrand, 2007). Vertical velocity was used as a surrogate of upwellings. For environmental variables, the degree of smoothness of model terms was restricted from 3 to 5 in order to assume a unimodal niche model (*sensu* Hutchinson, 1957), but allowing asymmetry since interactions between species and extreme environmental stress may cause skewed responses (Oksanen and Minchin, 2002). In this sense, GAMs provide a more realistic solution than rectilinear climate envelope models or ellipsoidal climate envelope GLMs (Oksanen and Minchin, 2002). The CPR phytoplankton indices (i.e. PCI, diatoms and dinoflagellates abundance) were tested individually as phytoplankton is a key food resource for *Calanus* spp. (Irigoien et al., 1998); however, because the data relative to these indices were not always available to cover the spatial and temporal domain as the other environmental variables, they were not used for spatial and temporal reconstruction of the habitat suitability model and they were not included in the overall model.

Month and geographic variables (i.e. latitude and longitude) are considered here as surrogates of population features or environmental factors not considered (Legendre, 1993). For instance, spatial terms might be proxies of overwintering areas since close vicinity to an overwintering site has been suggested to be the main prerequisite for a region or water mass to hold a large population of *C. finmarchicus* (e.g. Head et al., 2000; Torgersen and Huse, 2005; Speirs et al., 2004). Spatial terms (i.e. latitude and longitude) were considered with interaction and using a bivariate smooth function. Month information was considered as a categorical variable; thus, a parametric coefficient was estimated for each month. To analyse the temporal trend, year was considered as explanatory variable and its GAM smoothness term was restricted to 5 degrees of freedom.

We built and compared three different models for each species: 1) A spatial and temporal Model. A GAM using spatial (latitude, longitude) and temporal (month, year) terms only. This model is employed as data reconstruction method, thus, to identify trends on population over the analysed period. 2) An SST Model. A GAM based upon only SST. As this model is driven by SST trend, it serves to identify species habitat suitability shifts. The comparison of the output of this model with the previous one permits to verify whether populations have shifted due to sea warming or if only their habitat suitability has shifted. 3) A combined Model. A GAM based on spatial, temporal and environmental factors. As this model incorporates all factors, it has the potential to be the most accurate in predicting overall habitat suitability among the three model types, and it is used also to assess the relative contribution of spatio-temporal factors with respect to the environment. Several steps had been undertaken: first, we have built a GAM for each variable independently. Second, we have selected the best model by removing variables that are not statistically significant or explaining the deviance of species occurrence by less than 1%. The explained deviance, 1 - (residual deviance)/(null deviance), is the equivalent to R^2 in least squares models (Guisan and Zimmermann, 2000). Third, we have improved the model using a forward stepwise procedure, i.e. by adding variables according to the explained deviance, and removing those that do not improve significantly the model or less than 1%.

Model validation

We validated the models based on the cross-validation resampling procedure, which use independent data sets for model building and model validation (Burnham and Anderson, 2002). The comparison between the accuracy of the model (that using all observations to build the model) and that of cross-validated permits the detection of model overfitting, which highly reduce the use of such models for extrapolation. In particular, we used k-fold partitioning of a data set(Hijmans et al., 2012), where each record in the data set is randomly assigned to a group. In our case, group numbers are between 1 and k, with k=5, hence, 80% of the CPR observations are used for model building, and the remaining 20% (i.e. independent) observations are used for model validation in an iterative procedure that is repeated 5 times.

The accuracy of the model and the five replicate model cross-validations have been evaluated using Area Under the receiver operating characteristic Curve (AUC) (Fielding and Bell, 1997; Raes and ter Steege, 2007) and accuracy indices derived from confusion matrix (VanDerWal et al., 2012). To this end, first, the modelled probability of species presence was converted to either presence or absence using probability thresholds obtained using two criteria: sensitivity (true predicted presences) is equal to specificity (true predicted absences), and maximization of sensitivity plus specificity, following Jimenez-Valverde and Lobo (2007). Given the defined threshold value, a confusion matrix (also called an error matrix, Congalton, 1991), which represents a cross-tabulation of the modelled occurrence (presence/absence) against the observations data, was calculated. An overall accuracy measure was computed from the confusion matrix which is the proportion of the presence and absence records correctly identified. Both overall accuracy and AUC values range between 0.5 (random sorting) and 1 (perfect discrimination).

Time series analysis of the geographic gravity centre

For all three model types, the probability of species occurrence was predicted over the whole spatial and temporal domain. Subsequently, we computed the geographic gravity centre of the predicted maps of probability of presence of each species from January 1959 to December 2004. The gravity centre is defined as the mean geographic location of a population (Woillez et al., 2009). The changes in the gravity centre's coordinates (longitude and latitude) were used to describe the changes in the geographic distribution of the habitat suitability in the *Calanus* spp. along time. As a way to test the sensitivity of this approach to detect geographic shifts triggered by environmental change, first, this statistic was calculated from the habitat suitability models for each time step (i.e. a month) and subsequently represented along the seasonal cycle. Latitudinal trends estimated from these three models were compared with observed data (both abundance and presence/absence data), and sampling frequency.

RESULTS

Climate variability and change

The analysis of time series trends over the period 1959-2004 indicated that sea surface temperature at all latitudes analysed increased between 0.0240 and 0.0088 ºC yr^{-1} (p<0.0001, p=0.018, respectively). Specifically, the warming period started mainly at *circa* 1970 with a rate of increase of 0.028 ºC yr^{-1} (p<0.0001) as showed by the mean SST (Fig. 2a). The spatial difference of SST between cold (1969-1979) and warm (1998-2004) periods (Fig. 2b) showed that warming in the NW

Atlantic was more heterogeneous than in the NE Atlantic with three hotspots of warming and a region of slight cooling.

CPR data sampling frequency

Sampling frequency has a strong variability throughout years, with maximum effort in the 1960s and minimum in the 1980s (Fig. 3a). Mean sampling frequency at the beginning of the period is more concentrated in higher latitudes and decreases 3º on average over the period, with moderate variability (Fig. 3b). Mean sampling frequency is more concentrated in the eastern part of the North Atlantic during 1959-1961 and during 1987-1989, and in the western part in the remaining period (Fig. 3b). There is non linear trend in the sampling frequency for the geographic longitude along the time period.

Habitat models

First, each term (environmental, spatial or temporal) was separately tested for each species using GAM (Table 1). This indicates that PCI and total abundance of diatoms and dinoflagellates accounted for a limited deviance of species occurrence. Subsequently, the three model types were fitted to each species according to the methodology described and the explained deviance compared. In all *Calanus* spp., spatial and temporal models accounted for 33-45% of species occurrence, while environmental variables accounted for 17-31% (SI 1). Specifically, SST model explained between 26% and 10% of the variation according to species. Environmental factors contributed very little to the combined model (adding 0.9-2.2% to the explained variance), indicating that high covariation exists between both variables types and that spatial and temporal terms are key to reconstruct habitat suitability over the period. For the combined model, the estimated degrees of freedom, p-value for each selected variables, and the accuracy measures of cross-validation are indicated in Table 2.

According to the AUC and overall accuracy, models for *C. finmarchicus*, *C. glacialis* and *C. helgolandicus* have good agreement between occurrence predictions and observations (AUC: 0.77-0.88 and overall accuracy: 78-79%), while that for *C. hyperboreus* was slightly less accurate (AUC: 0.72, overall accuracy: 72%). The high accuracy values for cross-validated models, also compared to that of model using all observations (80-90%), indicate that models do not present overfitting. As an example, Fig. 4 shows the GAM response curves of the combined model for *C. helgolandicus* occurrence probability, while Fig. 5 shows the SST model compared with the spatial and temporal model for the same species in June, averaged by time periods. In particular from the SST model, it appears that the habitat suitability of *C. helgolandicus* at the southern limit nearby the Bay of Biscay shifted poleward from 1970s to 2000s, while the spatial and temporal model indicates a general expansion of the population in all directions, southward, northward, and offshore.

Seasonal analysis

In order to assess if the gravity centre index used is a good descriptor of the shift, first, the indices were applied to the *Calanus* spp. populations from the habitat suitability models (combined model) for each time step (i.e. a month) and then represented along the seasonal cycle (Fig. 6). Population gravity centre shifts poleward from April to August (average for the overall 1959-2004 period) and southward from September to February. This pattern is consistent in all four species, with low differences in the magnitude of this shift (i.e. from 2º of latitude range in *C. finmarchicus* to 4º in *C. helgolandicus* and *C. hyperboreus*). This shift corresponds to the population growth differential over the latitude, and not an advection of individuals. In the case of *C. finmarchicus*, *C. glacialis* and *C. hyperboreus* it also may correspond to the ascent of the overwintering population at the end of the diapause (Heath et al., 2004) rather than to a shift in the distribution of individuals remaining in surface during the winter (the CPR only samples the surface layer). The gravity centre index used for

Calanus spp. showed seasonal patterns which are consistent with the annual peaks reported for those taxa at different latitudes by other authors (Planque and Fromentin, 1996).

Temporal analysis

Population gravity centre indices throughout the years (Fig. 7, Table 3) permitted to infer the following trends for each species according to the comparison between models and observed data. For *C. glacialis*, all models and observed (presence/absence) data showed a slight shift to the South (Fig. 7a and e). This species presented relatively low occurrence in the data (i.e. *C. glacialis* was present in 5,023 samples within the entire spatial domain and time series, absent during 9 years) compared with other species (e.g. *C finmarchicus* recorded in 105,598 samples in all years). This species has its main geographic distribution at artic and subarctic regions; hence, enlarging the domain area of study beyond 65º is needed to confirm this result. For *C. hyperboreus*, observed data and the model based upon the spatial and temporal terms indicate a shift to the South (Fig. 7b and f). The combined model and the SST model showed no significant shift (Fig. 7b). This means that species distribution probably shifted slightly to the Equator, while its habitat suitability was not expected to shift. This species, which presented relatively low occurrence in the data (present in 3853 samples, absent during 4 years), has its main geographic distribution in the arctic and subarctic regions; hence, enlarging the domain area of study beyond 65º is needed to confirm this result. For *C. finmarchicus*, all models showed poleward shift (Fig. 7c and g). This means that species populations and its habitat suitability shifted poleward; hence, we can infer that population shift can be associated to sea warming. In particular, the spatial and temporal model indicates a population shift rate of 0.0073º latitude per year (8.1 km per decade) for the overall North Atlantic, and a slightly higher for the Northeast Atlantic (longitude between 30º W and 15º E) (16.5 km per decade) (Fig. 7c). On the contrary, observed data showed that the gravity centre has a tendency to shift to the South (Fig. 7g). This southward shift is due to the latitudinal decreasing trend in the sampling frequency (Fig. 3b, SI 2), particularly north of 64º Latitude in the North-eastern Atlantic, in recent years, see SI 2. For *C. helgolandicus*, habitat suitability based on SST model showed poleward shift since the 1970s; the combined model showed a similar result but the shift rate is less and starts from the 1980s (Fig. 7d). On the contrary, the model based upon spatial and temporal terms did not show a poleward shift. Observed data of *C. helgolandicus* showed slight southward shift for presence/absence data, and no shift considering abundance data (Fig. 7h). Overall, this means that species population probably did not shift poleward, and only its habitat suitability is shifted by sea warming.

DISCUSSION AND CONCLUSION

GAM models for the four *Calanus* spp. in the North Atlantic have been built to analyse species distribution shifts between 1959 and 2004. GAMs were previously used to investigate the influence of environmental factors on plankton standing stock in the North Sea (Llope et al., 2009; Llope et al., 2012). Concerning the species habitat suitability, the limitation of distance-based habitat models used in previous works (e.g. Helaouet and Beaugrand, 2007, 2009; Beaugrand et al., 2008, Helaouet and Beaugrand, 2009; Reygondeau and Beaugrand, 2011; Helaouët et al., 2011) to describe the asymmetry of ecological niche has been well solved by GAM models, which are usually more accurate according to model comparison studies (e.g. Elith et al., 2006). The models combining environmental and spatial factors have been validated using independent data sets and their reliability measure indicate moderate (72% for *C. hyperboreus*) to high accuracy performance (78-79% for *C. finmarchicus*, *C. glacialis* and *C. helgolandicus*). The reliability of our data reconstruction models and the gravity centres used here, encompassing the overall population in the study area, might improve previous estimates of shift rates based only upon observed data (e.g. Beaugrand et al., 2002).

Among the four analysed species, only *C. finmarchicus* showed a consistent poleward shift during the 1959-2004 period, as shown by all three models. This suggests that *C. finmarchicus* populations shifted poleward as a consequence of sea warming, since the SST model (i.e. habitat suitability) is consistent with the model with spatial and temporal terms (i.e. population data reconstruction) (see maps in SI 3). This poleward shift is, overall, in agreement with previous works (see a review in Richardson, 2008). However, the rate of northward movement detected in *C. finmarchicus* (8.1 km per decade for the overall North Atlantic, 16.5 per decade for the Northeast Atlantic) is substantially lower than the change in distribution indicated for zooplankton assemblages by previous works for the Northeast Atlantic (260 km per decade for the northward extension of zooplankton assemblages 14 species including the four *Calanus spp.* analysed here, Beaugrand et al., 2002)). The main differences between those studies are the taxa assemblage analysed, the statistic considered (distribution limits *versus* geographic centres), and the model algorithm used. The gravity centre considered here is more reliable to capture overall population movement since distribution limits may also change because overall increase in population abundance. The rate estimate here for *C. finmarchicus* is still higher than that reported for terrestrial species based on a study of 99 species of birds, butterflies and plants (6.1 km per decade, Parmesan and Yohe, 2003) but within that of rattlesnakes (4.3-24.2 km per decade, Lawing and Polly, 2011). On the contrary, the population centre gravity in the observed data of *C. finmarchicus* showed southward shift. This is most likely due to the lower sampling frequency at latitudes > 64˚N after the early-1980s (Fig. 3b), as shown by the long-term mean latitude of sampling frequency (SI 2a,b); indeed the Norwegian Sea, which is a core area of distribution for *C. finmarchicus* in the North East Atlantic, was poorly sampled between 1981 and 2004. Therefore, our data reconstruction modelling approach, which is supported by high model accuracy, shows its power in detecting latitudinal shifts even when observations are lacking due to discontinuous sampling.

Habitat suitability of *C. helgolandicus* based on SST showed poleward shift since 1970s. On the contrary, the model based upon spatial and temporal terms did not show poleward shift, but an expansion of the overall population in the North Sea, Atlantic margin and central N Atlantic since the 1970s (as shown by the predicted maps in Fig. 7d and by the increasing variance of the gravity centre not shown here for brevity). This means that *C. helgolandicus* population did not shift poleward, although its habitat suitability changed probably as a result of sea warming. The causes of *C. helgolandicus* population expansion in all directions, including southward, are still unclear; one could hypothesizes that it could be partially related to the general increase of phytoplankton biomass observed since the mid-1980s in the North East Atlantic (Raitsos et al., 2005; McQuatters-Gollop et al., 2011). This is supported by the fact that the CPR phytoplankton indices explained *C. helgolandicus* occurrence in a larger extent than for the other three species (Table 1). The expansion of *C. helgolandicus* includes its northern distribution limit in the North Sea where it has replaced *C. finmarchicus* since the 1990s, which has been interpreted as a result of warming of this region (Richardson, 2008). Changes in abundance are more difficult to attribute to global warming than are shifts in distribution or phenology (Richardson, 2008). Our approach helps to disentangle shifts in species distribution and shifts in their habitats, reconstructing species expected occurrence even when observations are not available.

Southward population movement of the artic species (*C. glacialis and C. hyperboreus*), that have their main geographic centre at NW Atlantic, is in agreement with previous works focused on the NW Atlantic (see artic and subarctic assemblages in Beaugrand et al., 2002, and *C. hyperboreus* in Johns et al., 2001). The southward shift of these two species would respond to cool water penetrating southward in the NW Atlantic (Richardson, 2008), in particular in the Scotian and Newfoundland shelf regions influenced by the outflow of freshwater from the Arctic (Head and Pepin, 2010; Licandro et al., 2011). The spatial difference of SST between cold (1969-1979) and warm (1998-2004) periods (Fig. 2B) showed that warming in the NW Atlantic (Labrador Sea) was more heterogeneous than in the NE Atlantic with three hotspots of warming and a region of cooling. This pattern could be related to the observed trend of the North Atlantic Oscillation (NAO) index towards positive values (see Beaugrand et al., 2002) that result in warmer winters in the NE Atlantic and colder winters in the NW Atlantic (Hurrel, 1995) and might explain why *C. glacialis* and *C. hyperboreus* are showing southward shift. On the other hand, these two artic species were less frequent in the time series (9 and 4 years without any presence for *C. glacialis* and *C. hyperboreus*, respectively) as their main geographic distribution is usually in artic and subarctic regions, out of the area sampled by the CPR; hence, enlarging the domain area of study beyond 65º is needed to confirm these results.

Latitudinal shift of species is not the only potential response to ocean warming. Marine fishes and invertebrates, for instance, can also respond to warming migrating to deeper waters (Cheung et al., 2013), similar to terrestrial species shifting their distribution to higher elevations within mountains (Engler et al., 2011). Using electronic tagging, Neat and Righton (2007) found that cod moved to cooler water at deeper depths. The limitations of our data based uniquely on surface sampling (Jónasdóttir and Koski, 2011) preclude analysing whether there is also a shift towards deeper waters. In particular, Williams (1985) and Jónasdóttir and Koski (2011) observed that when *C. helgolandicus* and *C. finmarchicus* co-occur, the latter preferred colder deeper waters remaining reproductively active, while the former stayed in the warmer surface waters. In *C. glacialis,* Niehoff & Hirche (2005) found that temperature increase in the surface layer apparently triggered the descent of the females to lower depths and the arrest of their reproductive activity. In *Neocalanus plumchrus*, the timing of the annual maximum peak biomass has shifted 60 days earlier in warm than in cold years over the past 50 years (Mackas et al., 1998). Such phenological change is probably a consequence of both increased survivorship of early cohorts and increase in physiological rates such as egg hatching, reproductive and growth rate (Richardson, 2008). According to the study by Helaouet and Beaugrand (2009), the application of the ecological niche theory predicts that for northern hemisphere species, warming should produce increased survivorship in the northern (i.e. at cooler waters) population side in respect with its optimal niche, while it will diminish survivorship at the southern (i.e. at warmer waters) population side. Similarly, in the case of competing species warming should produce increased competitive advantage four southern species with respect to northern species in overlapping areas. These two processes should cause latitudinal shift of the overall species distribution, thus, keeping pace with the shift of their suitable habitats. If vertical migration plays also a role in the climate response, even assuming that *Calanus* spp. could remain deeper ingesting an adequate ration of food, a drop in overall occurrence frequency at the two (northern-southern) sides of optimal (realised) niche should be observed in CPR surface-based data, which is not the case for *C. helgolandicus* according to our results.

Among the environmental factors, sea surface temperature is, in general, the one explaining most of the variance of species occurrence in the four *Calanus* spp. (especially in *C. glacialis*), in agreement with previous works (Beaugrand et al., 2013) and the view of temperature as the most broadly influential factor controlling biological processes (Brown et al., 2004). Other environmental factors that could be taken into account in future studies in order to improve trend analysis and habitat suitability models are horizontal currents, food resources and suitability of the overwintering habitat (Irigoien, 2004). As autonomous motility of copepods is spatially limited as compared with passive movement triggered by ocean currents, dispersal by this means might influence the probability of occurrence of a species at a given location from month to month. Phytoplankton indices used here and *Calanus* occurrence were poorly related according to our modelling approach as in previous attempts (e.g. Reygondeau and Beaugrand, 2011), either because those indices represents only part of the food available or because food is not a limiting factor. Phytoplankton is a key food source for calanoid species (Moller et al., 2012); hence, other phytoplankton indices (satellite-derived primary production) or other ways of modelling food resources in the habitat suitability model should be explored in the future. Further, factors affecting overwintering survival such as winter mixing depth or distribution of predators might also play a role in the final distribution (Irigoien, 2004).

Another relevant finding of this study is that environmental variables accounted for 17-31% of species occurrence, which is less than did spatial and temporal terms (33-45%) in all *Calanus* spp., with high covariation among both types of factors. This means that space and seasonality are key to describe the pelagic distribution of copepods. Also, since spatial and temporal terms can be partially a proxy of dispersal constrains, our results are in line with a balanced view between the importance of the role of dispersal limitation and of niche partitioning on the plankton community structure (see for instance Irigoien et al., 2011, for zooplankton, and Chust et al., 2013, for phytoplankton).

Since species habitat models developed here have high accuracy, according to model evaluation using independent data sets, they have also the potential to be applied to future climate change scenarios in order to assess warming impacts on zooplankton, and to assess the implications of changes at this trophic level versus top predators such as fish and cetaceans. As we have seen, warming can modify the distribution of marine organisms, which in turn, it can be propagated through the upper trophic levels. In a context of rapid alteration of marine ecosystems throughout the world (Pauly et al., 1998), future projections of ocean productivity, based on habitat species distribution, are needed for a detailed assessment of ocean health and benefits and for achieving or maintaining the good environmental status of the North Atlantic (see for instance the environmental status defined by the Marine Strategy Framework Directive, MSFD, European Commission, 2008).

In summary, our findings show that among the four *Calanus* spp. analysed in the North Atlantic during the 1959-2004 period, only *C. finmarchicus* had a consistent poleward shift estimated in 8.1 km per decade (16.5 km per decade for the Northeast Atlantic), triggered by sea warming, which is lower than previous works restricted to the Northeast Atlantic and considering zooplankton assemblages. Because of the sampling limitation of the CPR survey in the northern regions, it is not possible to clarify whether *C. finmarchicus* global gravity centre has displaced to the North or rather its southern distribution has retracted. Our model is highly accurate (80%), which has been validated by a subset of observational data. It shows its power in detecting latitudinal shifts even when changes in the sampling frequency may not ensure an adequate coverage of a region. On the contrary, *C. helgolandicus* population gravity centre did not shift poleward according to the results, although its northern distribution limit in the North Sea has shifted northward. *C. helgolandicus* is expanding in all directions probably influenced by multiple factors (e.g. phytoplankton increase, warming, their own population dynamics, biotic interactions, environmental variability). *C. glacialis* and *C. hyperboreus* based on the CPR sampling, present the geographic centres of their populations mainly in the NW Atlantic, showed a slight southward shift, probably responding to cool water penetrating south in the Labrador Current and the heterogeneity in the warming at NW Atlantic. Despite of the limitations of CPR data restricted to surface sampling, the long and spatially extensive biological data set, together with species occurrence models based upon a wide range of factors (climate, spatio-temporal) and tested in a combined and separate manner, have the potential to detect and accurately quantify latitudinal shifts and suggest potential causes.

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Tables

Table 1. Explained deviance of *Calanus* spp. occurrence by each factor.

	C. glacialis	*C. hyperboreus*	*C. finmarchicus*	*C. helgolandicus*
PCI	0.27	0.16	0.16	4.15
PCI + Diatoms + Dinoflagellates	0.51	1.41	2.41	6.41
SST	26.3	17.7	11.6	10.0
Salinity	19.4	10.7	11.4	2.05
Bathymetry	1.06	3.59	4.72	15.7
Vertical Velocity	0.53	1.32	1.09	5.47
Spatial terms (Lat:Long)	35.6	23.1	26.3	39.0
Month	3.78	19.3	3.91	0.55
Year	4.87	0.75	1.66	2.74

Table 2. Combined GAM models. Variables entered: Year, Month, Longitude, Latitude, Sea Surface Temperature (SST), Salinity, Bathymetry, Vertical Velocity. EDF: Estimated Degrees of Freedom. Thresholds for conversion of probability of species presence to either presence or absence in model validation: 0.05 (*C. glacialis*), 0.60 (*C. finmarchicus*), 0.03 (*C. hyperboreus*), 0.30 (*C. helgolandicus*).

Species	Variables selected	EDF	p-value	Overall explained deviance (%)	AUC (model with all observations / mean kfold cross-validation)	Accuracy (model with all observations / mean kfold cross-validation) (%)
C. glacialis	Year	3.979	$<1.10^{-15}$	42.6	0.888 / 0.774	89.1 / 78.2
	SST	1.361	$<1.10^{-15}$			
	Salinity	1.289	0.0019			
	Longitude	2.964	$<1.10^{-15}$			
	Month		10 months significant			
C. finmarchicus	Year	3.940	$<1.10^{-15}$	34.4	0.778 / 0.778	79.8 / 79.8
	SST	1.997	$<1.10^{-15}$			
	Long : Lat	14.957	$<1.10^{-15}$			
	Month		10 months significant			
C. hyperboreus	Year	2.759	$<1.10^{-15}$	46.0	0.889 / 0.717	90.5 / 72.2
	SST	1.979	$<1.10^{-15}$			
	Long : Lat	14.771	$<1.10^{-15}$			
	Month		9 months significant			
C. helgolandicus	Year	3.988	$<1.10^{-15}$	41.2	0.819 / 0.798	80.8 / 79.7
	SST	1.998	$<1.10^{-15}$			
	Long : Lat	14.950	$<1.10^{-15}$			

Table 3. Latitudinal shifts (° yr^{-1}) for each species and according to observed data and models between 1959 and 2004 in the North Atlantic.

	C. glacialis		*C. hyperboreus*		*C. finmarchicus*		*C. helgolandicus*	
	Trend	p-value	Trend	p-value	Trend	p-value	Trend	p-value
Observed data (Pres/Abs)	-0.0386	0.0369	-0.1194	0.0006	-0.0641	4.5e-06	-0.0304	0.0042
Observed data (Abundance)	-0.0174	0.3570	-0.0979	0.0252	-0.0483	0.0296	0.0119	0.4170
SST model	-0.0077	0.0178	-0.0024	0.2770	0.0086	1.9e-09	0.0119	0.0002
Spatial and temporal model	-0.0143	0.0136	-0.0044	<2e-16	0.0073	<2e-16	-0.0019	1.2e-06
Combined model	-0.0079	0.0049	-0.0020	0.5350	0.0123	<2e-16	0.0029	0.0261

Figure legends

Fig. 1. The North Atlantic basin. The domain of the studied area is 350º to 650º N and 750º W to 150º E. Source of Bathymetry: ETOPO1, NOAA, Amante and Eakins (2009). Transparent dots are those sampled in the overall period (1959-2004). Red dots are those sampled in 2004.

Fig. 2. A) Mean SST trend; B) Difference of SST between 1969-1979 (cold period) and 1998-2004 (warm period).

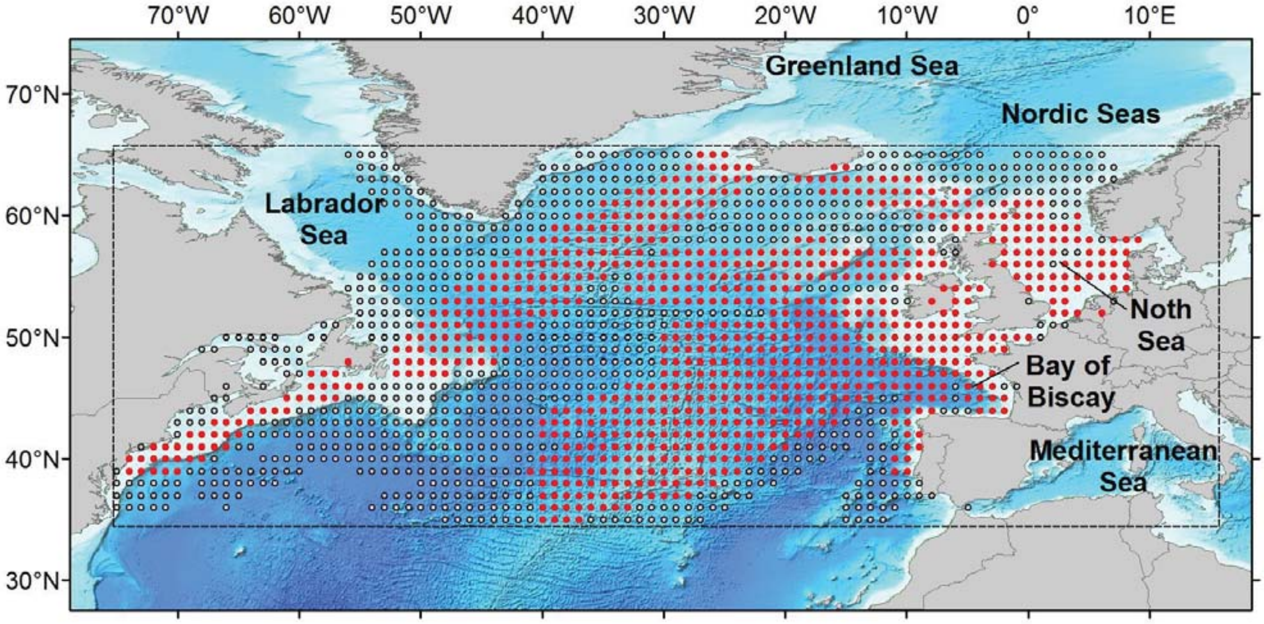
Fig. 3. Sampling frequency as a function of year (a), as a function of year and latitude (b), and as function of year and longitude (c). In b and c, the size of the circle is proportional to the sampling frequency, the black line indicates the mean value at the corresponding year, and the dotted line indicates the linear temporal trend.

Fig. 4. Response of C. helgolandicus occurrence probability for each variable of the combined model.

Fig. 5. Evolution of C. helgolandicus occurrence probability models (SST model, as habitat suitability model, and spatial and temporal model as population data reconstruction) between 1959 and 2004 (Month: June).

Fig. 6. Latitudinal shift of the population gravity centre during seasonal cycle (average for the overall 1959-2004 period; combined model). See text for explanation.

Fig. 7. Shift in latitude of the gravity centre of Calanus spp. population habitat suitability models (a, b, c, d) and of the observed annual average (e, f, g, h), according to abundance and presence/absence data. See estimations of trends (and their statistical significance) in Table 3.


70°W
60°W
50°W
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30°W
20°W
10°W
0°
10°E
70°N
60°N
50°N
40°N
30°N
Greenland Sea
Nordic Seas
Labrador Sea
Noth Sea
Bay of Biscay
Mediterranean Sea

Fig. 1.

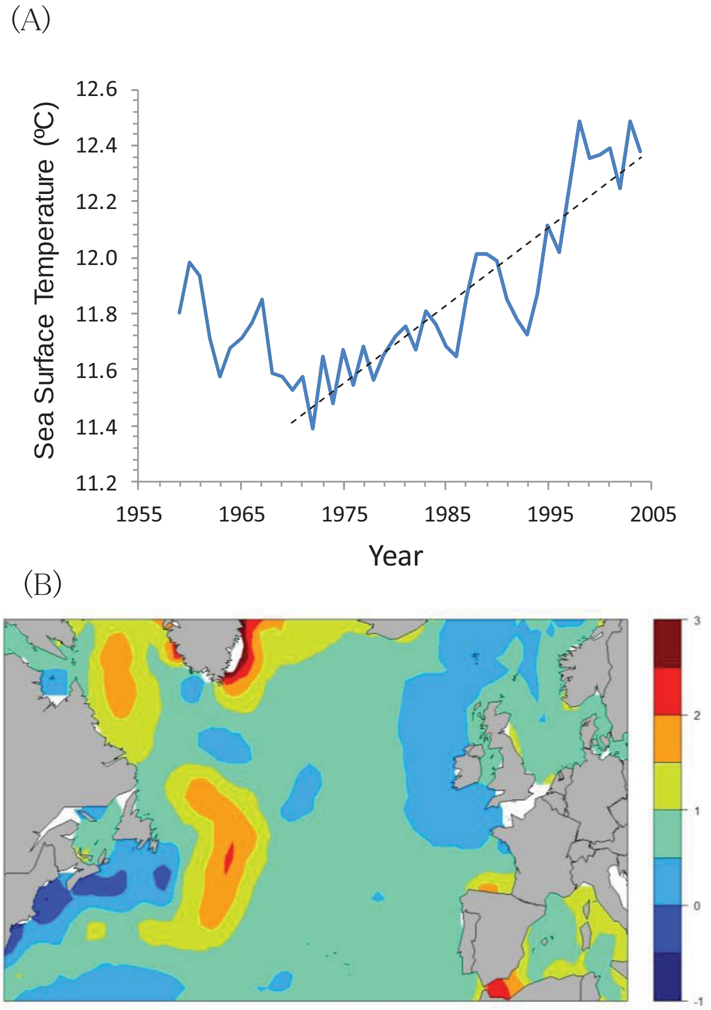

(A)
Sea Surface Temperature (ºC)
12.6
12.4
12.2
12.0
11.8
11.6
11.4
11.2
1955
1965
1975
1985
1995
2005
Year
(B)
3
2
1
0
-1

Fig. 2.

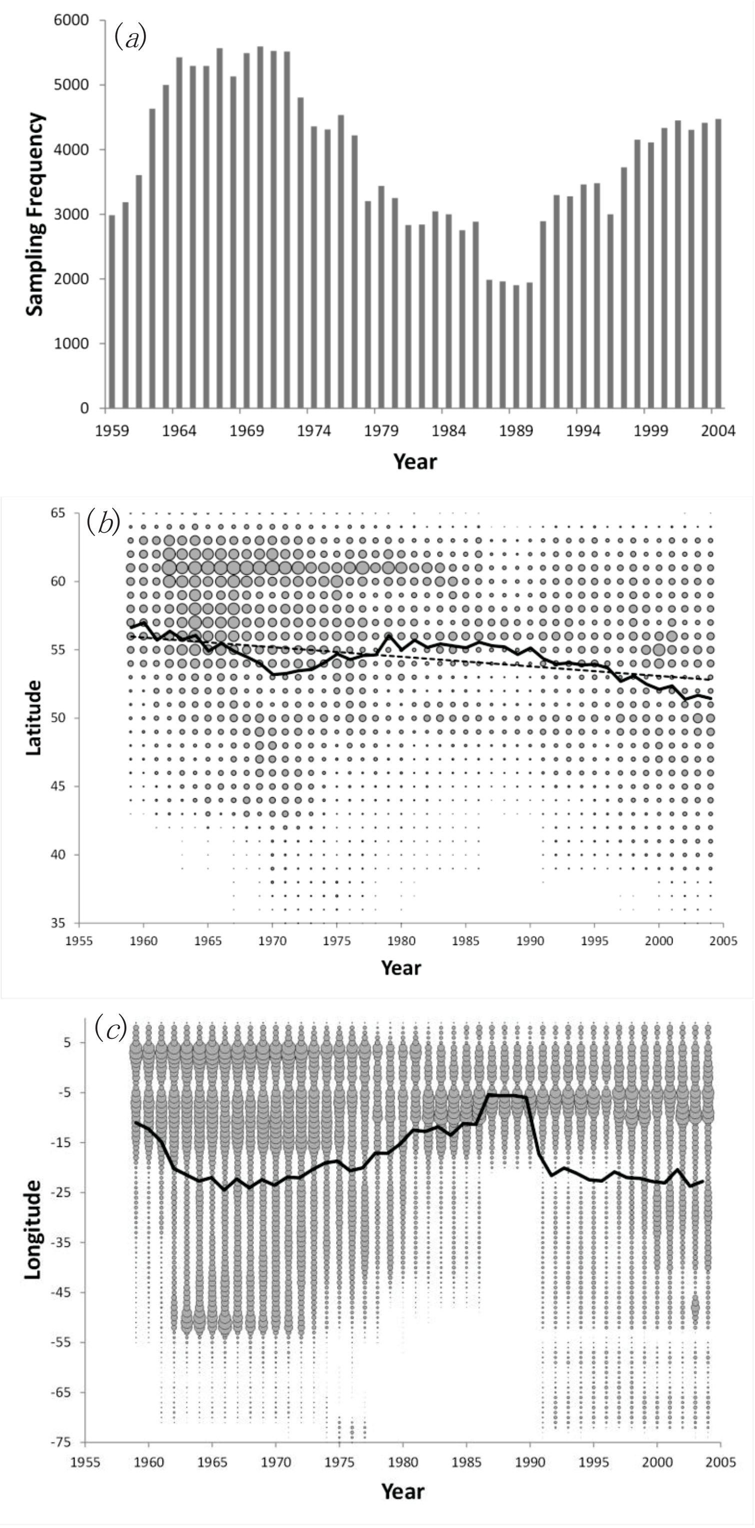

(a)
Sampling Frequency
6000
5000
4000
3000
2000
1000
0
1959
1964
1969
1974
1979
1984
1989
1994
1999
2004
Year
(b)
Latitude
65
60
55
50
45
40
35
1955
1960
1965
1970
1975
1980
1985
1990
1995
2000
2005
Year
(c)
Longitude
5
-5
-15
-25
-35
-45
-55
-65
-75
1955
1960
1965
1970
1975
1980
1985
1990
1995
2000
2005
Year

Fig. 3.

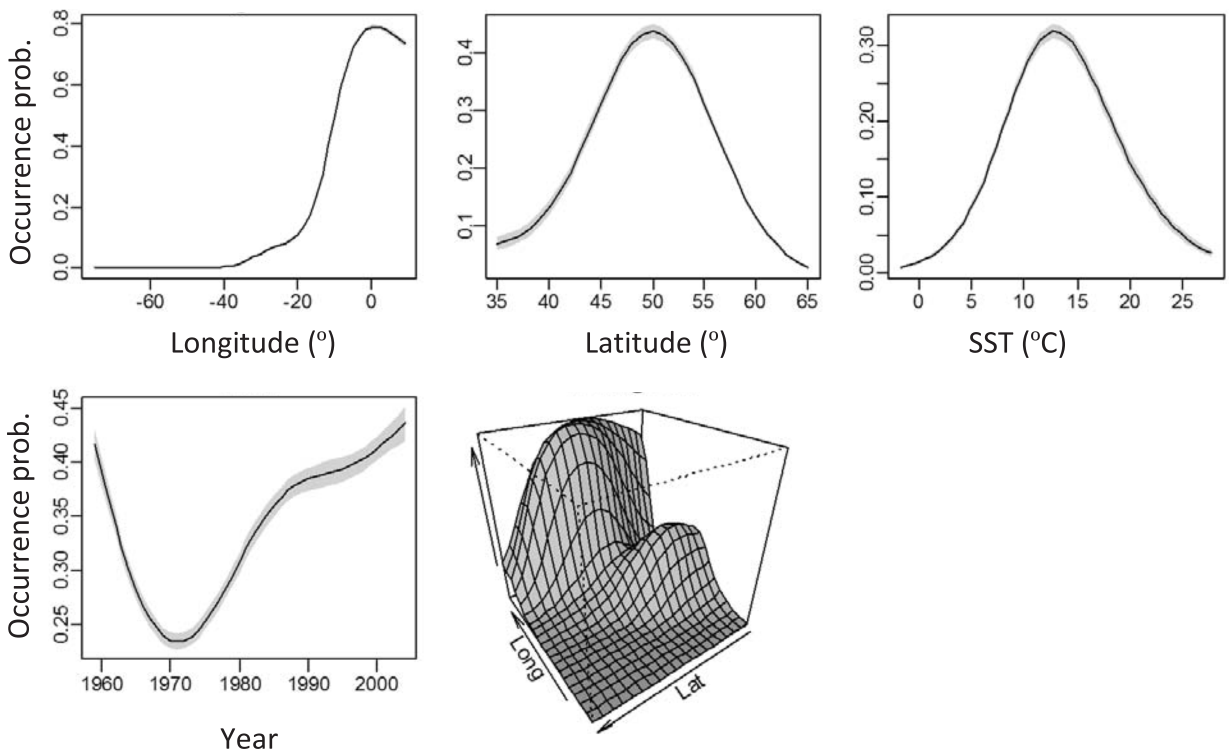

Occurrence prob.
0.0
0.2
0.4
0.6
0.8
-60
-40
-20
0
Longitude (°)
0.1
0.2
0.3
0.4
35
40
45
50
55
60
65
Latitude (°)
0.00
0.10
0.20
0.30
0
5
10
15
20
25
SST (°C)
Occurrence prob.
0.25
0.30
0.35
0.40
0.45
1960
1970
1980
1990
2000
Year
Long
Lat

Fig. 4.

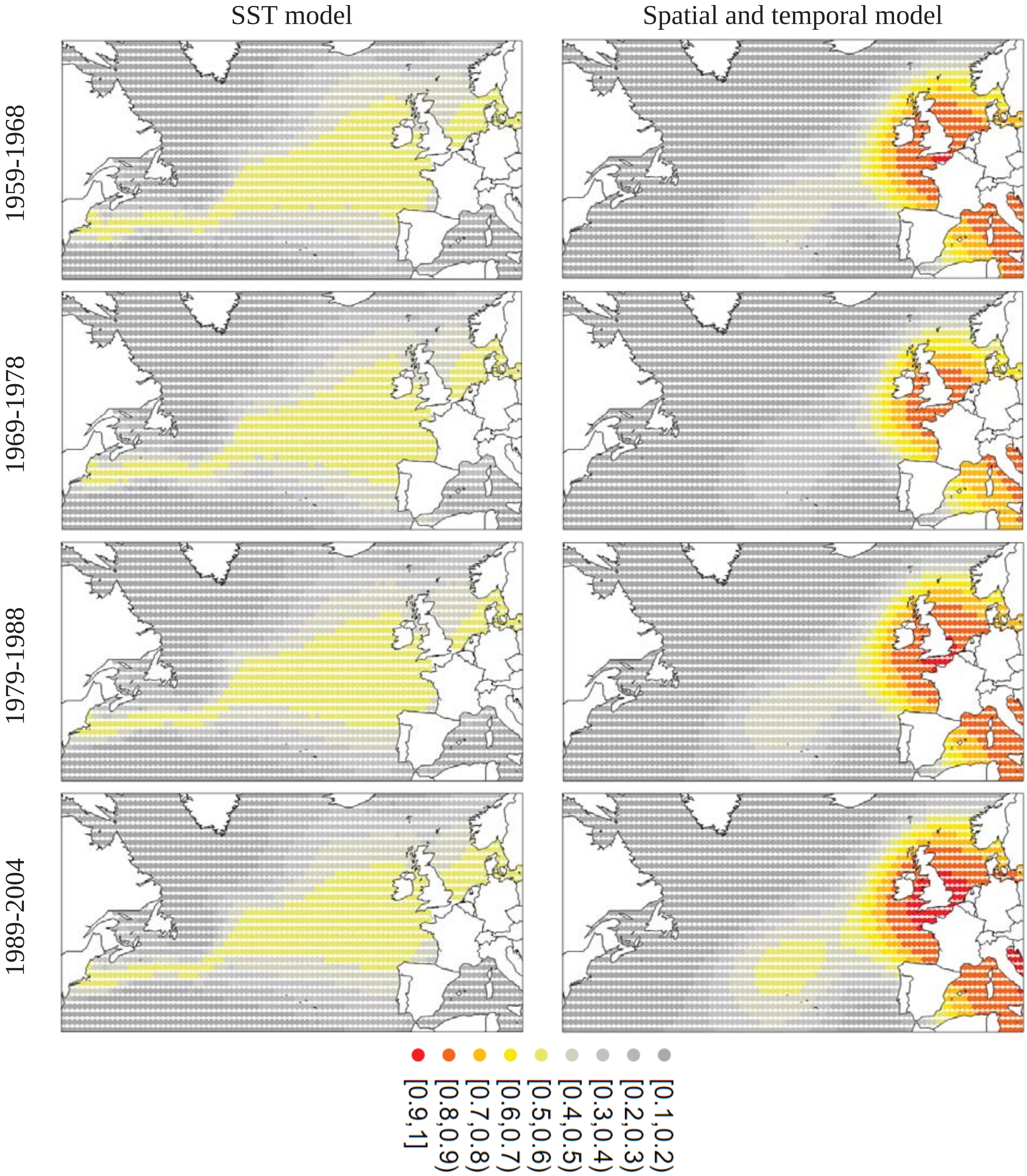

SST model
Spatial and temporal model
1959-1968
1969-1978
1979-1988
1989-2004
[0.9,1]
[0.8,0.9)
[0.7,0.8)
[0.6,0.7)
[0.5,0.6)
[0.4,0.5)
[0.3,0.4)
[0.2,0.3)
[0.1,0.2)

Fig. 5.

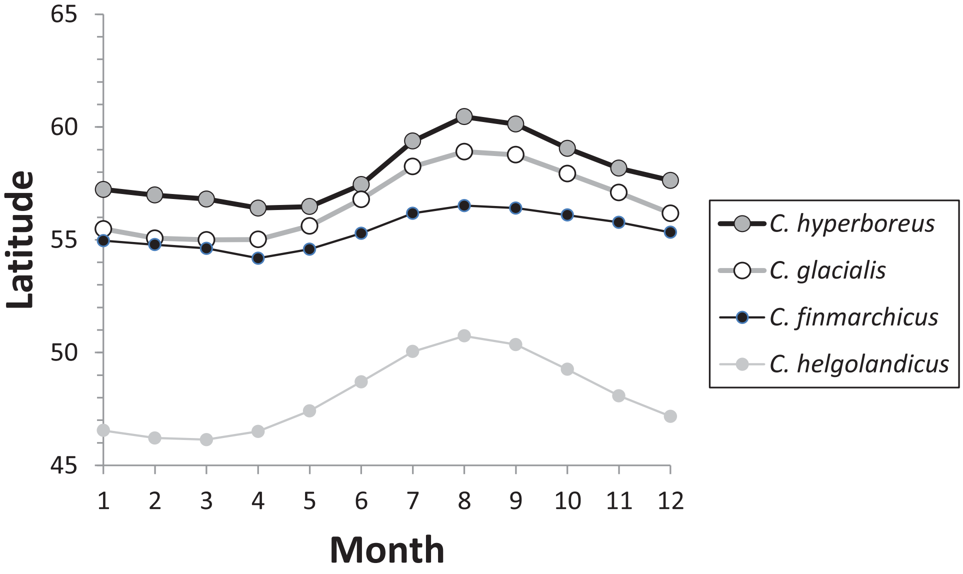

65
60
55
50
45
Latitude
1
2
3
4
5
6
7
8
9
10
11
12
Month
C. hyperboreus
C. glacialis
C. finmarchicus
C. helgolandicus

Fig. 6.

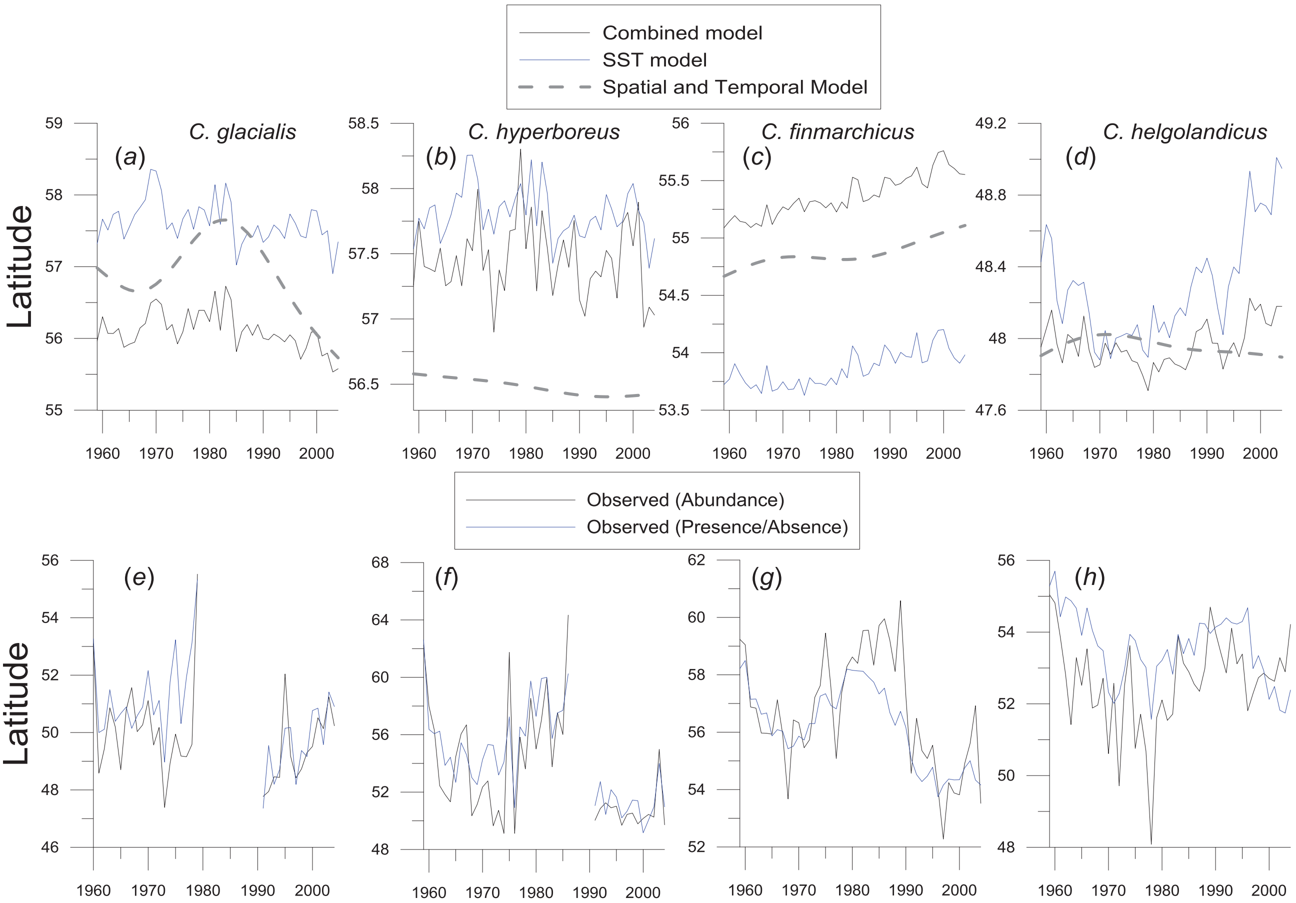
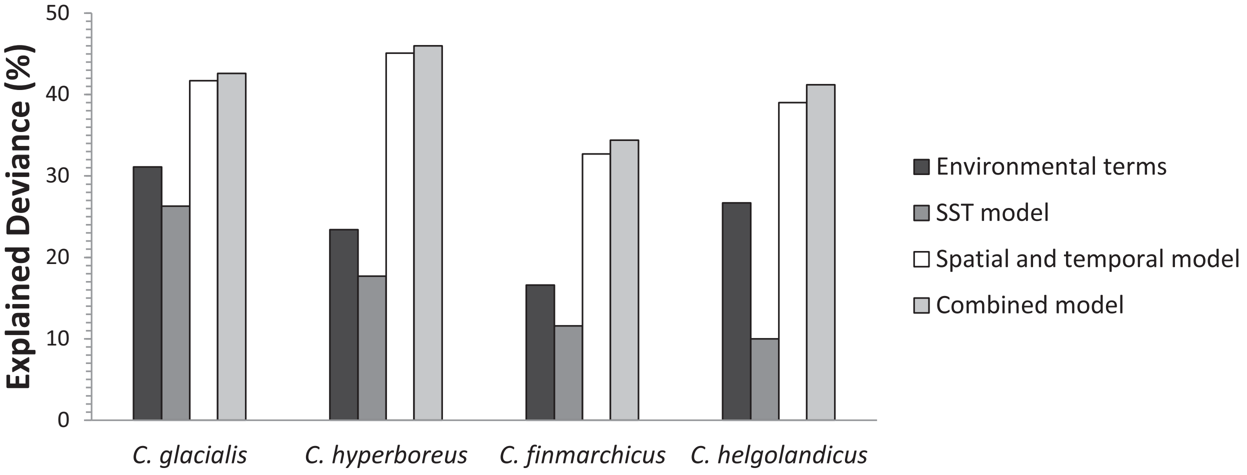
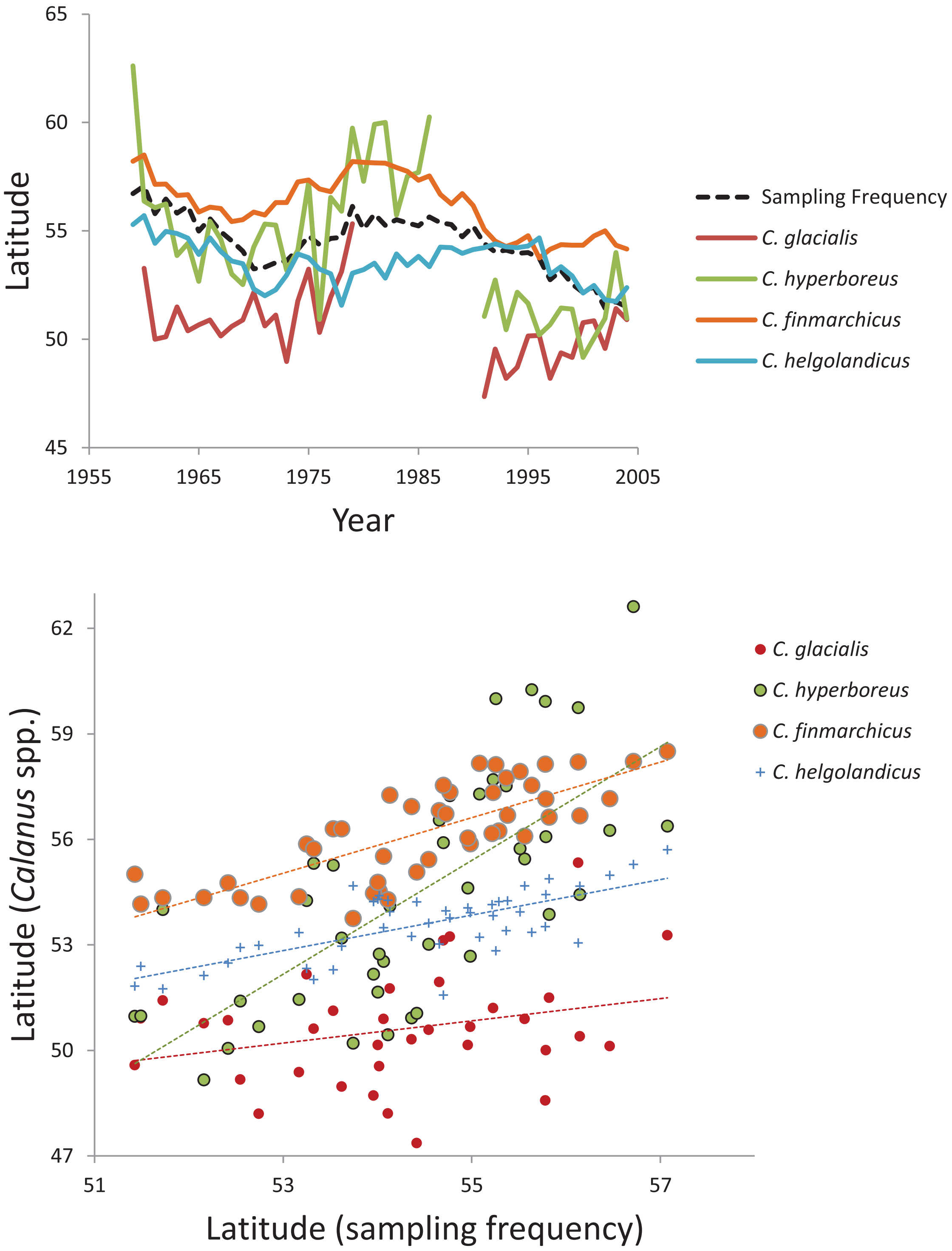

Combined model
SST model
Spatial and Temporal Model
Latitude
C. glacialis
(a)
C. hyperboreus
(b)
C. finmarchicus
(c)
C. helgolandicus
(d)
59
58
57
56
55
58.5
58
57.5
57
56.5
56
55.5
55
54.5
54
53.5
49.2
48.8
48.4
48
47.6
1960
1970
1980
1990
2000
Observed (Abundance)
Observed (Presence/Absence)
(e)
(f)
(g)
(h)
56
54
52
50
48
46
68
64
60
56
52
48
62
60
58
56
54
52

Fig. 7.

Supplementary Information 1. Explained deviance according to environmental variables, and the three models used (SST, spatial and temporal, and the combined model).



Supplementary Information 2. Mean latitude of sampling frequency and gravity centre of *Calanus* spp. of observed (Presence/Absence) data over the period (*a*) and linear regression analysis (*b*). Correlation coefficients: for *C. glacialis* (r^2=0.078, p=0.098), *C. hyperboreus* (r^2=0.498, p<0.0001), *C. finmarchicus* (r^2=0.61, p<0.0001), *C. helgolandicus* (r^2=0.499, p<0.0001).



Supplementary Information 3. Evolution of *C. finmarchicus* occurrence models (SST model, as habitat suitability model, and spatial and temporal model as population data reconstruction) between 1959 and 2004 (Month: June). Map key: orange is presence and grey color is absence.