
Modelling the future biogeography of North Atlantic zooplankton communities in response to climate change

Ernesto Villarino^{1,*}, Guillem Chust¹, Priscilla Licandro², Momme Butenschön³,
Leire Ibaibarriaga¹, Aitor Larrañaga⁴, Xabier Irigoien⁵

¹AZTI-Tecnalia, Marine Research Division, Txatxarramendi ugarteia z/g, 48395 Sukarrieta (Bizkaia), Spain

²Sir Alister Hardy Foundation for Ocean Science, The Laboratory, Citadel Hill, Plymouth PL1 2PB, UK

³Plymouth Marine Laboratory (PML), Prospect Place, Plymouth PL1 3DH, UK

⁴Laboratory of Stream Ecology, Department of Plant Biology and Ecology, University of the Basque Country, PO Box 644, 48080 Bilbao, Spain

⁵Red Sea Research Center, King Abdullah University of Science and Technology (KAUST), Thuwal 23955-6900, Saudi Arabia

*: Corresponding author : Ernesto Villarino, email address : evillarino@azti.es

Abstract:

Advances in habitat and climate modelling allow us to reduce uncertainties of climate change impacts on species distribution. We evaluated the impacts of future climate change on community structure, diversity, distribution and phenology of 14 copepod species in the North Atlantic. We developed and validated habitat models for key zooplankton species using continuous plankton recorder (CPR) survey data collected at mid latitudes of the North Atlantic. Generalized additive models (GAMs) were applied to relate the occurrence of species to environmental variables. Models were projected to future (2080–2099) environmental conditions using coupled hydroclimatic–biogeochemical models under the Intergovernmental Panel on Climate Change (IPCC) A1B climate scenario, and compared to present (2001–2020) conditions. Our projections indicated that the copepod community is expected to respond substantially to climate change: a mean poleward latitudinal shift of 8.7 km per decade for the overall community with an important species range variation (–15 to 18 km per decade); the species seasonal peak is expected to occur 12–13 d earlier for *Calanus finmarchicus* and *C. hyperboreus*; and important changes in community structure are also expected (high species turnover of 43–79% south of the Oceanic Polar Front). The impacts of the change expected by the end of the century under IPCC global warming scenarios on copepods highlight poleward shifts, earlier seasonal peak and changes in biodiversity spatial patterns that might lead to alterations of the future North Atlantic pelagic ecosystem. Our model and projections are supported by a temporal validation undertaken using the North Atlantic climate regime shift that occurred in the 1980s: the habitat model built in the cold period (1970–1986) has been validated in the warm period (1987–2004).

Keywords: Zooplankton ; Habitat suitability ; GAM ; Climate change ; North Atlantic ; Biogeography

INTRODUCTION

Plankton communities can quickly respond to climatic variability (e.g. Beaugrand et al. 2002a). Impacts of global warming affect the whole pelagic ecosystem from plankton to higher trophic levels (Richardson & Schoeman 2004, Beaugrand & Kirby 2010, Beaugrand 2012). Such impacts can result in poleward movements in species distribution (Johns et al. 2001, Perry et al. 2005, Parmesan 2006, Beaugrand et al. 2009, Chust et al. 2014a), shifts in phenology (Edwards & Richardson 2004, Moore et al. 2011) or changes in abundance and community structure (Molinero et al. 2008, Kirby & Beaugrand 2009, Chust et al. 2014b). Species responses to climate change may lead to local extinction and invasions, resulting in changes in the pattern of marine species richness and trophic mismatches (Cheung et al. 2009). Therefore, assessing how these biogeographic processes will change in the future is a key prerequisite to anticipate consequences of climate change on marine ecosystems.

Sea temperature is one of the most important physical variables structuring marine ecosystems. There is overwhelming evidence that the composition, abundance and phenology of plankton communities are closely linked to water temperature (Richardson 2008). Throughout the North Atlantic Ocean, a general increase in temperature has been observed in the past century (Beaugrand 2009) and future ocean temperatures have been forecasted to increase by coupled atmosphere–ocean general circulation models (AOGCMs). In particular, the North Atlantic has warmed faster than all other ocean basins, and climate change scenarios project sea surface temperature isotherms to shift up to 600 km northwards by the end of the 21st century (Lee et al. 2011).

Habitat suitability (species distribution) models (Guisan & Zimmermann 2000, Elith & Leathwick 2009) have been widely used to project how species ranges might change in the future. These models aim to define the species ecological niches by relating the occurrence of species to environmental variables (e.g. temperature, depth and phytoplankton) in the same area. They rely on the environmental niche concept of Hutchinson (1957), in which a multi-dimensional hypervolume is defined by the combination of multiple environmental conditions that requires a species population to survive and reproduce. Habitat suitability models have been widely used to project how species ranges might change in the future. Then, using projections from the Intergovernmental Panel on Climate Change (IPCC), we can investigate how environmental changes will affect future species distributions (Guisan & Thuiller 2005).

In the past decade, several studies using species distribution models and continuous plankton recorder (CPR) data with future climate change scenarios have been published. For example, Helaouët & Beaugrand (2009) forecasted a poleward movement of *Calanus finmarchicus* of 1° latitude by the end of the 21st century; Beaugrand et al. (2008) analysed the reasons behind the climate-driven ecosystem future shifts of cod, zooplankton and phytoplankton; Reygondeau & Beaugrand (2011) and Beaugrand et al. (2011) used the Non-Parametric Probabilistic Ecological Niche Model (NPPENM) to project *C. finmarchicus* distribution through the next century; while Beaugrand et al. (2013) investigated how climate-induced changes in temperatures will alter marine zooplankton both locally and globally. Most of these studies have used the NPPENM, which is based on the Mahalanobis distance (MD) algorithm (Mahalanobis 1936). A recent work by Chust et al. (2014a) shows that generalized additive models (GAMs) perform well in detecting latitudinal shifts of species and identifying the causes.

So far most of the bioclimatological research is concentrated on a single species (Bonnet et al. 2005, Beaugrand et al. 2007, Helaouët & Beaugrand 2007, Helaouët et al.

2011, Reygondeau & Beaugrand 2011, Beaugrand et al. 2013) and there are very few works at community level (Beaugrand et al. 2000, 2002b, 2009, Beaugrand & Ibañez 2002, Woodd-Walker et al. 2002). Yet, some of the publications analysed the historic plankton biogeographical shifts in the North Atlantic Ocean (e.g. Reygondeau & Beaugrand 2011). However, little is known about the future spatial distribution of copepod biodiversity, seasonal changes and latitudinal shift in the North Atlantic Ocean, despite their importance in marine food webs.

Here, we analysed a zooplankton community to detect future biogeographic changes in species distribution and phenology, and to identify spatial and temporal patterns of diversity. This will allow us to project the community shifts and their consequences in the North Atlantic Basin. In particular, our aim was to develop and validate habitat models in key zooplankton species using CPR survey data collected at mid latitudes of the North Atlantic (35 to 65° N, Fig. 1) to be reliably extrapolated to future climate scenarios. To do that, we built a model using the data from a cold period (1970–1986) and evaluated its performance under a warm regime (1987–2004). Subsequently, the model was used to project species distributions, community composition and phenological changes at the end of the century under climate change scenarios.

MATERIALS AND METHODS

Environmental data

A set of 7 environmental variables was used to build the N-dimensional ecological niches of copepod species and to predict their probability of occurrence over the North Atlantic Ocean: sea surface temperature (SST), sea surface salinity (SSS), bathymetry, oxygen, pH, sea surface phytoplankton biomass (Pc) and mixed layer depth (MLD). SST and SSS (salinity especially in coastal environments) are essential factors because of their recognized influence on spatial distribution of *Calanus* spp. (Mauchline 1998, Helaouët & Beaugrand 2009, Helaouët et al. 2011, Reygondeau & Beaugrand 2011). Bathymetry was selected because it has been suggested that it influences the distribution of some copepod species in regions such as the southern North Sea (Reygondeau & Beaugrand 2011). Phytoplankton is an important food source for *Calanus* spp. that dominates zooplankton biomass in the North Atlantic (Irigoien 2004, Møller et al. 2012, Melle et al. 2014). MLD is an important parameter for phytoplankton production and controls the spatial distribution of many plankton species (Longhurst 2007). Oceanic pH influences calcifying organisms such as coccolithophorids, foraminifers, corals and pteropods (Orr et al. 2005, Kroeker et al. 2010).

SST, SSS, Pc, oxygen and pH data were extracted from a 1960–2004 hindcast of an implementation of the **NEMO-ERSEM** model forced with atmospheric reanalysis data from the Drakkar Forcing Set 4 (DFS4) composite of **NCEP** and European Centre for Medium-Range Weather Forecasts (ECMWF) fields. MLD data were obtained from the Center for Marine and Atmospheric Sciences (ZMAW, Hamburg) and used as a proxy of water column stability. MLDs were obtained from vertical profiles of temperature and salinity (de Boyer Montégut et al. 2004), using the classical density criterion of 0.125 (Levitus 1983). Bathymetry was extracted from **ETOPO1** global model (NOAA). Data were organized in 1° longitude and 1° latitude grid resolution available for every month of the period 1970–2004.

Biological data

Data on the abundance (mean density ind. m⁻³) of 4 species (*Calanus finmarchicus*, *C. glacialis*, *C. helgolandicus* and *C. hyperboreus*) were obtained from the CPR database. The CPR survey is an upper-layer plankton monitoring programme that has regularly collected samples, at monthly intervals, in the North Atlantic and adjacent seas since 1946 (Warner & Hays 1994). The number of records collected for the 4 *Calanus* spp. from the CPR survey during the 1970 to 2004 period is shown in Fig. A1 in the Appendix.

These calanoids are key species in subarctic (*C. finmarchicus*) and temperate shelf-edge (*C. helgolandicus*) regions of the North Atlantic Ocean (Bonnet et al. 2005, Speirs et al. 2005). *C. helgolandicus* is considered to be a pseudo-oceanic species, i.e. a species that can be found in oceanic and neritic waters, but it is mostly abundant above the shelf edge (Beaugrand et al. 2002b). *C. glacialis* and *C. hyperboreus* are Arctic species, while *C. finmarchicus* is a subarctic species that overlaps in size range with *C. helgolandicus*. *C. hyperboreus* is the largest among them.

In order to have a better representation of the copepod community at North Atlantic Basin scale, data on another 10 copepod species (ind. m⁻³) (*Candacia armata*, *Centropages typicus*, *Centropages hamatus*, *Metridia lucens*, *Paraeuchaeta norvegica*, *Paraeuchaeta hebes*, *Pleuromamma borealis*, *Pleuromamma robusta*, *Pseudocalanus elongatus* and *Temora longicornis*) were downloaded from the National Marine Fisheries Service NMFS-COPEPOD global plankton database (www.st.nmfs.noaa.gov/copepod/data/sahfosatl/index.html) between 1995 and 1999. It is also based on CPR survey and it represents one-third of the CPR records collected in the same region. Those species were selected as they were the most abundant copepod taxa identified at species level (with more than 100 occurrences in the data set). The selected 14 species represent 49.3% of the total occurrences sampled in the community, hence, well representing the overall community in terms of abundance. All CPR data used in the present study were gridded within 35 to 65° N and -75° W to 2° E at 1 by 1° spatial resolution using the inverse-distance interpolation method, and analysed monthly.

Habitat modelling

We generated models based upon the prominent climate drivers for the most abundant 14 copepod species in the study area. First, model selection and validation was evaluated for 4 species (*Calanus finmarchicus*, *C. glacialis*, *C. helgolandicus* and *C. hyperboreus*) using the entire time series from 1970 to 2004. In particular, we compared GAMs with other habitat model algorithms (MD and MaxEnt), and validated the model using randomly independent data sets and comparing cold (1970–1986) with warm (1987–2004) climate regimes. That way we assessed the capacity of the model to be extrapolated to future climate. Second, we built habitat models on the other set of copepod species (10 species) in the same way as we did for the main 4 *Calanus* spp. using data from the 1995–1999 period. Thus, we built habitat models of 14 species to (1) evaluate the impacts of future climate change on community structure in the 2080–2099 period compared to present conditions (2001–2020), (2) quantify the poleward shift of species distribution, and (3) analyse phenological changes of the species in the North Atlantic Ocean at community level, with model outputs corresponding to the IPCC Special Report on Emissions Scenarios A1B global warming scenario (IPCC 2007).

Species distribution models assume that observations represent a species at equilibrium with its environment. Here, GAMs (Hastie & Tibshirani 1990, Wood 2006) were used to model occurrences for each of the 4 *Calanus* spp. as a function of environmental factors (SST, SSS, MLD, pH and bathymetry) and potential food resource (Pc). The strength of GAMs is due to their capacity to deal with highly non-linear relationships between the

response and the set of explanatory variables, allowing asymmetrical unimodal distributions, since interaction between species and extreme environmental gradients may cause skewed responses (Oksanen & Minchin 2002). GAMs also enable us to model the seasonal response of the species. A GAM using the binomial error distribution and logit function of the `mgcv` package in R (Wood 2006) was used to relate copepod presence–absence data and the explanatory environmental variables, following Chust et al. (2014a). The CPR data set used here includes 112 161 samples across the spatial domain and irregularly distributed at yearly and monthly intervals.

Prior to model building, we tested for collinearity between explanatory variables by calculating variance inflation factors (VIF) with the `AED` package in R (Zuur et al. 2009). We excluded any variable that had a VIF > 3, and then recalculated VIF for the remaining variables. We iterated this process until all variables had a VIF < 3. The variable most often thrown out was oxygen, which highly correlated with temperature, thus we excluded it from the subsequent analysis.

We built and compared different GAMs for each species to find the optimal set of explanatory variables. Variable importance was assessed first by removing variables that were not statistically significant and second, by adding and removing terms and noting the change in deviance or gain (>1%) in a forward stepwise procedure. For environmental variables, the degree of smoothness of model terms was restricted from 3 to 5 in order to assume a unimodal, ecologically meaningful niche model sensu Hutchinson (1957), but allowing asymmetry. After characterizing the ecological niche of each species, the environmental space was projected into geographical space and the probability of occurrence of *Calanus* spp. was calculated.

To prevent overfitting, we first restricted the degrees of smoothness to ecologically interpretable responses according to niche theory; second we analysed the response of species occurrence to each environmental predictor; and third we used cross-validation methods to evaluate the reliability of the models (see section below)

GAM vs. MD and MaxEnt

GAM has been also compared with other 2 habitat models (MaxEnt and MD algorithm) in order to assess its performance. Both MaxEnt and MD algorithm are ecological niche models using presence-only species records, although they can use absences to model validation. They are implemented in the `dismo` R package (Hijmans et al. 2013), which is specially designed to model species distributions that do not migrate or shift during seasonal cycle, since it uses static environmental layers. Contrary to MD algorithm and MaxEnt habitat model techniques, GAM presents the advantage to model the seasonal response of the species resulting in a more ‘dynamic’ habitat modelling technique. Hence, only for the purpose of comparing performances of GAM with MaxEnt and MD algorithms, we reduced the data set into a unique spatial layer by accumulating occurrences of all years and months. The MD algorithm technique for a given point expresses the distance between this point and the species optimum in the ecological space (Farber & Kadmon 2003, Calenge et al. 2008, Nogués-Bravo et al. 2008, Etherington et al. 2009). MaxEnt uses the principle of maximum entropy to estimate a set of functions that relate environmental variables and habitat suitability in order to approximate the niche and potential geographic distribution of the species (Phillips et al. 2006). MaxEnt model minimizes the relative entropy between 2 probability densities (presence data and the landscape data) defined in a covariate space (Elith & Leathwick 2009, 2011). Although MaxEnt has been widely used in terrestrial species (e.g.

Graham & Hijmans 2006, Monterroso et al. 2009, Young et al. 2009, Yates et al. 2010), applications in pelagic species are still scarce.

Model validation

The 3 models used were validated using independent data sets for model building and model validation (Burnham & Anderson 2002). We validated the models in 2 ways: (1) k -fold random resampling, and (2) temporal cross-validation. In the first procedure, the data is first partitioned into k equally sized segments or folds. Subsequently, k iterations of training and validation are performed so that within each iteration a different fold of the data is held-out for validation while the remaining $k - 1$ folds are used for model fitting (Hijmans 2012). We used $k = 5$, hence, 80% of the CPR observations were used for model building, and the other 20% (i.e. independent) for model validation in an iterative procedure that was repeated 5 times. Hold-out validation avoids the overlap between training data and test data, yielding a more accurate estimate for the generalization performance of the algorithm. The comparison between the accuracy (the proportion of true results) of the model (all observations) and that of cross-validated results also permits the detection of model overfitting, which reduce the usefulness of such models for extrapolation.

Second, the North Atlantic regime shift in the 1980s (Reid et al. 2001, Beaugrand 2004, deYoung et al. 2004) was taken into account to perform a temporal cross-validation of the models (i.e. the second procedure of model validation). A wide range of studies have investigated the North Atlantic and North Sea climate decadal fluctuations that affect phytoplankton (Edwards et al. 2001, Reid et al. 2001, Beaugrand & Reid 2003), zooplankton (Beaugrand et al. 2002, Beaugrand 2003, 2004) and fish populations (Alheit & Hagen 1997, Reid et al. 2001). To this end, we performed a Wilcoxon rank sum test (Wilcoxon 1945) between a cold period from 1970 to 1986 (mean SST: $11.64 \pm \text{SE } 0.12^\circ\text{C}$) and a warm period from 1987 to 2004 (mean SST: $12.10 \pm \text{SE } 0.26^\circ\text{C}$) and defined in our time series 2 different climatic regimes ($p < 0.0001$) (Fig. 2). Subsequently, we built the models and compared the 4 *Calanus* spp. between cold (1970–1986) and warm (1987–2004) periods. We tested the habitat model predictive capacity validating the cold period into the warm period and vice versa, using the area under the receiver operating characteristic curve (AUC) (Hanley & McNeil 1982, Raes & ter Steege 2007), and confusion matrix accuracy assessment indices (VanDerWal et al. 2011) (see section below). This approach enabled us not only to explore the model behaviour for different climates but also to see to what degree of reliability we can project the model to future warmer climate conditions. The temporal cross-validation was undertaken only to the 4 *Calanus* spp., since the NMFS-COPEPOD time series (1995–1999) including the other set of 10 copepod species is too short.

Model evaluation

We assessed the predictive performance of the overall model and the held-out folds using the AUC, a measure of the ability of the predictions to discriminate presence from absence, and accuracy indices derived from confusion matrix. To this end, the species presence modelled probability was converted to either presence or absence using probability thresholds following 2 criteria: sensitivity (true predicted presences) = specificity (true predicted absences), and maximization of sensitivity plus specificity, as reported in Jiménez-Valverde & Lobo (2007). Thus, the cases above this threshold are assigned to presences, and below to absences. Given the threshold value, a confusion matrix was calculated yielding outputs of correctly identified records of presence and absence to have an overall accuracy estimate of model performance. Overall accuracy ranges from 0 to 100% and AUC values from 0.5 (random sorting) to 1 (perfect discrimination). Accuracy is a good indicator of

model performance since it is the proportion of true results, either true positive or true negative, in a population.

Climatic scenario for the 21st century

In order to assess the copepod response to climate change, selected habitat models were projected to future conditions and thresholds were applied to the resulting probability maps. We used modelled environmental predictors (SST, SSS and Pc) from the DKRZ-CERA database (<http://cera-www.dkrz.de>) at IPCC A1B scenario for the 2001–2099 period. More in detail, we used the Hamburg Ocean Carbon Cycle (HAMOCC) model for the phytoplankton, and the Max Planck Institute's Ocean General Circulation Model (MPIOM) (JungCLAUS et al. 2013) for the physical set up. HAMOCC, embedded into MPIOM, simulates the oceanic cycles of carbon and other biogeochemical elements (Ilyina et al. 2013). Technical details of the ocean model MPIOM can be found in Marsland et al. (2003).

Assessing impacts of climate change on copepods

The impacts of climate change on copepods were assessed by estimating latitudinal shifts of each species, phenological changes and spatial patterns of biodiversity indices.

The latitudinal shift (km) of the species was calculated by comparing the geographic centre of gravity of its suitable area for present (2001–2020) and future scenarios (2080–2099). The centre of gravity is defined as the mean geographic location of a population (Wuillez et al. 2009). Gravity centres of habitat models showing well-separated east to west population patches (*C. armata*, *C. hamatus* and *P. hebes*) were calculated separately and then averaged. We assumed unlimited copepod dispersal to estimate the extent of gain or loss of suitable space from present to future modelled conditions.

We computed the changes in the seasonal cycle or phenology of *Calanus* spp. by analysing the difference in terms of days on the annual maxima of the copepods' probabilities of occurrence in both present and future conditions. The timing of the peak was determined as the date when the modelled species occurrences reached the annual maximum. Monthly mean species occurrences were used to build a GAM fitted function (with a Gaussian link and cyclic cubic regression spline) to predict the seasonal peaks, and to quantify the phenological shifts in days.

We carried out a seasonal quantitative analysis only on *C. hyperboreus* and *C. finmarchicus* since their predicted phenological patterns matched relatively well with observed ones. We did not perform any phenology analysis in the NMFS-COPEPOD set of species either, due to time series shortness.

Changes in local biodiversity were assessed in terms of species turnover, colonization and extinction. In particular, we mapped 4 biodiversity components of change: (1) stability, i.e. the number of species that were present or absent at both present and future scenarios at each pixel; (2) extinction, i.e. the number of species that were present at present and were absent in the future; (3) colonization, i.e. the number of species that were absent at present and present in the future; and (4) turnover, i.e. the number of species that suffer either colonization or extinction.

Species assemblages were categorized following Beaugrand et al. (2009) in 2 main groups: (1) the 'cold-water species assemblage', including the cold-temperate mixed water (*Pleuromamma robusta*), subarctic (*Calanus finmarchicus*) and Arctic (*Calanus hyperboreus* and *Calanus glacialis*) species assemblages, and (2) the 'warm-water species assemblage', including the warm-temperate oceanic and pseudo-oceanic (*Pleuromamma borealis*,

Paraeuchaeta norvegica, *Metridia lucens* and *Paraeuchaeta hebes*), the temperate pseudo-oceanic (*Centropages typicus*, *Candacia armata* and *Calanus helgolandicus*) and continental shelf (*Pseudocalanus elongatus*, *Temora longicornis* and *Centropages typicus*). This simplified way of proceeding enabled us to understand which set of species was more affected by environmental change.

RESULTS

Future environmental changes

MPIOM SST model projections forecasted an average (\pm SD) increase of $1.54 \pm 0.35^\circ\text{C}$ (Wilcoxon rank sum test, $p < 0.0001$) from 2001–2020 to 2080–2099 in the North Atlantic study area (Fig. 3). Our spatial examination of changes in SST reveals regional differences. For instance, SST increased by 4 to 6°C in areas of the Gulf Stream extension and the Newfoundland continental shelf, south of the Oceanic Polar Front (i.e. $60\text{--}45^\circ\text{W}$ and $43\text{--}48^\circ\text{N}$). On the other hand, in some areas of the subarctic region south of the Labrador Current in the North Atlantic Gyre (i.e. $40\text{--}30^\circ\text{W}$ and $55\text{--}60^\circ\text{N}$), SST is expected to decrease between 1 and 0°C .

The HAMOCC biogeochemical model projects a general Pc decrease by the end of century in the North Atlantic. Results showed a clear east to west asymmetry on Pc changes, with strong negative differences (-30 to -20 mg C m^{-3}) along the east of the Oceanic Polar Front, from the subarctic region south of Iceland down to the Bay of Biscay and the Southern European shelf edge (i.e. $25\text{--}5^\circ\text{W}$ and $38\text{--}60^\circ\text{N}$). In turn, a slight increase in Pc ($0\text{--}10\text{ mg C m}^{-3}$) is projected along the Flemish Cup area and extending through the Oceanic Polar Front (i.e. $50\text{--}40^\circ\text{W}$ and $43\text{--}50^\circ\text{N}$) (Fig. 3).

GAM habitat models

We evaluated the response of the *Calanus* spp. to each explanatory variable individually using GAMs (Table 1). SST was the most important environmental driver in the *Calanus* spp. environmental space, followed by SSS, depth and Pc. Oceanic pH and MLD explained less deviance of species occurrence, although pH was considered in the model selection as it accounted for more than 1% of deviance for all models.

Habitat suitability models were constructed for the 4 *Calanus* spp. (Fig. 4). All the subsequent environmental variables, i.e. SST, SSS, depth, pH and Pc, were included in all models except for *C. glacialis* (without pH and Pc) and for *C. helgolandicus* (without Pc).

The random cross-validation of models is shown in Table 2. The habitat models in the 4 *Calanus* spp. showed a slight drop in the accuracy measure if we compare all observations (74–85%) vs. the k -fold cross-validation (69–85%); this is owing to a slight signal of model overfitting. Here, *C. helgolandicus* showed low overall deviance explained (25.4%) in the habitat suitability models, whilst the other species deviance explained was higher: *C. finmarchicus* (46.9%), *C. glacialis* (34.1%) and *C. hyperboreus* (42.3%).

The temporal cross-validation enabled us to assess the model reliability to be extrapolated to different climates. Results have shown that model accuracy is relatively good (75–84%) for the models built in the cold period and extrapolated and validated in the warm period (Table 3). Therefore, species models can be used to be projected in future climate simulations with relative confidence.

GAM habitat models for the non-*Calanus* spp. set of copepods (Table 4) showed a slightly lower accuracy (64–74%) than for the 4 *Calanus* spp. Moderate deviance explained

was found in *Centropages typicus* (25.4%), *Centropages hamatus* (28.7%), *Paraeuchaeta norvegica* (27.5%), *Paraeuchaeta hebes* (35.4%) and *Temora longicornis* (24.9%). For the remaining set of species the deviance explained was lower (17.5–7.7%), as were the accuracy values. The difference in the accuracy values of the model using all the observations (76–63%) and those cross-validated (53–57%) indicated a slight overfitting in these latter models (Table 4).

Model comparison: GAM vs. MD and MaxEnt

MaxEnt ranked first in terms of model accuracy or performance, followed by GAM and MD, with similar values for *C. glacialis* and *C. helgolandicus* but higher values for GAM in *C. hyperboreus* and *C. finmarchicus* (Fig. 5).

However, we have shown that GAM, which is a presence–absence-based model, predicts correctly the potential distribution of *C. glacialis* along the Labrador Sea, Newfoundland shelf and the Davis Strait, where it is abundant according to Head et al. (2003) and Pomerleau et al. (2014), whilst both MaxEnt and MD predicted absence (Fig. A2 in the Appendix).

Latitudinal shift under climate change scenarios

Despite the different thermal window of each of the 14 species analysed, all centres of gravity have been located in the central temperate part (45–55° N) of the North Atlantic Ocean, both at present and future periods (Figs. 6 & 7). Distribution centroids of most of our studied species were projected to shift poleward under climate change (Table 5). All copepod assemblages showed a northward shift of 0.1–13.5 km per decade for the shelf-sea association species (*Paraeuchaeta hebes*, *Paraeuchaeta norvegica* and *Temora longicornis*), of 3.7–11.3 km per decade in the Arctic and subarctic association (*Calanus hyperboreus*, *Calanus glacialis* and *Calanus finmarchicus*) and of 1.9–17.8 km for temperate or warm-water species association (*Metridia lucens*, *Pleuromamma robusta*, *Pleuromamma borealis*, *Calanus helgolandicus*, *Centropages typicus* and *Candacia armata*). A southward migration in centre of gravity of ca. 11–15.4 km per decade was found in other shelf-sea and temperate association species (*Pseudocalanus elongatus* and *Centropages hamatus*). On average, a poleward community shift of 8.7 km per decade was predicted, with an important species range variation (–15 to 18 km per decade). Poleward shifts of the warm-temperate copepod assemblage were more important than the range contraction of the subarctic and Arctic species assemblage. These shift rates were generally associated with a reduction located at the southern edge of the species spatial distribution. Such changes could be linked to regional SST warming.

At species level, projections revealed a poleward shift with a slight contraction of the southern limit of habitat suitability distribution of the *C. finmarchicus*, *C. glacialis* and *C. hyperboreus*, and a shelfward constriction of *C. helgolandicus*, disappearing from oceanic warm waters south of the Oceanic Polar Front (Fig. 7).

The average northward retreat is more clearly seen in *C. finmarchicus*, *C. glacialis* and *C. hyperboreus*, with local projected shifts of up to 25–70 km per decade in the southern limits of their distribution. We observed that the probabilities of *C. finmarchicus* occupying large areas of the Labrador Sea and Baffin Bay will increase considerably by the end of the century, as well as in the northern North Atlantic Gyre and the Irminger Current. The *C. hyperboreus* and *C. glacialis* map showed a similar pattern: their distribution will be mainly reduced northwestward, from Labrador to Newfoundland and the Greenland Sea. The ecological niche of *C. finmarchicus* and *C. glacialis* will suffer an important habitat reduction

in the warm-temperate waters of the central North Atlantic around the Gulf Stream and the North Atlantic Drift provinces, with potential local extinctions. A mean poleward migration of *C. glacialis* of 11.3 km per decade is estimated, much more acute than in *C. finmarchicus* (3.7 km per decade). Its habitat suitability will probably respond to future warmer SST shifting northward to the Irminger Current, Faroe–Shetland Channel and Norwegian Trench (Figs. 6 & 7). A noticeable habitat gain in *C. glacialis* is predicted in the northern subarctic region, south of Iceland and the northern European shelf edge; this has contributed to a higher poleward shift of the centroid. Future projections of *C. hyperboreus* habitat suitability have also indicated a reduction in the southwestern edge of its spatial distribution where the species might face extinction. It will have a straightforward climatic response with a poleward mean latitudinal shift of ca. 8 km per decade. The species might disappear also from the southward flow of the **East Greenland Current**. Our models also predicted that *C. helgolandicus* might disappear from the warm-temperate subtropical areas of the North Atlantic and some areas of the Bay of Biscay and southern European shelf edge, and that it will colonize the North Atlantic Drift province and the east of the Oceanic Polar Front, with a relatively high net northward movement of ca. 18 km per decade (Figs. 6 & 7).

Ecological niche models of warm-temperate pseudo-oceanic (*Candacia armata* and *Centropages typicus*) and continental shelf assemblages (*Pseudocalanus elongatus*) also project a habitat gain in the temperate North Atlantic and along the Gulf Stream and North Atlantic Current. The warm-temperate *Pleuromamma borealis* and the cold mixed water *Pleuromamma robusta* also will gain habitat in the Oceanic Polar Front and subarctic region of the North Atlantic. The temperate *Paraeuchaeta norvegica* might face local extinction along the southern limits of its distribution. The overall suitable habitat is therefore expected to increase in these temperate-warm and shelf species assemblages. The habitat suitability of other sets of studied species did not show any latitudinal shift, but rather an east to west asymmetry: *Centropages hamatus* might colonize the Bay of Biscay and the southern European shelf edges, and *Paraeuchaeta hebes* would become extinct from the North Sea and the southern European shelf edge. The model explained deviance for *M. lucens* is too low (7.7%) to draw conclusions on its habitat suitability change.

The warm-temperate and continental shelf sets of species assemblages have shown the highest local northward shifts. Southern temperate regions are becoming warmer and are expected to provide suitable habitat for the warm-temperate and temperate pseudo-oceanic species assemblages. Thus, overall, warm species assemblages will respond faster to climatic change and cold species assemblages will retract their core distribution northward at a slower pace.

Phenology changes under climate change scenarios

Our projections showed an earlier timing of predicted occurrences of the annual maxima of 12 d in both copepod species (*C. finmarchicus* annual maxima at present was 15 April and in future was 3 April; *C. hyperboreus* at present was 27 April and in future was 15 April) (Fig. 8).

Species turnover under climate change scenarios

Results have shown a high species turnover area (4–11 species) south of the Oceanic Polar Front (42.8–78.5%) compared with the overall North Atlantic (ca. 10%), covering vast areas of the centre of the North Atlantic Drift and extending up to the northern boundary of the influence of the Mediterranean water (Fig. 9D). Another moderate turnover rate (2–4 species, 21.4%) was found in coastal zones of southern Bay of Biscay and in the continental

shelf current. High intensity of species invasion (3 to 5 new species) was projected to be concentrated **along through** the Oceanic Polar Front (Fig. 9C). Local extinctions were projected to be most common (3–6 species lost) in temperate waters of the North Atlantic, south of the Oceanic Polar Front and by the northern boundary of the influence of Mediterranean water (Fig. 8B). Areas of high turnover overlap with areas of both highest SST and Pc changes between present and future periods (Fig. 3), and also correspond relatively well with the southern edge of the cold-temperate, subarctic and Arctic species assemblage (*C. hyperboreus*, *C. glacialis* and *C. finmarchicus*), and the northern biogeographic boundaries of the warm-temperate species assemblage (*C. armata* and *C. typicus*) (Fig. 7).

DISCUSSION

Habitat suitability models

Habitat suitability modelling enabled us to identify 3 key environmental variables (SST, SSS and depth) that determine the present distribution of *Calanus* spp. SST is, in general, the environmental driver explaining most of the variance of species occurrence in the 4 *Calanus* spp. (especially in *C. glacialis*) habitat models. Previous niche-model-related works (Beaugrand et al. 2013, Chust et al. 2014a) showed similar results. It is interesting to pinpoint that models also included Pc and pH. Pc seems to be a controlling factor in the probability of occurrence and distribution of *C. hyperboreus* and *C. finmarchicus*, but not of *C. glacialis* and *C. helgolandicus*. **These variables** have not been used frequently in zooplankton habitat modelling to date, **since they explain low variance of *Calanus* spp. occurrence, as has been shown in previous attempts** (e.g. Reygondeau & Beaugrand 2011). This is probably because Pc represents only a part of the food available and because food is not a limiting factor above the mixed layer depth.

The MD and MaxEnt species distribution models failed in predicting the spatial distribution of *C. glacialis* along the Labrador Sea, Newfoundland shelf and the Davis Strait, probably because the CPR routes do not regularly cover the northern Labrador Sea area and these types of models are based only on the presence points while not accounting for absence points. Instead, GAM has proved to be a useful and accurate model to quantify the ecological niche of *Calanus* spp. in the North Atlantic. This conclusion is based on (1) the accuracy values of random (69–85%) and temporal (74–85%) validation, (2) its flexibility to incorporate seasonal variability, and (3) its performance comparing both accuracy values and spatial distribution maps with MaxEnt and MD algorithms. The relatively good accuracy of temporal cross-validation enabled us to use confidently the GAM-based habitat models generated for *Calanus* spp. in the future climate simulation.

It should be noted that there are some local differences (especially south of the Oceanic Polar Front) between the GAM habitat models built with the NEMO-ERSEM model and the MPIOM-HAMOCC for the present time in the 4 *Calanus* spp. The latter habitat suitability models are biased, having their gravity centres located farther south. However, since we are using the same model (MPIOM-HAMOCC) to make the projections at future and present conditions, then differences in environmental covariates will stay relative and vary accordingly in time.

One of the limitations of the niche modelling approach is that in principle it does not include the effects of dispersal that can play a significant role in the distribution of plankton (Irigoien et al. 2011, Chust et al. 2103). However, it has to be taken into account that when we use field distribution data to build the model we partially include such effects, albeit in an indirect way. **Some of the areas where we find a species, and therefore model as suitable**

niche, may actually be suitable due to transport, not because of the environmental conditions. Therefore, the model is likely to let zooplankton distribute in a wider area than its optimal niche.

Latitudinal shift

This study showed that the Hutchinson's ecological niche of *C. finmarchicus* and that of *C. helgolandicus* will keep well separated in the future. This species niche separation was well described for the historic CPR data set (1942–2002) in Helaouët & Beaugrand (2007). The modelled spatial distribution of *C. finmarchicus* showed that this species mainly occurred in areas above the Oceanic Polar Front (Dietrich 1964). It has a broader tolerance interval than its congener *C. helgolandicus* (Helaouët & Beaugrand 2007), though it is able to support larger environmental variations. In fact, it co-occurs with the Arctic *C. glacialis* and *C. hyperboreus* (Hirche 1991) at the northern edge of its distribution, i.e. north of Iceland, while in the northeastern North Atlantic, the North Sea and in the southern part of the Norwegian Sea, it co-occurs with *C. helgolandicus* (Conover 1988). Results also showed that the biogeographical range of *C. glacialis* and *C. hyperboreus* will be rather similar. The present biogeographic features of *C. finmarchicus*, *C. hyperboreus* and *C. glacialis* have been relatively well resolved by our habitat models. *C. helgolandicus*, instead, is more adapted to the temperate waters of the Atlantic Westerly Winds Biome (Longhurst 1998), although our projections have shown that it will mainly present along shelf edges in the Mediterranean, the Northeast Atlantic, the North Sea and south of Iceland. The ecological niche of this species will respond fast to climate change, from local extinction in the warming waters of the temperate west North Atlantic to colonization in waters of the Newfoundland continental shelf. Therefore, *C. helgolandicus* can be considered a **climate-sensitive species**.

Our GAM models projected a plankton community poleward latitudinal shift of 8.7 km per decade on average, within the range of 1.4–28 km per decade estimated by Cheung et al. (2009) for marine fishes and invertebrates, but substantially less than the 190 km per decade estimation of Sorte et al. (2010) for 129 marine species. At species level, the rate of northward movement projected in *C. finmarchicus* (3.7 km per decade) is considerably lower than the change in distribution suggested by Helaouët & Beaugrand (2009) for nearly the same area, period and climate change scenario (1° latitude and ca. 111 km per decade). The main differences between those studies and ours are the taxa assemblage analysed, the statistic considered (distribution limits vs. geographic centres) and the model algorithm used.

In this study, the use of GAMs to predict the habitat suitability of the species has been limited to a geographical subset in the North Atlantic; hence, the biogeographic range of the species is not fully represented. This limitation results in an underestimation of the poleward mean latitudinal shift of the species. Not all the species are projected to shift northward: *Centropages hamatus* (15.4 km per decade) and *Pseudocalanus elongatus* (11 km per decade) will shift southward by the end of century. This could be because the southern colonized area of these 2 species is larger compared to the north area, yielding a net southward migration. SST is not the main driving effect in the distribution of these 2 continental shelf species assemblages (6.6% out of the total 28.7% explained deviance in *C. hamatus* and 1.0% out of 17.6% in *P. elongatus*) and other environmental variables, such as P_c , appear to be more important. We think that although covering the whole biogeographic range of the species is preferable, the estimation of gravity centre considered here is relatively reliable to capture population shifts.

Phenology changes

Our models predicted an advance in the annual peaks of 12–13 d between **present time** and the end of the 21st century for *C. finmarchicus* and *C. hyperboreus*, which is in line with previous studies highlighting the advance in spring seasonal peaks for zooplankton time series; Edwards & Richardson (2004) reported a 10 d advance in annual maxima in North Sea copepods from 1958 to 2002, while Greve et al. (2004) estimated an annual peak occurring 37 d earlier in Helgoland Road cladocerans from 1975 to 1999.

Zooplankton timing variability is often linked with temperature and/or Pc during the preceding weeks or **month** (Ji et al. 2010). For taxa that have their maximum occurrences or abundances and activity in spring–summer like *C. finmarchicus* and *C. hyperboreus*, the usual pattern is ‘earlier when warmer’ (Edwards & Richardson 2004, Mackas et al. 2007). Our projected seasonal peak of the 2 species is also occurring earlier, responding to a climate warming trend by the end of the century; these changes may propagate higher up in the food web.

Results of the phenology model showed that after the SST seasonal peak by mid-April, zooplankton maxima will occur: *C. finmarchicus* and *C. hyperboreus* showed a positive relationship with a ‘sudden’ increase in SST by the beginning of April. On the other hand, modelled phytoplankton blooms will only advance a week from the present to 2100 (data not shown), which presumably shows a higher dependency on day length and light intensity rather than temperature (Eilertsen & Wyatt 2000). Results also showed that phytoplankton blooms will occur 1 or 2 wk later than *C. finmarchicus* and *C. hyperboreus* annual peaks, underlining the higher dependence of these copepods on temperature rather than food availability. Melle et al. (2014) also reported positive relationships between maximum abundances of *C. finmarchicus* and maximum temperatures in the North Atlantic, with no clear relationship with Pc maximum.

The aforementioned phenology studies as well as our modelled phenology approach are spatially limited because they take into account only a subset of the entire geographic range of the species. If the overall distribution area had been analysed, we would not expect to obtain substantial shifts in phenology, since the species would shift poleward in the future to a similar thermal window where it could succeed. On the contrary, local studies of zooplankton phenology (e.g. Mackas et al. 1998) in a subarctic Pacific station (Bornhold et al. 1998, in the Strait of Georgia), reported higher shifts (30–60 d), since local environmental changes are subjected to more variability and the climatic response of the species will be more pronounced. Our spatial scale is in-between local and entire biogeographic range studies, which might explain the intermediate mean shifts values found.

Species turnover

Habitat models projected that the boundaries of species biogeographic domains are prone to suffer higher extinction or colonization rates. These areas with high turnover of species coincide with a large predicted SST increase by the end of century, where warm species assemblages could benefit to settle their populations there, while the southern limits of the cold subarctic and Arctic species assemblages will retract.

These projections, which follow basic constraints on the eco-physiology of animals (Tewksbury et al. 2008), **support the theory** that marine communities at the extreme ends of their ecological niche are especially sensitive to local extinction due to climate change. The retreat of the southern biogeographical limits of species leads to a general range constriction, and the poleward expansion of the species in the subpolar regions is limited by the availability of suitable habitats. The Oceanic Polar Front (Dietrich 1964) has acted as a sharp boundary for shelf edges and warm-temperate species associations limiting dispersal

northward. These predicted species turnover patterns will trigger changes in the community structure of copepods, which are key species at the base of the marine food webs, and these changes may propagate through higher trophic levels (Kirby & Beaugrand 2009, Chust et al. 2014b), having an ecosystem-wide effect on the North Atlantic marine provinces.

Model uncertainties and implications

Our study projects the spatial distribution of a representative subset of the North Atlantic copepod community. We have gained new insights on where the species are potentially able to expand or extinct locally. GAM-based distributions of *Calanus* spp. in the 1970–2004 period are in agreement with the observed spatial distribution from CPR surveys (Helaouët & Beaugrand 2007), conventional sampling data sets (Heath et al. 2004, Reygondeau & Beaugrand 2011), CPR data reconstruction studies (Chust et al. 2014a) and with other distribution studies inferred from models (Speirs et al. 2005, Durbin & Kane 2007, Kane & Prezioso 2008, Hinder et al. 2014). Therefore, the general agreement of our models with occurrence records and other modelled distribution studies supports the view that climatic (mainly SST), and also SSS, depth and biological (phytoplankton) factors are enough to provide a first approximation of niche shifts under climate warming (Pearson & Dawson 2003, Araújo & Guisan 2006).

In their simplest form, habitat suitability models are limited, since they ignore the adaptive potential of species. Indeed, there is some evidence that species may adapt to changing conditions with a rapid genetic response to natural selection instead of a direct reaction of the species following their ecological niche (Lavergne et al. 2010, Dam 2013). This has been documented for small and spatially isolated zooplankton such as *Calanus helgolandicus* (Yebra et al. 2011), or chaetognats (Peijnenburg et al. 2006) in the Northeast Atlantic, Mediterranean and Black Sea, but not in the North Atlantic for *C. finmarchicus* (Provan et al. 2007). On the other hand, niche conservatism has been observed on palaeoclimatic scales (Crisp et al. 2009). In this sense, we assumed that on the time scale of this study, zooplankton have a limited evolutionary response capability to climate change (Helaouët & Beaugrand 2009, Reygondeau & Beaugrand 2011, Stegert et al. 2010). Therefore, our projections assume no thermal adaptation of the species (sensu population fitness) to a changing environment. This assumption is supported by a recent study (Hinder et al. 2014) revealing that *C. finmarchicus* and *C. helgolandicus* show a lack of thermal adaptation to rising temperatures. Species that fail to acclimatize physiologically or evolve genetically to increasing temperature will either move northward following their habitats (Walther et al. 2002, Parmesan & Yohe 2003, Hickling et al. 2006, Parmesan 2005, 2006, Thomas 2010) or become extinct (Thomas et al. 2004).

Successful shifting species may have characteristics similar to those postulated for successful introduced species, such as high dispersal rates, climatic tolerances and competitive abilities (Nyberg & Wallentinus 2005). However, we have considered the Hutchinson fundamental niche concept with unlimited dispersal of species that does not consider species competition processes.

There are uncertainties related to our projections: first, to the climate model itself; second, to the habitat model; and third, to the coupling of both. Moreover, our models do not incorporate other ecological processes such as dispersal limitation (in a direct way) and population dynamics. Future research efforts should focus on including these 2 mechanisms in the habitat modelling frame, in the same way as has already been done for fishes and invertebrates (e.g. Cheung et al. 2009). The application of the combined analytical methods

beyond those traditionally used by ecologists will shed new light on the understanding of climate impacts on plankton communities.

We have addressed a community of copepods with different ecological requirements, though the use of statistical models (GAMs) is a more suitable approach than that of mechanistic models. GAMs offer the possibility to investigate the effect of climate change on multiple species without requiring sophisticated and time-consuming mechanistic models that depend on detailed knowledge of vital rates and life traits for each species (e.g. in *C. finmarchicus* or *C. helgolandicus* in Maps et al. 2011; see also Melle et al. 2014).

In summary, projections of 14 main copepod species in the North Atlantic by the end of the century under climate change scenarios indicate: (1) a prevailing poleward shift of most of the studied species, with poleward community shift of 8.7 km per decade on average, with an important species range variation from –15 to 18 km per decade; (2) an area characterized by high species turnover of local colonization and extinction located south of the Oceanic Polar Front where SST is projected to increase by the end of the century; and (3) an earlier seasonal peak of copepods in response to the ocean warming trend. All these changes may propagate higher up in the food web. The precision of projection changes is subjected to limitations of the data set, mainly for those species with low occurrences and with short time period.

Acknowledgements.

This research was funded by the European Commission (Contract No. 264933, EURO-BASIN: European Union Basin-Scale Analysis, Synthesis and Integration) and the Basque Government (Department Deputy of Agriculture, Fishing and Food Policy). We acknowledge CliSAP-Integrated Climate Data Center and NOAA for providing climate and bathymetry data, respectively. E.V. has benefited from a PhD Scholarship granted by the Iñaki Goenaga-Technology Centres Foundation. We are grateful to present and past staff of SAHFOS who have contributed to the maintenance of the CPR time series. The authors also wish to acknowledge Markus Kreuz, who has actively contributed providing data from HAMOCC and MPIOM models through DKRZ (www.dkrz.de/). This is contribution XXX from AZTI-Tecnalia Marine Research Division.

LITERATURE CITED

- <jrn>Alheit J, Hagen E (1997) Long-term climate forcing of European herring and sardine populations. *Fish Oceanogr* 6:130–139 [doi:10.1046/j.1365-2419.1997.00035.x](https://doi.org/10.1046/j.1365-2419.1997.00035.x)</jrn>
- <jrn>Araújo MB, Guisan A (2006) Five (or so) challenges for species distribution modelling. *J Biogeogr* 33:1677–1688 [doi:10.1111/j.1365-2699.2006.01584.x](https://doi.org/10.1111/j.1365-2699.2006.01584.x)</jrn>
- <jrn>Beaugrand G (2003) Long-term changes in copepod abundance and diversity in the North-East Atlantic in relation to fluctuations in the hydroclimatic environment. *Fish Oceanogr* 12:270–283 [doi:10.1046/j.1365-2419.2003.00248.x](https://doi.org/10.1046/j.1365-2419.2003.00248.x)</jrn>
- <jrn>Beaugrand G (2004) The North Sea regime shift: evidence, causes, mechanisms and consequences. *Prog Oceanogr* 60:245–262 [doi:10.1016/j.pocean.2004.02.018](https://doi.org/10.1016/j.pocean.2004.02.018)</jrn>
- <jrn>Beaugrand G (2009) Decadal changes in climate and ecosystems in the North Atlantic Ocean and adjacent seas. *Deep-Sea Res Part II* 56:656–673 [doi:10.1016/j.dsr2.2008.12.022](https://doi.org/10.1016/j.dsr2.2008.12.022)</jrn>
- <jrn>Beaugrand G (2012) Unanticipated biological changes and global warming. *Mar Ecol Prog Ser* 445:293–301 [doi:10.3354/meps09493](https://doi.org/10.3354/meps09493)</jrn>

- <jrn>Beaugrand G, Ibañez F (2002) Spatial dependence of calanoid copepod diversity in the North Atlantic Ocean. *Mar Ecol Prog Ser* 232:197–211 [doi:10.3354/meps232197](https://doi.org/10.3354/meps232197)</jrn>
- <jrn>Beaugrand G, Kirby RR (2010) Climate, plankton and cod. *Glob Change Biol* 16:1268–1280 [doi:10.1111/j.1365-2486.2009.02063.x](https://doi.org/10.1111/j.1365-2486.2009.02063.x)</jrn>
- <jrn>Beaugrand G, Reid PC, Ibañez F, Planque B (2000) Biodiversity of North Atlantic and North Sea calanoid copepods. *Mar Ecol Prog Ser* 204:299–303 [doi:10.3354/meps204299](https://doi.org/10.3354/meps204299)</jrn>
- <jrn>Beaugrand G, Reid PC, Ibañez F, Lindley JA, Edwards M (2002a) Reorganization of North Atlantic marine copepod biodiversity and climate. *Science* 296:1692–1694 [PubMed doi:10.1126/science.1071329](https://pubmed.ncbi.nlm.nih.gov/117111329/)</jrn>
- <jrn>Beaugrand G, Ibañez F, Lindley JA, Reid PC (2002b) Diversity of calanoid copepods in the North Atlantic and adjacent seas: species associations and biogeography. *Mar Ecol Prog Ser* 232:179–195 [doi:10.3354/meps232179](https://doi.org/10.3354/meps232179)</jrn>
- <jrn>Beaugrand G, Lindley JA, Helaouet P, Bonnet D (2007) Macroecological study of *Centropages typicus* in the North Atlantic Ocean. *Prog Oceanogr* 72:259–273 [doi:10.1016/j.pocean.2007.01.002](https://doi.org/10.1016/j.pocean.2007.01.002)</jrn>
- <jrn>Beaugrand G, Edwards M, Brander K, Luczak C, Ibañez F (2008) Causes and projections of abrupt climate-driven ecosystem shifts in the North Atlantic. *Ecol Lett* 11:1157–1168 [PubMed](https://pubmed.ncbi.nlm.nih.gov/1781157/)</jrn>
- <jrn>Beaugrand G, Christophe L, Martin E (2009) Rapid biogeographical plankton shifts in the North Atlantic Ocean. *Glob Change Biol* 15:1790–1803 [doi:10.1111/j.1365-2486.2009.01848.x](https://doi.org/10.1111/j.1365-2486.2009.01848.x)</jrn>
- <jrn>Beaugrand G, Lenoir S, Ibañez F, Manté C (2011) A new model to assess the probability of occurrence of a species, based on presence-only data. *Mar Ecol Prog Ser* 424:175–190 [doi:10.3354/meps08939](https://doi.org/10.3354/meps08939)</jrn>
- <jrn>Beaugrand G, Mackas D, Goberville E (2013) Applying the concept of the ecological niche and a macroecological approach to understand how climate influences zooplankton: advantages, assumptions, limitations and requirements. *Prog Oceanogr* 111:75–90 [doi:10.1016/j.pocean.2012.11.002](https://doi.org/10.1016/j.pocean.2012.11.002)</jrn>
- <jrn>Bonnet D, Richardson A, Harris R, Hirst A and others (2005) An overview of *Calanus helgolandicus* ecology in European waters. *Prog Oceanogr* 65:1–53 [doi:10.1016/j.pocean.2005.02.002](https://doi.org/10.1016/j.pocean.2005.02.002)</jrn>
- <jrn>Bornhold E, Mackas D, Harrison P (1998) Interdecadal variations in developmental timing of the copepod *Neocalanus plumchrus* (Marukawa) in the Strait of Georgia. *EOS Trans Am Geophys Union* 79: (Abstract)</jrn>
- <bok>Burnham KP, Anderson DR (2002) Model selection and multi-model inference: a practical information-theoretic approach, Vol. Springer</bok>
- <jrn>Calenge C, Darmon G, Basille M, Loison A, Jullien JM (2008) The factorial decomposition of the Mahalanobis distances in habitat selection studies. *Ecology* 89:555–566 [PubMed doi:10.1890/06-1750.1](https://pubmed.ncbi.nlm.nih.gov/1890061750.1/)</jrn>
- <jrn>Cheung WWL, Lam VWY, Sarmiento JL, Kearney K, Watson R, Pauly D (2009) Projecting global marine biodiversity impacts under climate change scenarios. *Fish Fish* 10:235–251 [doi:10.1111/j.1467-2979.2008.00315.x](https://doi.org/10.1111/j.1467-2979.2008.00315.x)</jrn>

- <jrn>Chust G, Irigoien X, Chave J, Harris RP (2013) Latitudinal phytoplankton distribution and the neutral theory of biodiversity. *Global Ecol Biogeogr* 22:531–543 [doi:10.1111/geb.12016](https://doi.org/10.1111/geb.12016)</jrn>
- <jrn>Chust G, Castellani C, Licandro P, Ibaibarriaga L, Sagarminaga Y, Irigoien X (2014a) Are *Calanus* spp. shifting poleward in the North Atlantic? A habitat modelling approach. *ICES J Mar Sci* 71:241–253 [doi:10.1093/icesjms/fst147](https://doi.org/10.1093/icesjms/fst147)</jrn>
- <jrn>Chust G, Allen JI, Bopp L, Schrum C and others (2014b) Biomass changes and trophic amplification of plankton in a warmer ocean. *Glob Change Biol* 20:2124–2139 [PubMed](https://pubmed.ncbi.nlm.nih.gov/25011111/) [doi:10.1111/gcb.12562](https://doi.org/10.1111/gcb.12562)</jrn>
- <jrn>Conover RJ (1988) Comparative life histories in the genera *Calanus* and *Neocalanus* in high latitudes of the northern hemisphere. *Hydrobiologia* 167–168:127–142 [doi:10.1007/BF00026299](https://doi.org/10.1007/BF00026299)</jrn>
- <jrn>Crisp MD, Arroyo MTK, Cook LG, Gandolfo MA and others (2009) Phylogenetic biome conservatism on a global scale. *Nature* 458:754–756 [PubMed](https://pubmed.ncbi.nlm.nih.gov/19111111/) [doi:10.1038/nature07764](https://doi.org/10.1038/nature07764)</jrn>
- <jrn>Dam HG (2013) Evolutionary adaptation of marine zooplankton to global change. *Annu Rev Mar Sci* 5:349–370 [PubMed](https://pubmed.ncbi.nlm.nih.gov/24111111/) [doi:10.1146/annurev-marine-121211-172229](https://doi.org/10.1146/annurev-marine-121211-172229)</jrn>
- <jrn>de Boyer Montégut C, Madec G, Fischer AS, Lazar A, Iudicone D (2004) Mixed layer depth over the global ocean: an examination of profile data and a profile-based climatology. *J Geophys Res C* 109:C12003, [doi:10.1029/2004JC002378](https://doi.org/10.1029/2004JC002378)</jrn>
- <jrn>deYoung B, Harris R, Alheit J, Beaugrand G, Mantua N, Shannon L (2004) Detecting regime shifts in the ocean: data considerations. *Prog Oceanogr* 60:143–164 [doi:10.1016/j.pocean.2004.02.017](https://doi.org/10.1016/j.pocean.2004.02.017)</jrn>
- <jrn>Dietrich G (1964) Oceanic polar front survey. *Rev Geophys* 2:291–308</jrn>
- <jrn>Durbin E, Kane J (2007) Seasonal and spatial dynamics of *Centropages typicus* and *C. hamatus* in the western North Atlantic. *Prog Oceanogr* 72:249–258 [doi:10.1016/j.pocean.2007.01.008](https://doi.org/10.1016/j.pocean.2007.01.008)</jrn>
- <jrn>Edwards M, Richardson, AJ (2004) Impact of climate change on marine pelagic phenology and trophic mismatch. *Nature* 430:881–884 [PubMed](https://pubmed.ncbi.nlm.nih.gov/15111111/)</jrn>
- <jrn>Edwards M, Reid P, Planque B (2001) Long-term and regional variability of phytoplankton biomass in the Northeast Atlantic (1960–1995). *ICES J Mar Sci* 58:39–49 [doi:10.1006/jmsc.2000.0987](https://doi.org/10.1006/jmsc.2000.0987)</jrn>
- <jrn>Eilertsen HC, Wyatt T (2000) Phytoplankton models and life history strategies. *S Afr J Mar Sci* 22:323–338 [doi:10.2989/025776100784125717](https://doi.org/10.2989/025776100784125717)</jrn>
- <jrn>Elith J, Leathwick JR (2009) Species distribution models: ecological explanation and prediction across space and time. *Annu Rev Ecol Evol Syst* 40:677–697 [doi:10.1146/annurev.ecolsys.110308.120159](https://doi.org/10.1146/annurev.ecolsys.110308.120159)</jrn>
- <jrn>Elith J, Phillips SJ, Hastie T, Dudík M, Chee YE, Yates CJ (2011) A statistical explanation of maxent for ecologists. *Divers Distrib* 17:43–57 [doi:10.1111/j.1472-4642.2010.00725.x](https://doi.org/10.1111/j.1472-4642.2010.00725.x)</jrn>
- <jrn>Etherington TR, Ward AI, Smith GC, Pietravalle S, Wilson GJ (2009) Using the Mahalanobis distance statistic with unplanned presence-only survey data for

- biogeographical models of species distribution and abundance: a case study of badger setts. *J Biogeogr* 36:845–853 [doi:10.1111/j.1365-2699.2008.02041.x](https://doi.org/10.1111/j.1365-2699.2008.02041.x)</jrn>
- <jrn>Farber O, Kadmon R (2003) Assessment of alternative approaches for bioclimatic modeling with special emphasis on the Mahalanobis distance. *Ecol Model* 160:115–130 [doi:10.1016/S0304-3800\(02\)00327-7](https://doi.org/10.1016/S0304-3800(02)00327-7)</jrn>
- <jrn>Graham CH, Hijmans RJ (2006) A comparison of methods for mapping species ranges and species richness. *Global Ecol Biogeogr* 15:578–587 [doi:10.1111/j.1466-8238.2006.00257.x](https://doi.org/10.1111/j.1466-8238.2006.00257.x)</jrn>
- <jrn>Greve W, Reiners F, Nast J, Hoffmann S (2004) Helgoland Roads meso- and macrozooplankton time-series 1974 to 2004: lessons from 30 years of single spot, high frequency sampling at the only off-shore island of the North Sea. *Helgol Mar Res* 58:274–288 [doi:10.1007/s10152-004-0191-5](https://doi.org/10.1007/s10152-004-0191-5)</jrn>
- <jrn>Guisan A, Thuiller W (2005) Predicting species distribution: offering more than simple habitat models. *Ecol Lett* 8:993–1009 [doi:10.1111/j.1461-0248.2005.00792.x](https://doi.org/10.1111/j.1461-0248.2005.00792.x)
- <jrn>Guisan A, Zimmermann NE (2000) Predictive habitat distribution models in ecology. *Ecol Model* 135:147–186 [doi:10.1016/S0304-3800\(00\)00354-9](https://doi.org/10.1016/S0304-3800(00)00354-9)</jrn>
- <jrn>Hanley JA, McNeil BJ (1982) The meaning and use of the area under a receiver operating characteristic (roc) curve. *Radiology* 143:29–36 [PubMed](https://pubmed.ncbi.nlm.nih.gov/7063747/) [doi:10.1148/radiology.143.1.7063747](https://doi.org/10.1148/radiology.143.1.7063747)</jrn>
- <bok>Hastie TJ, Tibshirani RJ (1990) Generalized additive models, Vol. Taylor & Francis</bok>
- <jrn>Head EJH, Harris LR, Yashayaev I (2003) Distributions of *Calanus* spp. and other mesozooplankton in the Labrador Sea in relation to hydrography in spring and summer (1995–2000). *Prog Oceanogr* 59:1–30 [doi:10.1016/S0079-6611\(03\)00111-3](https://doi.org/10.1016/S0079-6611(03)00111-3)</jrn>
- <jrn>Heath MR, Boyle PR, Gislason A, Gurney WSC and others (2004) Comparative ecology of over-wintering *Calanus finmarchicus* in the northern North Atlantic, and implications for life-cycle patterns. *ICES J Mar Sci* 61:698–708</jrn>
- <jrn>Helaouët P, Beaugrand G (2007) Macroecology of *Calanus finmarchicus* and *C. helgolandicus* in the North Atlantic Ocean and adjacent seas. *Mar Ecol Prog Ser* 345:147–165 [doi:10.3354/meps06775](https://doi.org/10.3354/meps06775)</jrn>
- <jrn>Helaouët P, Beaugrand G (2009) Physiology, ecological niches and species distribution. *Ecosystems* 12:1235–1245 [doi:10.1007/s10021-009-9261-5](https://doi.org/10.1007/s10021-009-9261-5)</jrn>
- <jrn>Helaouët P, Beaugrand G, Reid PC (2011) Macrophysiology of *Calanus finmarchicus* in the North Atlantic Ocean. *Prog Oceanogr* 91:217–228 [doi:10.1016/j.pocean.2010.11.003](https://doi.org/10.1016/j.pocean.2010.11.003)</jrn>
- <jrn>Hickling R, Roy DB, Hill JK, Fox R, Thomas CD (2006) The distributions of a wide range of taxonomic groups are expanding polewards. *Glob Change Biol* 12:450–455 [doi:10.1111/j.1365-2486.2006.01116.x](https://doi.org/10.1111/j.1365-2486.2006.01116.x)</jrn>
- <jrn>Hijmans RJ (2012) Cross-validation of species distribution models: removing spatial sorting bias and calibration with a null model. *Ecology* 93:679–688 [PubMed](https://pubmed.ncbi.nlm.nih.gov/22811111/) [doi:10.1890/11-0826.1](https://doi.org/10.1890/11-0826.1)</jrn>
- <eref>Hijmans RJ, Phillips S, Leathwick J, Elith J (2013) Dismo: species distribution modeling. R package version 0.8-17. <http://CRAN.R-project.org/package=dismo></eref>

- <jrn>Hinder SL, Gravenor MB, Edwards M, Ostle C and others (2014) Multi-decadal range changes vs. thermal adaptation for North East Atlantic oceanic copepods in the face of climate change. *Glob Change Biol* 20:140–146 [PubMed](#) [doi:10.1111/gcb.12387](https://doi.org/10.1111/gcb.12387)</jrn>
- <jrn>Hirche HJ (1991) Distribution of dominant calanoid copepod species in the Greenland Sea during late fall. *Polar Biol* 11:351–362 [doi:10.1007/BF00239687](https://doi.org/10.1007/BF00239687)</jrn>
- <conf>Hutchinson G (1957) Concluding remarks. *Cold Spring Harbour Symp Quantitative Biology* 22:415–427</conf>
- <jrn>Ilyina T, Six KD, Segschneider J, Maier-Reimer E, Li H, Núñez-Riboni I (2013) Global ocean biogeochemistry model HAMOCC: model architecture and performance as component of the MPI-Earth system model in different CMIP5 experimental realizations. *J Adv Model Earth Syst* 5:287–315 [doi:10.1029/2012MS000178](https://doi.org/10.1029/2012MS000178)</jrn>
- <edb>IPCC (2007) Summary for policymakers. In: Solomon S, Qin D, Manning M, Chen Z and others (eds) *Climate change 2007: the physical science basis. Contribution of working group I to the fourth assessment report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge, p 1–18</edb>
- <jrn>Irigoiien X (2004) Some ideas about the role of lipids in the life cycle of *Calanus finmarchicus*. *J Plankton Res* 26:259–263 [doi:10.1093/plankt/fbh030](https://doi.org/10.1093/plankt/fbh030)</jrn>
- <jrn>Irigoiien X, Chust G, Fernandes JA, Albaina A, Zarauz L (2011) Factors determining the distribution and beta diversity of mesozooplankton species in shelf and coastal waters of the Bay of Biscay. *J Plankton Res* 33:1182–1192 [doi:10.1093/plankt/fbr026](https://doi.org/10.1093/plankt/fbr026)</jrn>
- <jrn>Ji R, Edwards M, Mackas DL, Runge JA, Thomas AC (2010) Marine plankton phenology and life history in a changing climate: current research and future directions. *J Plankton Res* 32:1355–1368 [PubMed](#) [doi:10.1093/plankt/fbq062](https://doi.org/10.1093/plankt/fbq062)</jrn>
- <jrn>Jiménez-Valverde A, Lobo JM (2007) Threshold criteria for conversion of probability of species presence to either–or presence–absence. *Acta Oecol* 31:361–369 [doi:10.1016/j.actao.2007.02.001](https://doi.org/10.1016/j.actao.2007.02.001)</jrn>
- <jrn>Johns DG, Edwards M, Batten SD (2001) Arctic boreal plankton species in the Northwest Atlantic. *Can J Fish Aquat Sci* 58:2121–2124 [doi:10.1139/f01-156](https://doi.org/10.1139/f01-156)</jrn>
- <jrn>Jungclaus JH, Fischer N, Haak H, Lohmann K and others (2013) Characteristics of the ocean simulations in the Max Planck Institute Ocean Model (MPIOM) the ocean component of the MPI-Earth system model. *J Adv Model Earth Syst* 5:422–446 [doi:10.1002/jame.20023](https://doi.org/10.1002/jame.20023)</jrn>
- <jrn>Kane J, Prezioso J (2008) Distribution and multi-annual abundance trends of the copepod *Temora longicornis* in the US northeast shelf ecosystem. *J Plankton Res* 30:619–632 [doi:10.1093/plankt/fbn026](https://doi.org/10.1093/plankt/fbn026)</jrn>
- <jrn>Kirby RR, Beaugrand G (2009) Trophic amplification of climate warming. *Proc R Soc Lond B* 276:4095–4103 [doi:10.1098/rspb.2009.1320](https://doi.org/10.1098/rspb.2009.1320)</jrn>
- <jrn>Kroeker KJ, Kordas RL, Crim RN, Singh GG (2010) Meta-analysis reveals negative yet variable effects of ocean acidification on marine organisms. *Ecol Lett* 13:1419–1434 [PubMed](#) [doi:10.1111/j.1461-0248.2010.01518.x](https://doi.org/10.1111/j.1461-0248.2010.01518.x)</jrn>
- <jrn>Lavergne S, Mouquet N, Thuiller W, Ronce O (2010) Biodiversity and climate change: integrating evolutionary and ecological responses of species and communities. *Annu Rev Ecol Evol Syst* 41:321–350 [doi:10.1146/annurev-ecolsys-102209-144628](https://doi.org/10.1146/annurev-ecolsys-102209-144628)</jrn>

- <jrn>Lee S-K, Park W, van Sebille E, Baringer MO and others (2011) What caused the significant increase in Atlantic Ocean heat content since the mid-20th century? *Geophys Res Lett* 38:L17607, doi:10.1029/2011GL048856 [doi:10.1029/2011GL048856](https://doi.org/10.1029/2011GL048856)</jrn>
- <jrn>Levitus S (1983) Climatological atlas of the world ocean. *Eos Trans Am Geophys Union* 64:962–963, doi:10.1029/EO064i049p00962-02 [doi:10.1029/EO064i049p00962-02](https://doi.org/10.1029/EO064i049p00962-02)</jrn>
- <bok>Longhurst AR (2007) Ecological geography of the sea, 2nd edn. Academic Press, Burlington, MA, p 51–70</bok>
- <jrn>Mackas DL, Goldblatt R, Lewis AG (1998) Interdecadal variation in developmental timing of *Neocalanus plumchrus* populations at ocean station P in the subarctic North Pacific. *Can J Fish Aquat Sci* 55:1878–1893 [doi:10.1139/f98-080](https://doi.org/10.1139/f98-080)</jrn>
- <jrn>Mackas DL, Batten S, Trudel M (2007) Effects on zooplankton of a warmer ocean: recent evidence from the Northeast Pacific. *Prog Oceanogr* 75:223–252 [doi:10.1016/j.pocean.2007.08.010](https://doi.org/10.1016/j.pocean.2007.08.010)</jrn>
- <unknown>Mahalanobis PC (1936) On the generalized distance in statistics. *Proc Natl Inst Sci India* 2:49–55</unknown>
- <jrn>Maps F, Pershing AJ, Record NR (2011) A generalized approach for simulating growth and development in diverse marine copepod species. *ICES J Mar Sci* 69:370–379 [doi:10.1093/icesjms/fsr182](https://doi.org/10.1093/icesjms/fsr182)</jrn>
- <jrn>Marsland SJ, Haak H, JungCLAUS JH, Latif M, Röske F (2003) The Max-Planck-Institute global ocean/sea ice model with orthogonal curvilinear coordinates. *Ocean Model* 5:91–127 [doi:10.1016/S1463-5003\(02\)00015-X](https://doi.org/10.1016/S1463-5003(02)00015-X)</jrn>
- <edb>Mauchline J (1998) Preface. In: Mauchline J (ed) *Advances in marine biology*, Vol. 33. Academic Press, p x </edb>
- <jrn>Melle W, Runge JA, Head E, Plourde S and others (2014) The North Atlantic Ocean as habitat for *Calanus finmarchicus*: environmental factors and life history traits. *Prog Oceanogr* 129:244–284 [doi:10.1016/j.pocean.2014.04.026](https://doi.org/10.1016/j.pocean.2014.04.026)</jrn>
- <jrn>Molinero JC, Ibanez F, Souissi S, Buecher E, Dallot S, Nival P (2008) Climate control on the long-term anomalous changes of zooplankton communities in the northwestern Mediterranean. *Glob Change Biol* 14:11–26 [doi:10.1111/j.1365-2486.2007.01469.x](https://doi.org/10.1111/j.1365-2486.2007.01469.x)</jrn>
- <jrn>Møller EF, Maar M, Jónasdóttir SH, Nielsen TG, Tönnesson K (2012) The effect of changes in temperature and food on the development of *Calanus finmarchicus* and *Calanus helgolandicus* populations. *Limnol Oceanogr* 57:211–220 [doi:10.4319/lo.2012.57.1.0211](https://doi.org/10.4319/lo.2012.57.1.0211)</jrn>
- <jrn>Monterroso P, Brito JC, Ferreras P, Alves PC (2009) Spatial ecology of the European wildcat in a Mediterranean ecosystem: dealing with small radio-tracking datasets in species conservation. *J Zool* 279:27–35 [doi:10.1111/j.1469-7998.2009.00585.x](https://doi.org/10.1111/j.1469-7998.2009.00585.x)</jrn>
- <jrn>Moore PJ, Thompson RC, Hawkins SJ (2011) Phenological changes in intertidal con-specific gastropods in response to climate warming. *Glob Change Biol* 17:709–719 [doi:10.1111/j.1365-2486.2010.02270.x](https://doi.org/10.1111/j.1365-2486.2010.02270.x)</jrn>
- <jrn>Nogués-Bravo D, Rodríguez J, Hortal J, Batra P, Araújo MB (2008) Climate change, humans, and the extinction of the woolly mammoth. *PLoS Biol* 6:e79 [PubMed](https://pubmed.ncbi.nlm.nih.gov/16811111/) [doi:10.1371/journal.pbio.0060079](https://doi.org/10.1371/journal.pbio.0060079)</jrn>

- <jrn>Nyberg C, Wallentinus I (2005) Can species traits be used to predict marine macroalgal introductions? *Biol Invasions* 7:265–279 [doi:10.1007/s10530-004-0738-z](https://doi.org/10.1007/s10530-004-0738-z)</jrn>
- <jrn>Oksanen J, Minchin PR (2002) Continuum theory revisited: what shape are species responses along ecological gradients? *Ecol Model* 157:119–129 [doi:10.1016/S0304-3800\(02\)00190-4](https://doi.org/10.1016/S0304-3800(02)00190-4)</jrn>
- <jrn>Orr JC, Fabry VJ, Aumont O, Bopp L and others (2005) Anthropogenic ocean acidification over the twenty-first century and its impact on calcifying organisms. *Nature* 437:681–686 [PubMed](https://pubmed.ncbi.nlm.nih.gov/16258111/) [doi:10.1038/nature04095](https://doi.org/10.1038/nature04095)</jrn>
- <edb>Parmesan C (2005) Biotic response: range and abundance changes. In: Lovejoy TE, Hannah, L (eds) *Climate change and biodiversity*. Yale University Press, New Haven, CT, p 41–55</edb>
- <jrn>Parmesan C (2006) Ecological and evolutionary responses to recent climate change. *Annu Rev Ecol Syst* 37:637–669 [doi:10.1146/annurev.ecolsys.37.091305.110100](https://doi.org/10.1146/annurev.ecolsys.37.091305.110100)</jrn>
- <jrn>Parmesan C, Yohe G (2003) A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421:37–42 [PubMed](https://pubmed.ncbi.nlm.nih.gov/12575711/) [doi:10.1038/nature01286](https://doi.org/10.1038/nature01286)</jrn>
- <jrn>Pearson RG, Dawson TP (2003) Predicting the impacts of climate change on the distribution of species: Are bioclimate envelope models useful? *Global Ecol Biogeogr* 12:361–371 [doi:10.1046/j.1466-822X.2003.00042.x](https://doi.org/10.1046/j.1466-822X.2003.00042.x)</jrn>
- <jrn>Peijnenburg KT, Fauvelot C, Breeuwer JA, Menken SB (2006) Spatial and temporal genetic structure of the planktonic *Sagitta setosa* (chaetognatha) in European seas as revealed by mitochondrial and nuclear DNA markers. *Mol Ecol* 15:3319–3338 [PubMed](https://pubmed.ncbi.nlm.nih.gov/16711111/) [doi:10.1111/j.1365-294X.2006.03002.x](https://doi.org/10.1111/j.1365-294X.2006.03002.x)</jrn>
- <jrn>Perry AL, Low PJ, Ellis JR, Reynolds JD (2005) Climate change and distribution shifts in marine fishes. *Science* 308:1912–1915 [PubMed](https://pubmed.ncbi.nlm.nih.gov/16258111/) [doi:10.1126/science.1111322](https://doi.org/10.1126/science.1111322)</jrn>
- <jrn>Phillips SJ, Anderson RP, Schapire RE (2006) Maximum entropy modeling of species geographic distributions. *Ecol Model* 190:231–259 [doi:10.1016/j.ecolmodel.2005.03.026](https://doi.org/10.1016/j.ecolmodel.2005.03.026)</jrn>
- <jrn>Pomerleau C, Nelson RJ, Hunt BPV, Sastri AR, Williams WJ (2014) Spatial patterns in zooplankton communities and stable isotope ratios ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) in relation to oceanographic conditions in the sub-Arctic Pacific and western Arctic regions during the summer of 2008. *J Plankton Res* 36:757–775 [doi:10.1093/plankt/fbt129](https://doi.org/10.1093/plankt/fbt129)</jrn>
- <jrn>Provan JIM, Beatty GE, Maggs CA, Savidge G (2007) Expressed sequence tag-derived microsatellites for the cool-water marine copepod *Calanus finmarchicus*. *Mol Ecol Notes* 7:1369–1371 [doi:10.1111/j.1471-8286.2007.01889.x](https://doi.org/10.1111/j.1471-8286.2007.01889.x)</jrn>
- <jrn>Raes N, ter Steege H (2007) A null-model for significance testing of presence-only species distribution models. *Ecography* 30:727–736 [doi:10.1111/j.2007.0906-7590.05041.x](https://doi.org/10.1111/j.2007.0906-7590.05041.x)</jrn>
- <jrn>Reid PC, Borges Md F, Svendsen E (2001) A regime shift in the North Sea circa 1988 linked to changes in the North Sea horse mackerel fishery. *Fish Res* 50:163–171 [doi:10.1016/S0165-7836\(00\)00249-6](https://doi.org/10.1016/S0165-7836(00)00249-6)</jrn>
- <jrn>Reygondeau G, Beaugrand G (2011) Future climate-driven shifts in distribution of *Calanus finmarchicus*. *Glob Change Biol* 17:756–766 [doi:10.1111/j.1365-2486.2010.02310.x](https://doi.org/10.1111/j.1365-2486.2010.02310.x)</jrn>

- <jrn>Richardson AJ (2008) In hot water: zooplankton and climate change. *ICES J Mar Sci* 65:279–295 [doi:10.1093/icesjms/fsn028](https://doi.org/10.1093/icesjms/fsn028)</jrn>
- <jrn>Richardson AJ, Schoeman DS (2004) Climate impact on plankton ecosystems in the Northeast Atlantic. *Science* 305:1609–1612 [PubMed doi:10.1126/science.1100958](https://pubmed.ncbi.nlm.nih.gov/1100958/)</jrn>
- <jrn>Sorte CJB, Williams SL, Carlton JT (2010) Marine range shifts and species introductions: comparative spread rates and community impacts. *Global Ecol Biogeogr* 19:303–316 [doi:10.1111/j.1466-8238.2009.00519.x](https://doi.org/10.1111/j.1466-8238.2009.00519.x)</jrn>
- <jrn>Speirs DC, Gurney WSC, Heath MR, Wood SN (2005) Modelling the basin-scale demography of *Calanus finmarchicus* in the North-east Atlantic. *Fish Oceanogr* 14:333–358 [doi:10.1111/j.1365-2419.2005.00339.x](https://doi.org/10.1111/j.1365-2419.2005.00339.x)</jrn>
- <jrn>Stegert C, Ji R, Davis CS (2010) Influence of projected ocean warming on population growth potential in two North Atlantic copepod species. *Prog Oceanogr* 87:264–276 [doi:10.1016/j.pocean.2010.09.013](https://doi.org/10.1016/j.pocean.2010.09.013)</jrn>
- <jrn>Tewksbury JJ, Huey RB, Deutsch CA (2008) Putting the heat on tropical animals. *Science* 320:1296–1297 [PubMed doi:10.1126/science.1159328](https://pubmed.ncbi.nlm.nih.gov/1159328/)</jrn>
- <jrn>Thomas CD (2010) Climate, climate change and range boundaries. *Divers Distrib* 16:488–495 [doi:10.1111/j.1472-4642.2010.00642.x](https://doi.org/10.1111/j.1472-4642.2010.00642.x)</jrn>
- <jrn>Thomas CD, Cameron A, Green RE, Bakkenes M and others (2004) Extinction risk from climate change. *Nature* 427:145–148 [PubMed doi:10.1038/nature02121](https://pubmed.ncbi.nlm.nih.gov/101038/)</jrn>
- <unknown>VanDerWal J, Falconi L, Januchowski S, Shoo L, Storlie C (2011) SDMtools: species distribution modelling tools: tools for processing data associated with species distribution modelling exercises. R package version 1</unknown>
- <jrn>Walther G-R, Post E, Convey P, Menzel A and others (2002) Ecological responses to recent climate change. *Nature* 416:389–395 [PubMed doi:10.1038/416389a](https://pubmed.ncbi.nlm.nih.gov/101038/)</jrn>
- <jrn>Warner AJ, Hays GC (1994) Sampling by the continuous plankton recorder survey. *Prog Oceanogr* 34:237–256 [doi:10.1016/0079-6611\(94\)90011-6](https://doi.org/10.1016/0079-6611(94)90011-6)</jrn>
- <jrn>Wilcoxon F (1945) Individual comparisons by ranking methods. *Biom Bull* 1:80–83 [doi:10.2307/3001968](https://doi.org/10.2307/3001968)</jrn>
- <jrn>Wuillez M, Rivoirard J, Petitgas P (2009) Notes on survey-based spatial indicators for monitoring fish populations. *Aquat Living Resour* 22:155–164 [doi:10.1051/alr/2009017](https://doi.org/10.1051/alr/2009017)</jrn>
- <bok>Wood S (2006) Generalized additive models: an introduction with R, Vol. Taylor & Francis</bok>
- <jrn>Woodd-Walker RS, Ward P, Clarke A (2002) Large-scale patterns in diversity and community structure of surface water copepods from the Atlantic Ocean. *Mar Ecol Prog Ser* 236:189–203 [doi:10.3354/meps236189](https://doi.org/10.3354/meps236189)</jrn>
- <jrn>Yates CJ, McNeill A, Elith J, Midgley GF (2010) Assessing the impacts of climate change and land transformation on *banksia* in the south west Australian floristic region. *Divers Distrib* 16:187–201 [doi:10.1111/j.1472-4642.2009.00623.x](https://doi.org/10.1111/j.1472-4642.2009.00623.x)</jrn>
- <jrn>Yebra L, Bonnet D, Harris RP, Lindeque PK, Peijnenburg KTCA (2011) Barriers in the pelagic: population structuring of *Calanus helgolandicus* and *C. euxinus* in European waters. *Mar Ecol Prog Ser* 428:135–149 [doi:10.3354/meps09056](https://doi.org/10.3354/meps09056)</jrn>

<jrn>Young BE, Franke I, Hernandez PA, Herzog SK, Paniagua L, Tovar C, Valqui T (2009) Using spatial models to predict areas of endemism and gaps in the protection of Andean slope birds. *Auk* 126:554–565 doi:10.1525/auk.2009.08155</jrn>

<bok>Zuur AF, Ieno EN, Walker N (2009) Mixed effects models and extensions in ecology with R, Vol. Springer-Verlag, New York, NY</bok>

Table 1. Generalized additive model. Explained deviance (%) of *Calanus* spp. occurrence in the North Atlantic Basin according to each environmental factor. SST: sea surface temperature, SSS: sea surface salinity, Pc: surface phytoplankton biomass, Chl *a*: chlorophyll *a*, MLD: mixed layer depth

	SST	SSS	O ₂	pH	Pc	Chl <i>a</i>	MLD	Depth
<i>C. finmarchicus</i>	14.2	15.1	18.9	4.4	6.2	6.1	0.6	5.5
<i>C. helgolandicus</i>	11.3	5.4	3.4	1.8	0.4	0.3	2.8	14.1
<i>C. glacialis</i>	29.6	25.5	25.9	1.9	4.2	3.2	0.7	0.1
<i>C. hyperboreus</i>	21.5	13.0	30.8	6.6	16.5	12.0	0.3	4.8

Table 2. Evaluation of generalized additive models (yearly accumulated) with *k*-fold cross-validation. Variables entered: sea surface temperature (SST), sea surface salinity (SSS), bathymetry, surface phytoplankton biomass (Pc) and pH. Thresholds for conversion of probability of species presence to either presence or absence in model validation: 0.08 (*Calanus hyperboreus*), 0.11 (*C. glacialis*), 0.48 (*C. helgolandicus*) and 0.63 (*C. finmarchicus*). Values in the AUC column refer to model with all observations/mean *k*-fold cross-validation. Values in the accuracy column refer to model with all observations/mean *k*-fold cross-validation (%). edf: estimated degrees of freedom. All *p* < 0.001.

Species	Variables selected	edf	Overall deviance explained (%)	AUC	Accuracy
<i>C. hyperboreus</i>	SST	1.99	42.3	0.845/0.698	85.34/69.84
	SSS	1.00			
	Depth	2.17			
	pH	1.96			
	Pc				
<i>C. glacialis</i>	SST	1.95	34.1	0.816/0.642	81.90/71.25
	SSS	2.88			
	Depth	1.00			
<i>C. helgolandicus</i>	SST	1.99	25.4	0.749/0.754	74.94/75.40
	SSS	2.99			
	Depth	2.85			
	pH	1.97			
<i>C. finmarchicus</i>	SST	1.97	46.9	0.852/0.851	85.19/85.13
	SSS	2.74			
	Depth	2.88			
	pH	1.83			
	Pc				

Table 3. Evaluation of generalized additive models (yearly accumulated) with temporal cross-validation. Models built in cold period validated in warm period. Variables entered: sea surface temperature (SST), sea surface salinity (SSS), bathymetry, surface phytoplankton biomass (Pc) and pH. Values in the AUC column refer to model with all observations/mean k -fold cross-validation. Values in the accuracy column refer to model with all observations/mean k -fold cross-validation (%). edf: estimated degrees of freedom

Species	Variables selected	edf	p	Overall explained deviance (%)	AUC	Accuracy
<i>Calanus hyperboreus</i>	SST	1.99	<2e-16			
	SSS	1.00				
	Depth	2.90				
	pH	1.98				
	Pc					
				48.1	0.845/0.807	85.34/80.80
<i>C. glacialis</i>	SST	1.73	<2e-16			
	SSS	2.84				
	Depth	1	0.0143			
				30.7	0.816/0.691	81.90/74.33
<i>C. helgolandicus</i>	SST	1.99	<2e-16			
	SSS	2.99				
	Depth	2.95				
	pH	1.98				
				27.3	0.749/0.745	74.94/74.83
<i>C. finmarchicus</i>	SST	1.95	<2e-16			
	SSS	2.87				
	Depth	2.80				
	pH	2				
	Pc					
				45.2	0.852/0.857	85.19/85.73

Table 4. Generalized additive models for the period 1995–1999. All observation-based models vs. k -fold cross-validated models. Threshold for conversion of probability of species presence to either presence or absence in model validation: 0.09 (*Candacia armata*), 0.24 (*Centropages typicus*), 0.07 (*Centropages hamatus*), 0.35 (*Metridia lucens*), 0.14 (*Paraeuchaeta norvegica*), 0.1 (*Paraeuchaeta hebes*), 0.1 (*Pleuromamma borealis*), 0.08 (*Pleuromamma robusta*), 0.2 (*Pseudocalanus elongatus*) and 0.26 (*Temora longicornis*). Values in the AUC column refer to model with all observations/mean k -fold cross-validation. Values in the accuracy column refer to model with all observations/mean k -fold cross-validation (%). edf: estimated degrees of freedom

Species	Variables selected	edf	p	Overall explained deviance (%)	AUC	Accuracy
<i>Candacia armata</i>	SST	1.80	6.49E–08	15.4	0.738/0.558	75.1/55.9
	SSS	1	0.000589			
	Depth	1.79	4.60E–10			
<i>Centropages typicus</i>	SST	1.002	<2e–16	25.4	0.761/0.730	76.2/73.0
	SSS	1	0.000587			
	Depth	2.413	<2e–16			
	pH	1.965	2.12E–08			
<i>Centropages hamatus</i>	SST	1.95	1.67E–05	28.7	0.846/0.747	80.3/74.7
	SSS	1.96	2.46E–05			
	Depth	2.62	7.84E–06			
	pH	1.88	9.46E–06			
<i>Metridia lucens</i>	SST	1.98	6.74E–11	7.65	0.637/0.574	63.3/57.4
	SSS	2.70	1.87E–07			
	Depth	2.92	2.06E–06			
	pH	1.89	1.17E–05			
<i>Paraeuchaeta norvegica</i>	SST	1.99	6.44E–07	27.5	0.783/0.644	78.2/64.4
	SSS	2.71	5.68E–16			
	Depth	2.95	<2e–16			
	pH	1.86	2.67E–07			
<i>Paraeuchaeta hebes</i>	SST	1.96	1.12E–08	35.4	0.854/0.700	84.5/70.0
	SSS	2.88	0.0896			
	Depth	2.75	1.80E–15			
	pH	1.44	6.87E–11			
	SST	1.95	7.37E–08	23.3	0.770/0.672	78.3/67.3
	Depth	2.59	1.22E–10			
	pH	1.89	6.82E–06			
<i>Pleuromamma borealis</i>	SST	1.91	1.68E–05	15.7	0.767/0.530	76.7/53.0
	Depth	2.29	9.25E–12			
	pH	1.81	0.0231			
<i>Pleuromamma robusta</i>	SST	1.93	1.20E–04			
	Depth	2.74	9.54E–09			

	pH	1	0.0028			
<i>Pseudocalanus elongatus</i>	SST	1.35	2.78E-02	11.4	0.713/0.530	71.3/52.9
	SSS	2.88	3.93E-05			
	Depth	2.49	<2e-16			
	pH	1.79	1.01E-08			
	Pc			17.5	0.723/0.631	71.8/63.1
<i>Temora longicornis</i>	SST	1.00	8.93E-04			
	SSS	1.26	6.83E-15			
	Depth	2.61	<2e-16			
	pH	1.40	1.52E-06	24.9	0.779/0.730	78.1/73.1

Table 5. Latitudinal and longitudinal shift of the species in the North Atlantic by taking into account the gravity centre of each. The shift is calculated as the distance (km) between the gravity centre of each species at present (2001–2020) and in the future (2080–2099)

Species	Latitudinal shift (km per decade)	Longitudinal shift (km per decade)
<i>Calanus finmarchicus</i>	3.7	8.1
<i>Calanus glacialis</i>	11.3	15.1
<i>Calanus helgolandicus</i>	17.8	0.8
<i>Calanus hyperboreus</i>	7.8	-11.9
<i>Candacia armata</i> subpopulations ^a	1.9	-10.8
<i>Centropages hamatus</i> subpopulations ^a	-15.4	-3.7
<i>Centropages typicus</i>	2.2	-0.8
<i>Metridia lucens</i>	7.3	-14.7
<i>Paraeuchaeta hebes</i> subpopulations ^a	13.5	-5.6
<i>Paraeuchaeta norvegica</i>	12.8	9.6
<i>Pleuromamma borealis</i>	7.2	-4.7
<i>Pleuromamma robusta</i>	11.2	-3.4
<i>Pseudocalanus elongatus</i>	-11.0	-20.6
<i>Temora longicornis</i>	0.1	14.6

^aThe gravity centres of *Candacia armata*, *Centropages hamatus* and *Paraeuchaeta hebes* are calculated by taking into account the individual subpopulation patches of each species and averaging them

Fig. 1. The North Atlantic Basin. The domain of the studied area is 35 to 65° N and 75° W to 2° E. Source of bathymetry: ETOPO1, NOAA, Amante and Eakins (2009). (Dots) continuous plankton recorder sampling points of *Calanus finmarchicus*, *C. helgolandicus*, *C. glacialis* and *C. hyperboreus* in the 1970–2004 period

Fig. 2. Mean sea surface temperature time series. Cold (1970–1896) and warm (1987–2004) periods are indicated

Fig. 3. Difference models of (A) sea surface temperature and (B) P_c sea surface phytoplankton biomass for present (2001–2020) and future (2080–2099) periods

Fig. 4. Occurrence models of *Calanus* spp. in the 1970–2004 period. Orange: presence; grey: absence. (A) *C. finmarchicus*, (B) *C. helgolandicus*, (C) *C. glacialis* and (D) *C. hyperboreus*

Fig. 5. Accuracy of each different model according to the 4 *Calanus* spp.. GAM: generalized additive model

Fig. 6. Latitudinal shift of species in the North Atlantic by taking into account the gravity centre of each. Position of the gravity centre at present (2001–2020)(blue circles); position of the gravity centre for the future (2080–2099)(red circles); 1: *Calanus glacialis*; 2: *Calanus hyperboreus*; 3: *Calanus finmarchicus*; 4: *Calanus helgolandicus*; 5: *Candacia armata*; 6: *Centropages typicus*; 7: *Centropages hamatus*; 8: *Paraeuchaeta norvegica*; 9: *Paraeuchaeta hebes*; 10: *Metridia lucens*; 11: *Pleuromamma borealis*; 12: *Pleuromamma robusta*; 13: *Pseudocalanus elongatus*; 14: *Temora longicornis*

Fig. 7. Habitat suitability models for each of the species at present (2001–2020) and in future conditions (2080–2099). Green: colonization area, species was absent in present and present in future; red: extinction area, species was present at present and absent in future; orange: present in both periods; grey: absent in both periods; 1: *Calanus glacialis*; 2: *Calanus hyperboreus*; 3: *Calanus finmarchicus*; 4: *Calanus helgolandicus*; 5: *Candacia armata*; 6: *Centropages typicus*; 7: *Centropages hamatus*; 8: *Paraeuchaeta norvegica*; 9: *Paraeuchaeta hebes*; 10: *Metridia lucens*; 11: *Pleuromamma borealis*; 12: *Pleuromamma robusta*; 13: *Pseudocalanus elongatus*; 14: *Temora longicornis*

Fig. 8. (A) *Calanus finmarchicus* and (B) *C. hyperboreus* continuous plankton recorder (CPR) number of observations vs. the habitat model predictions for the CPR sampling area in 1970 to 2004. Predicted occurrence phenology of (C) *C. finmarchicus* and (D) *C. hyperboreus* at present (2001–2020) and future (2080–2099) in the whole study area. Vertical **dotted lines** represent the seasonal peak of each species at each period

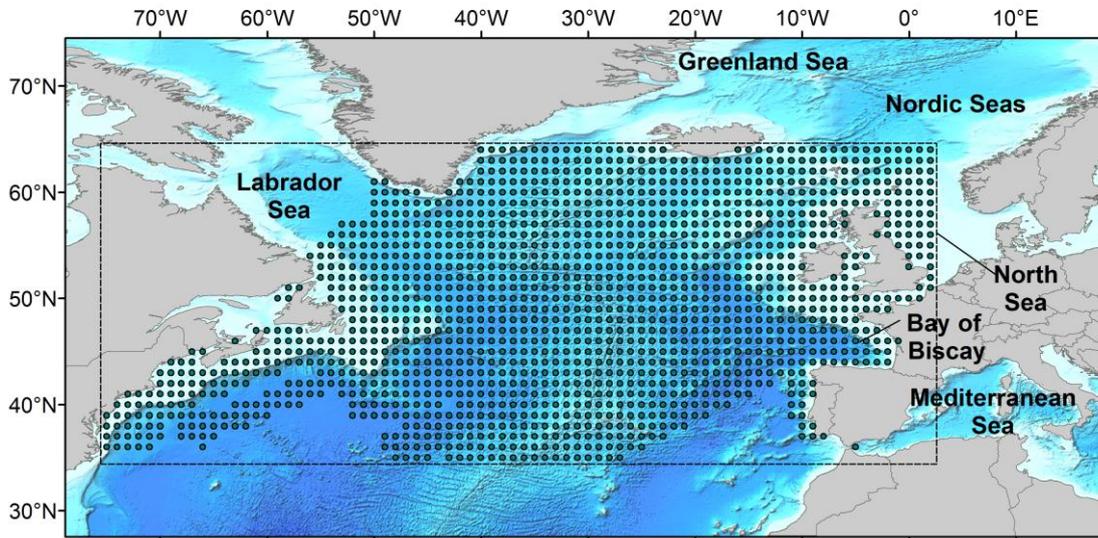
Fig. 9. (A) Species richness model at present (2001–2020). (B) Colonization model: number of new species that will occur at each pixel by 2080–2099. (C) Extinction model: number of species that will disappear at each pixel by 2080–2099. (D) Turnover model: number of species that will either colonize or go extinct at each pixel by 2080–2099

Appendix

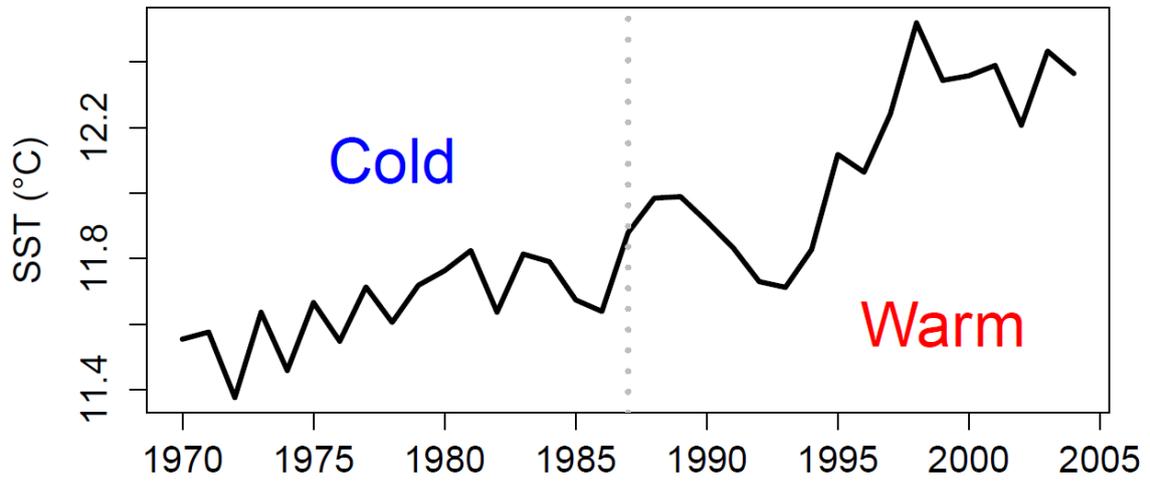
Fig. A1. Number of *Calanus* spp. occurrences from continuous plankton recorder survey for the 1970–2004 period: (A) *C. finmarchicus*, (B) *C. helgolandicus*, (C) *C. glacialis* and (D) *C. hyperboreus*

Fig. A2. Presence–absence model of *Calanus* spp. in the 1970–2004 period (all months and years aggregated). **Orange: presence; grey: absence.** (A) *C. finmarchicus*, (B) *C. helgolandicus*, (C) *C. glacialis* and (D) *C. hyperboreus*. Models: (I.) generalized additive model, (II.) MaxEnt and (III.) Mahalanobis

F.1

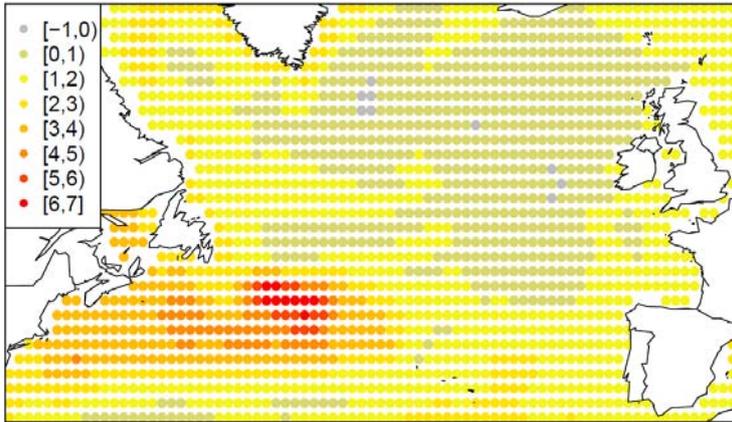


F2

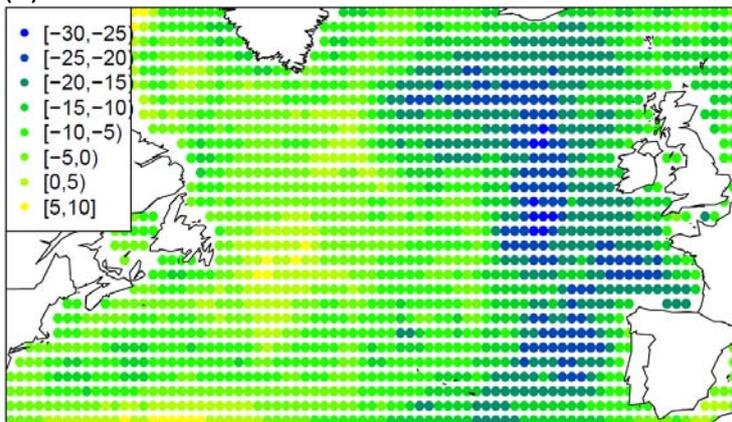


F.3

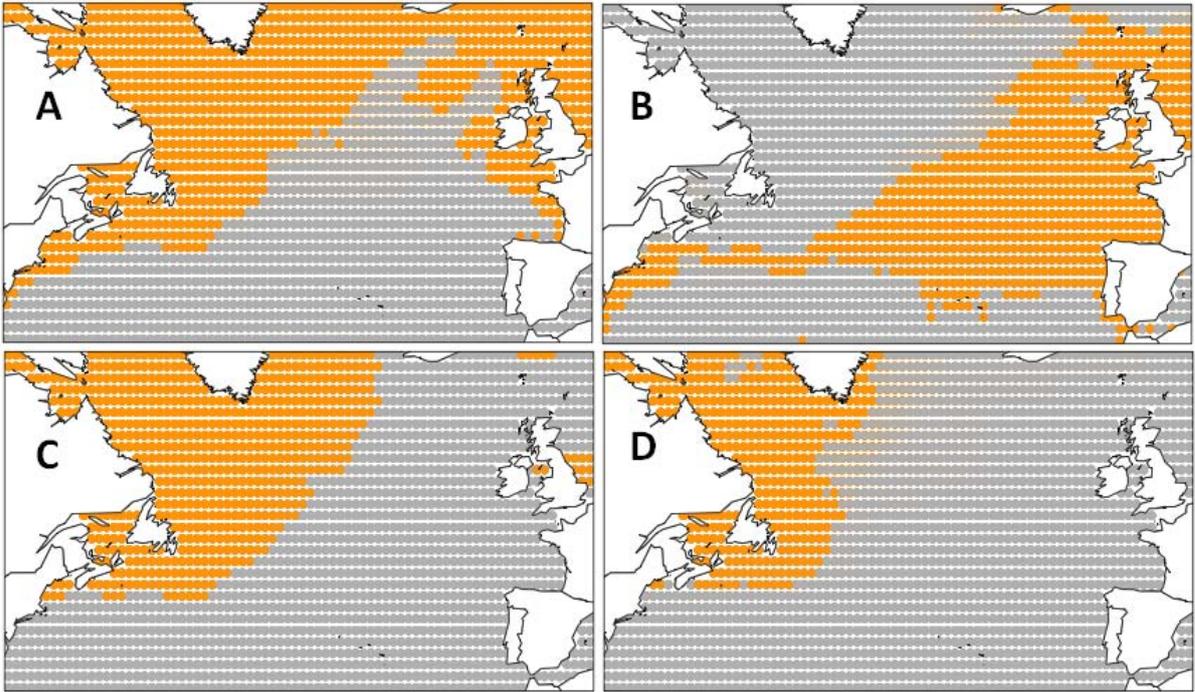
(A)



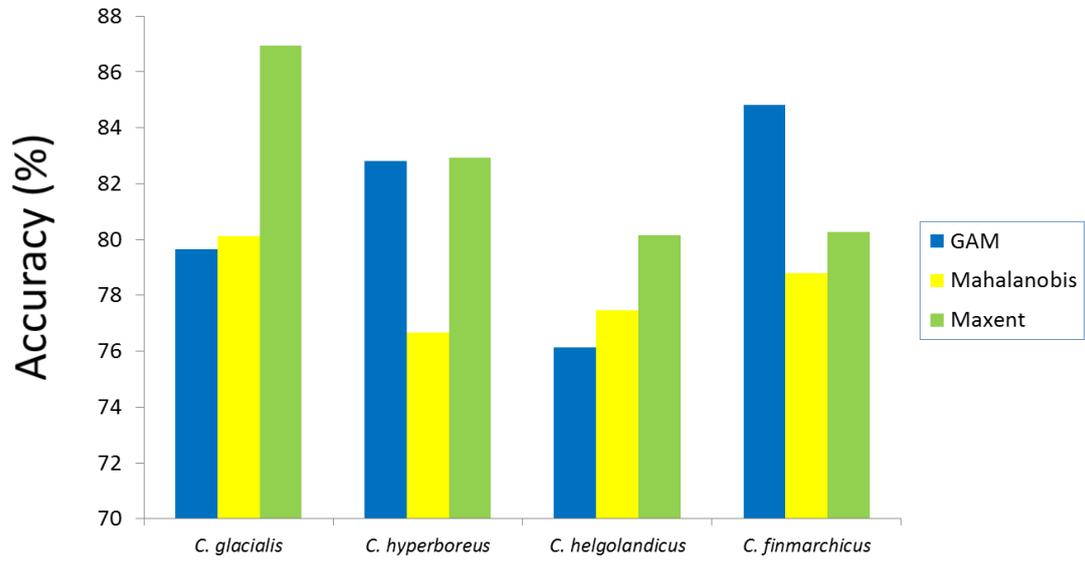
(B)



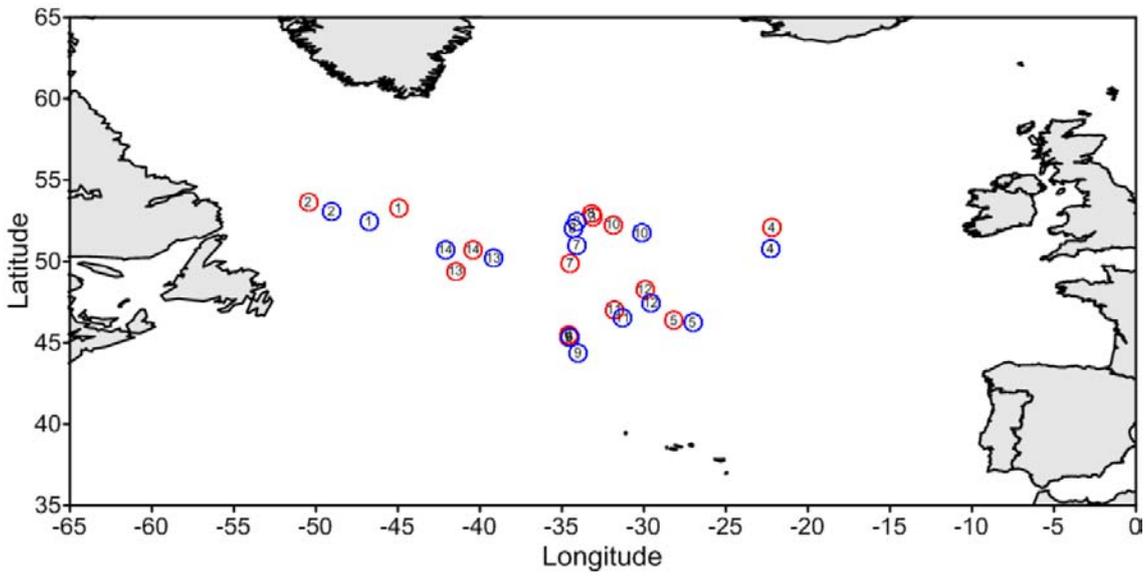
F4.



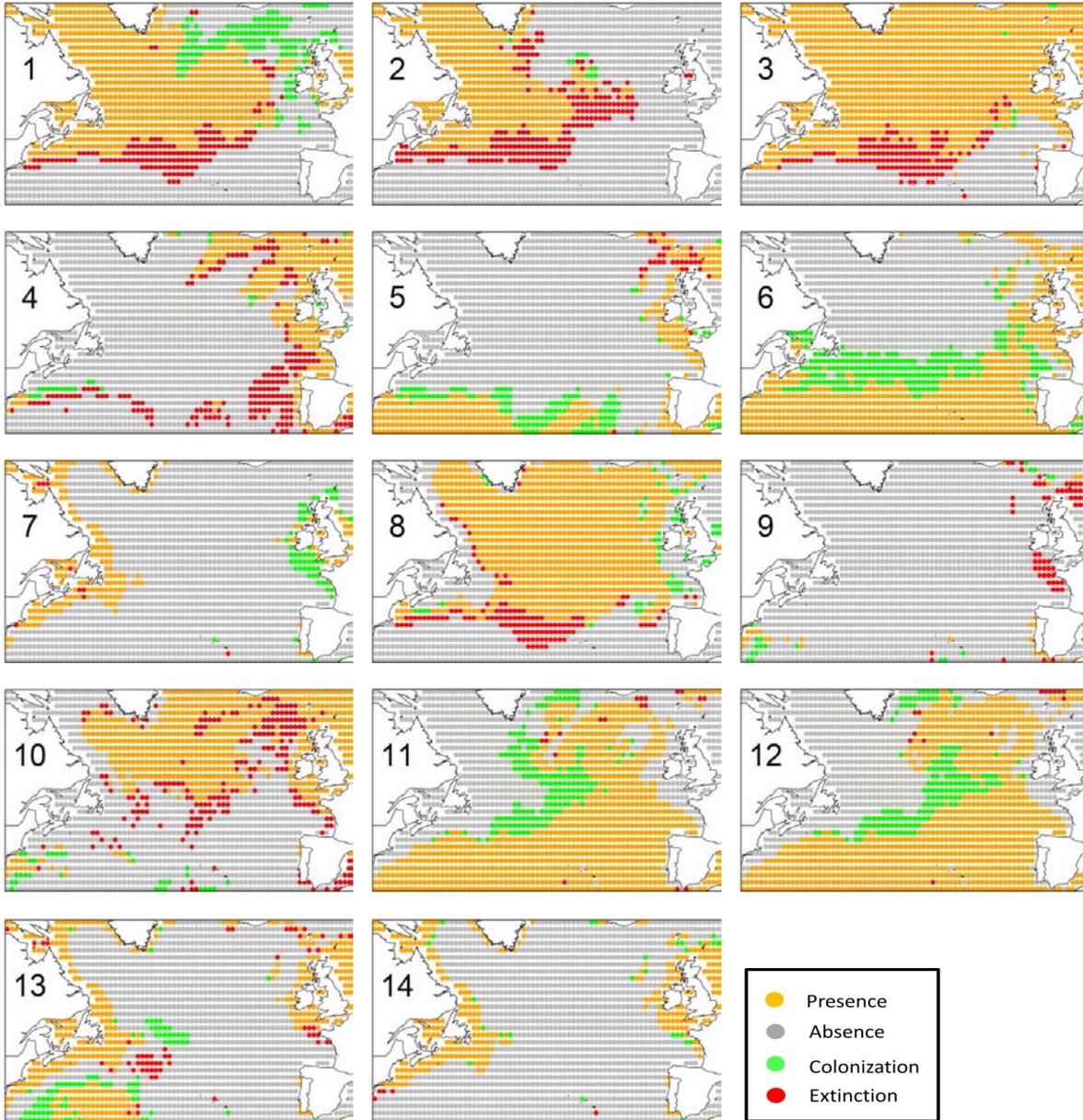
F.5



F.6

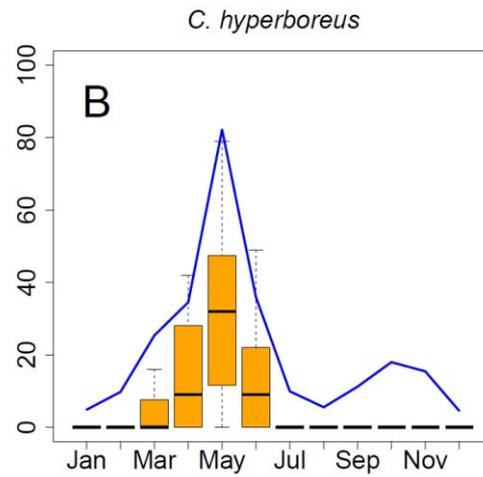
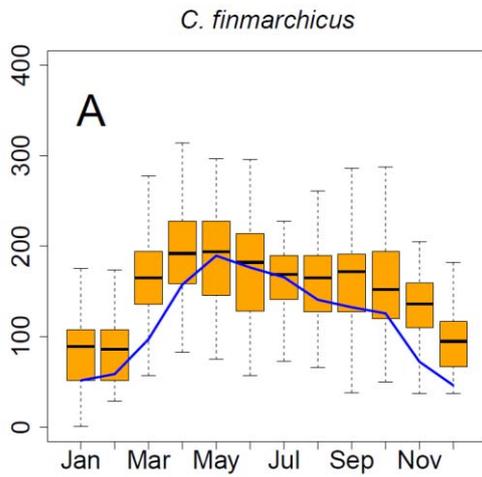
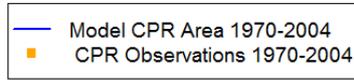


F.7

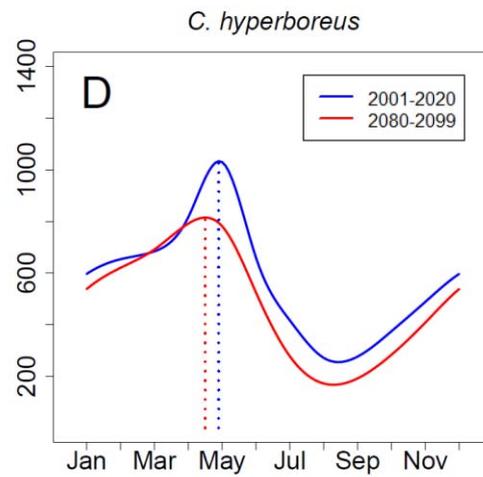
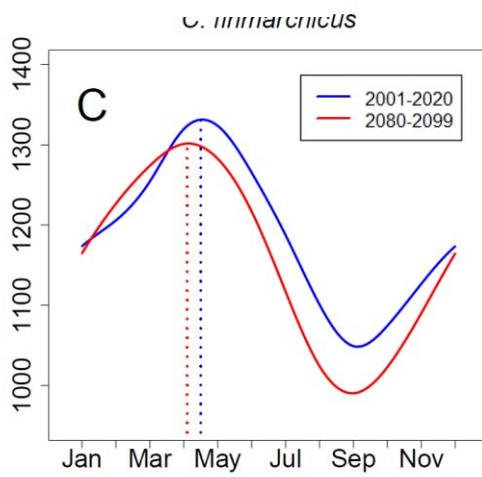


F.8

Occurrences

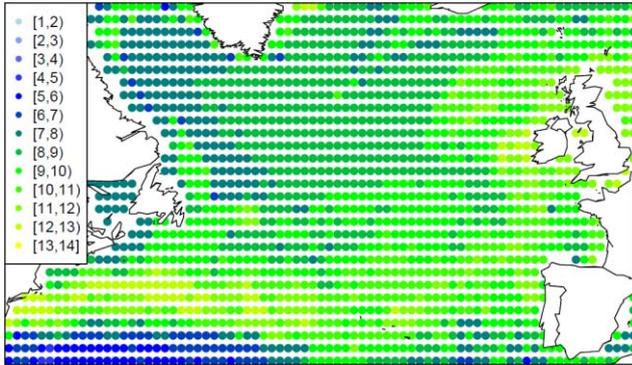


Predicted occurrences

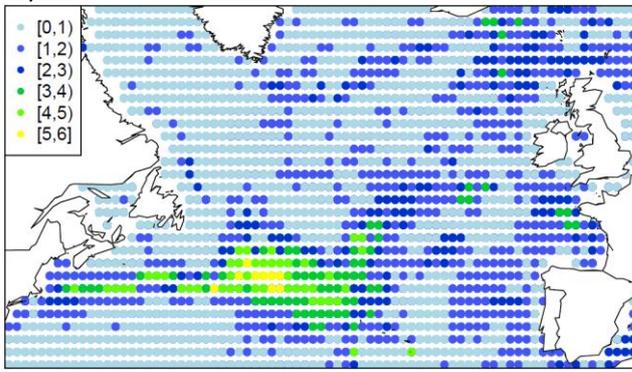


F.9

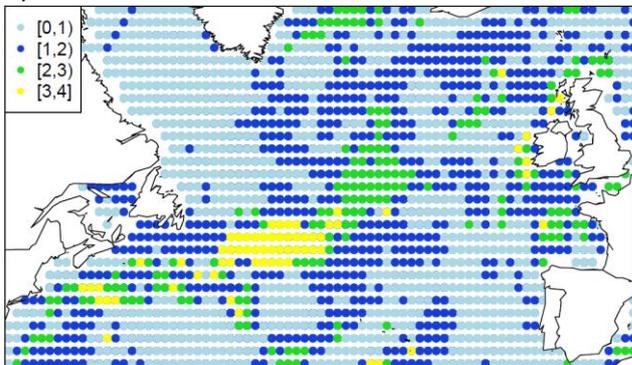
A) Species richness (2001-2020)



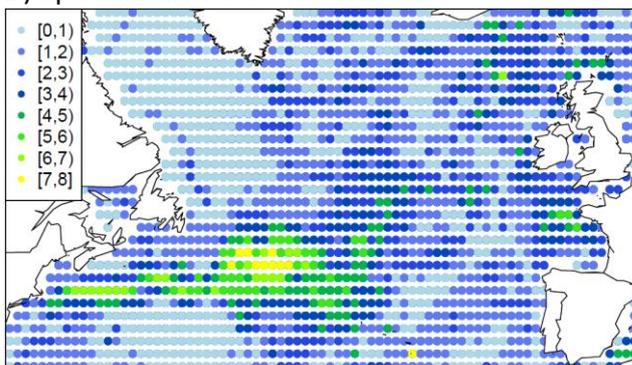
B) Extinction



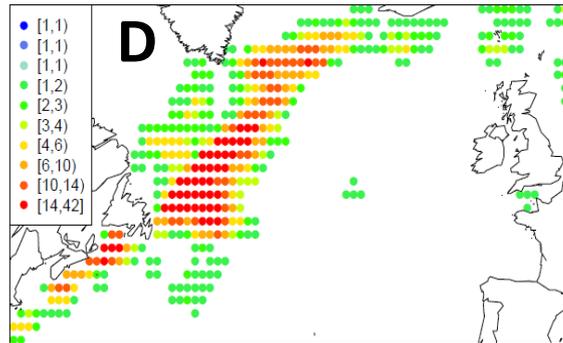
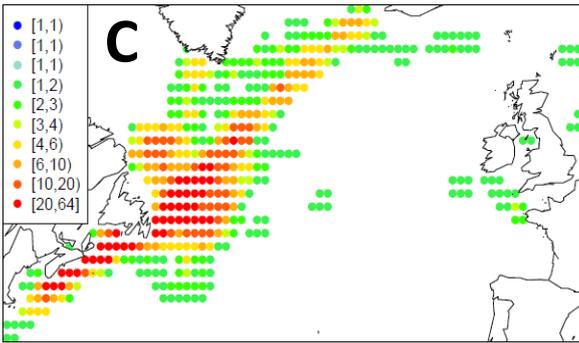
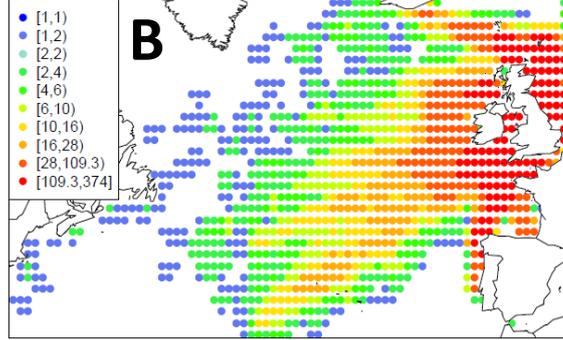
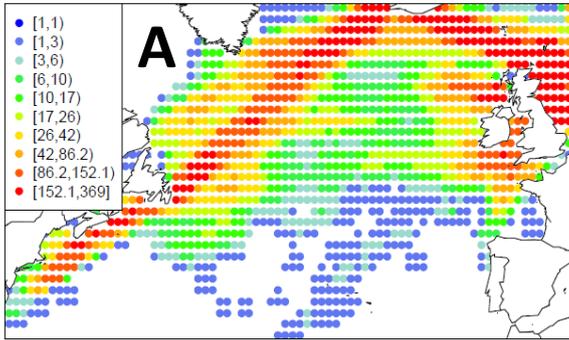
C) Colonization



D) Species turnover

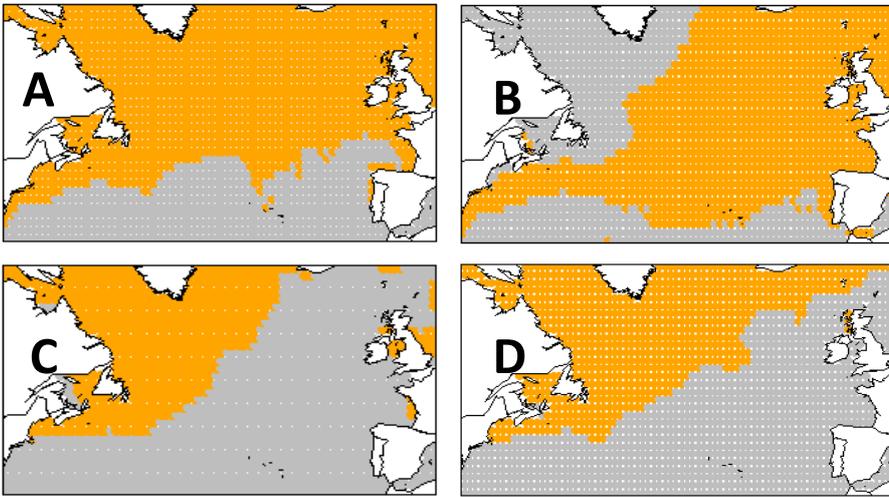


F.S1

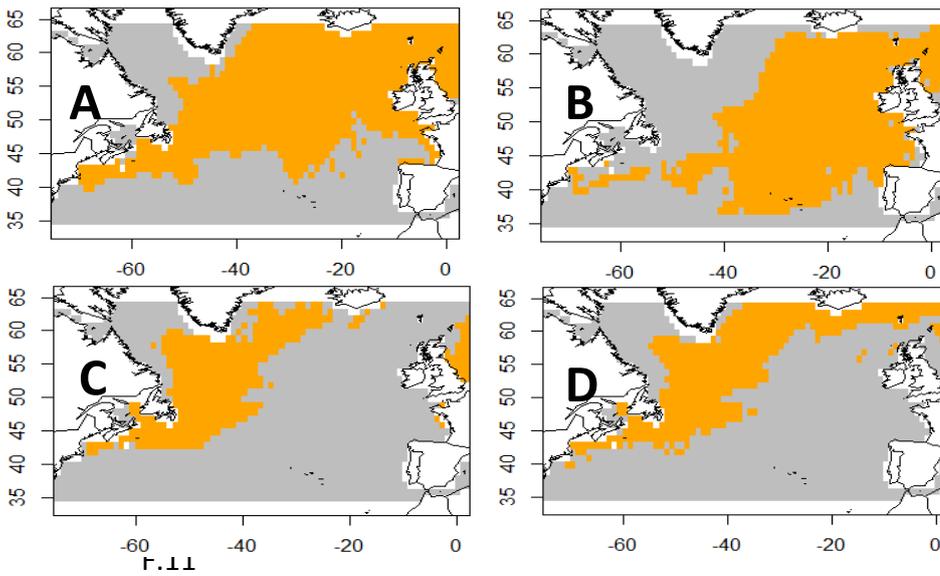


F.S2

1.



2.



3.

