



Original Articles

Multi-model ensemble projections of climate change effects on global marine biodiversity

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Species distribution models (SDMs) are important tools to explore the effects of future global changes in biodiversity. Previous studies show that variability is introduced into projected distributions through alternative datasets and modelling procedures. However, a multi-model approach to assess biogeographic shifts at the global scale is still rarely applied, particularly in the marine environment. Here, we apply three commonly used SDMs (AquaMaps, Maxent, and the Dynamic Bioclimate Envelope Model) to assess the global patterns of change in species richness, invasion, and extinction intensity in the world oceans. We make species-specific projections of distribution shift using each SDM, subsequently aggregating them to calculate indices of change across a set of 802 species of exploited marine fish and invertebrates. Results indicate an average poleward latitudinal shift across species and SDMs at a rate of 15.5 and 25.6 km decade⁻¹ for a low and high emissions climate change scenario, respectively. Predicted distribution shifts resulted in hotspots of local invasion intensity in high latitude regions, while local extinctions were concentrated near the equator. Specifically, between 10°N and 10°S, we predicted that, on average, 6.5 species would become locally extinct per 0.5° latitude under the climate change emissions scenario Representative Concentration Pathway 8.5. Average invasions were predicted to be 2.0 species per 0.5° latitude in the Arctic Ocean and 1.5 species per 0.5° latitude in the Southern Ocean. These averaged global hotspots of invasion and local extinction intensity are robust to the different SDM used and coincide with high levels of agreement.

Keywords: climate change, hotspots, marine biodiversity, multi-model approach, species distribution modelling.

Introduction

The latest assessment by the Intergovernmental Panel on Climate Change projects sea surface temperature (SST) to warm from 1°C (Representative Concentration Pathway, or RCP 2.6) to more than 3°C (RCP 8.5) by 2081–2100, relative to 1986–2005 (IPCC, 2013). Although ocean warming is predicted to be the greatest in the upper 700 m (IPCC, 2013), mixing and advection processes will gradually transfer the additional heat to deeper waters, with observations since 1961 showing average temperature to be increasing to a depth of 3000 m (Levitus *et al.*, 2000). As ectothermic marine species rely on a characteristic temperature window within their natural environment (Portner, 2001), there is increasing concern for species' ability to survive long-term changes in the mean climatic conditions, as well as increased climatic variability, acidification, and expansion of oxygen minimum zones (Orr *et al.*, 2005;

Fabry *et al.*, 2008; Cheung *et al.*, 2011). Observations and theory have indicated that marine fish and invertebrates frequently undergo shifts in distribution in response to changing environmental factors, in directions that are most commonly towards higher latitudes (Parmesan and Yohe, 2003; Perry *et al.*, 2005; Hiddink and ter Hofstede, 2008; Doney *et al.*, 2012; Poloczanska *et al.*, 2013), deeper waters (Dulvy *et al.*, 2008), and in general, following temperature velocity (Pinsky *et al.*, 2013). These responses to ocean–atmospheric changes have been projected to lead to altered patterns of species richness (Cheung *et al.*, 2009), changes in community structure (MacNeil *et al.*, 2010), ecosystem function (Petchev *et al.*, 1999), and consequential changes in marine goods and services (Cheung and Sumaila, 2008; Sumaila *et al.*, 2011; Madin *et al.*, 2012). In the marine environment, patterns of species richness are strongly related to environmental factors such

as temperature and nitrate concentration (Macpherson, 2002). It is therefore likely that the intensity of climate change impacts will vary geographically according to changes in key habitat types and the sensitivity of species inhabiting them (Roessig *et al.*, 2004; Harley *et al.*, 2006; Munday *et al.*, 2008; Cheung *et al.*, 2009).

Species distribution models (SDMs) have been widely applied to evaluate the likely responses of species to climate change, and assess the resulting impacts on biodiversity or ecosystem services in both the terrestrial (Polce *et al.*, 2013; Warren *et al.*, 2013) and marine environments (Cheung *et al.*, 2010). SDMs combine data indicating the current occurrence of a species with environmental parameters to form a bioclimatic envelope for that species. The bioclimatic envelope may thus be defined as the set of physical and biological conditions suitable for a given species (Hutchinson, 1957). Projecting this envelope under scenarios of climate change subsequently allows its potential shift in distribution to be estimated. However, alternative SDMs and input data frequently lead to variability in projections (Warren *et al.*, 2013; Jones *et al.*, 2013a), and the need to explicitly consider the inherent uncertainties and assumptions within the modelling procedure is frequently highlighted (Brander *et al.*, 2013; Jones *et al.*, 2013a). Although variation attributable to alternative SDMs has been found to be a large source of uncertainty in estimating species' range shifts under climate change (Jones *et al.*, 2013a, b), few studies have attempted to incorporate this uncertainty into model evaluations and outcomes, and none has done so at a global scale for a large number of species.

Here, we apply SDMs to project the future distributions and latitudinal shifts of a set of 802 marine fish and invertebrate species under scenarios of climate change. This set comprises species exploited by fisheries, which generally include those species that are more abundant. We thereby evaluate global patterns of local extinction and invasion, and identify areas where climate change may thus have the greatest impact on biodiversity and community structure. We use the term "local extinction" to refer to a species ceasing to exist in a particular location, despite existing elsewhere (Townsend Peterson *et al.*, 2002; Dulvy *et al.*, 2003; Cheung *et al.*, 2009), while invasion indicates the expansion of a species into an area not previously occupied by it (Rahel and Olden, 2008; Cheung *et al.*, 2009). To evaluate and incorporate the uncertainty attributable to alternative SDM procedures, we apply three models that are among the most commonly applied SDMs in the marine environment and were designed to cope with issues of data quality and quantity. These are Maxent (Phillips *et al.*, 2004; Phillips, 2008), AquaMaps (Kaschner *et al.*, 2006, 2011), and the Dynamic Bioclimate Envelope Model (Cheung *et al.*, 2011). We examine whether projections from multiple SDMs will result in estimates of shifts in the distribution of marine biodiversity that are different from previous projections using a single model only. In particular, we hypothesize that local extinctions will be concentrated in lower, equatorial latitudes, while invasions are more common near the poles (Cheung *et al.*, 2009). Moreover, using a multi-model approach will highlight where predictions are most robust to variations in SDM (Jones *et al.*, 2013b).

Material and methods

Modelling approaches

We applied the three SDMs, Maxent, AquaMaps, and the Dynamic Bioclimate Envelope Model (DBEM), to predict the distributions of a set of marine fish and invertebrates at a global scale. These SDMs have previously been applied and tested at a regional scale (Jones

et al., 2012, 2013a) and have been shown to be suited to modelling the distribution of marine species, for which data and knowledge are frequently scarce (Jones *et al.*, 2012). AquaMaps and Maxent use generative statistical procedures to determine species' environmental envelopes from species occurrence data and a suite of environmental variables. Species occurrence data are represented by presence data only, which is considered more appropriate when absence data are likely to be inaccurate. Although absence data are occasionally available for marine species, they are not available for many of the species modelled here. The two models, contrasting each other in the algorithms used (Jones *et al.*, 2012), were applied to predict the "current" distributions of the set of species using 30-year averaged environmental data centred on 1985 (1970–1999). The third model, the DBEM (Cheung *et al.*, 2011), combines statistical and mechanistic approaches in predicting species' distributions. First, a species' current distribution is predicted using the *Sea Around Us Project* model (Close *et al.*, 2006), thereby restricting a species' distribution using known parameters, geographic limits, or habitat preferences ("filters"). Filters were applied for FAO area, habitat, latitudinal limits, and depth. The DBEM then uses the predicted current distribution to define a species' bioclimatic envelope by its "preference profile" (the relative suitability of difference environmental values) for each environmental variable, again using environmental data averaged between 1970 and 1999. Detailed descriptions of the three SDMs are provided in the Supplementary data and publications indicated.

Having trained the three models on current environmental data to calculate the environmental envelope for each species, as described above and in greater detail in the Supplementary data, environmental envelopes were projected under climate change scenarios to predict annual distributions up to 2059. Projections were then used to calculate average estimates of change, as described below. Seasonal data (April–February and October–March) were used to model both summer and winter distributions for pelagic species, respectively, these then being averaged to assess annual patterns of distribution shift, consistent with demersal species.

Species' occurrence data

Data were obtained for exploited fish and invertebrates in the world oceans. Presence-only species occurrence data were obtained from the Ocean Biogeographic System (OBIS, <http://www.iobis.org/>), accessed in 2013. Occurrence records were spatially aggregated on a 0.5° latitude × 0.5° longitude grid and filtered to omit points occurring in non-verified FAO areas and outside validated depth limits using FishBase (Froese and Pauly, 2011). Species data were cleaned as described in the Supplementary data, and species with fewer than ten occurrence records were discarded, resulting in a set of 802 species.

Projecting distribution shifts under climate change

Projections of oceanographic variables from the Geophysical Fluid Dynamics Laboratory's Earth System Model (version 2.1, GFDL ESM2.1; Dunne *et al.*, 2010) were applied to project species distributions using the three SDMs. Oceanographic variables for predicting species distributions using Maxent and AquaMaps were bathymetry; sea surface temperature (SST); seabed temperature (SBT); salinity; ice; primary productivity; and distance to coast. In addition, the DBEM uses O₂ concentration to simulate changes in growth and body weight as described in the Supplementary data. The original data were interpolated and regridded onto 0.5° latitude × 0.5° longitude resolution using the nearest neighbour

method. Two scenarios used in the 5th Assessment Report of IPCC were used: RCP 2.6 (van Vuuren *et al.*, 2006, 2007) and RCP 8.5 (Riahi *et al.*, 2007). RCP 2.6 is characterized by a peak in greenhouse gases in mid-20th century, before a decline that results in a reduction in GHG levels over time (van Vuuren *et al.*, 2007). Conversely, RCP 8.5 is characterized by increasing emissions over time, leading to high GHG concentrations by the end of the century (Riahi *et al.*, 2007). A threshold value was used to exclude low values of relative habitat suitability in each prediction, with values lower than the threshold being set to 0. The threshold applied was that of the minimum relative habitat suitability value predicted across the set of species occurrence points, for each species. The effect of applying a threshold on results obtained is explored below.

Models were previously tested and validated using the area under the curve of the receiver operating characteristic plot test statistic, as well as the Point Biserial Coefficient (Zheng and Agresti, 2000; Jones *et al.*, 2012). However, as this only allows evaluation of a model's ability to portray a species' distribution in the current period, hindcast environmental and oceanographic data were obtained using a historical (1959–2004) simulation of ocean conditions using the GFDL ESM2.1 forced with re-analysis data (hindcast data). The three SDMs were trained on 30-year averaged data centred on 1985 and projected using annual environmental data from years 1982 to 2006. Observations were obtained for a set of species in the Bering Sea from Mueter and Litzow (2008) and distribution shifts were compared at the community level. GFDL hindcast data for SST and ice concentration were further compared with observation data obtained from the MET Office UK Hadley Centre (Rayner *et al.*, 2003) and the variation between anomalies examined to assess the accuracy of these modelled data.

Latitudinal shifts

Latitudinal centroids were calculated for each species in each year using Equation (1; Cheung *et al.*, 2009):

$$C = \frac{\sum_{i=1}^n \text{Lat}_i \times \text{Abd}_i}{\sum_{i=1}^n \text{Abd}_i}, \quad (1)$$

where Lat_i is the latitude of the centre of each $0.5^\circ \text{ lat} \times 0.5^\circ \text{ long}$ spatial cell, Abd_i its predicted relative environmental suitability, and n the total number of cells (Cheung *et al.*, 2009). The annual latitudinal shift for each species was calculated as the difference between latitudinal centroids (Δx , calculated in km) in consecutive years using Equation (2; Cheung *et al.*, 2009):

$$\Delta x = (C_m - C_n) \times \frac{\pi}{180} \times r, \quad (2)$$

where $r = 6378.2$ km, the approximate radius of the earth, and C_m and C_n are the latitudinal centroids in years m and n . Estimates of annual latitudinal shift for every year between 1970 and 2060 were used to calculate the average decadal shift per species.

Changes in species richness

We investigated likely impacts of climate change on potential global patterns of biodiversity. The latitudinal trend in species richness is well established in both terrestrial and marine environments (Macpherson, 2002). A change in this pattern resulting from species-specific shifts in distribution may have implications for species interactions as well as affecting the availability of commercially targeted species to fisheries. First, we calculated species

richness (number of occurring species) within each $0.5^\circ \text{ lat} \times 0.5^\circ \text{ long}$ grid cell by overlaying global distribution maps of each of the 802 species. This was done for two periods, using averaged projected distributions for each species: 1991–2010 (“current”, “2000”) and 2040–2059 (“future”, “2050”), and the latitudinal averages were calculated for each SDM for RCP 2.6 and RCP 8.5 emissions scenario.

Second, we explored the changing pattern of species richness in terms of the frequency of local extinctions and invasions in each $0.5^\circ \text{ lat} \times 0.5^\circ \text{ long}$ grid cell. Species occurrence data available for the marine environment are biased towards temperate regions in the Northern hemisphere as well as shelf seas, coastal and surface waters (Mora *et al.*, 2008). As this would have resulted in species distribution maps also being unevenly distributed, the number of species invading or going locally extinct in each cell was standardized, giving the invasion intensity (I) [Equation (3)] and local extinction intensity (E) [Equation (4)], thereby expressing values as a percentage of the number of species initially present in each cell (Cheung *et al.*, 2009).

$$I_{i,y} = \frac{n_{i,y}^I}{n_i + 1}. \quad (3)$$

$$E_{i,y} = \frac{n_{i,y}^E}{n_i + 1}. \quad (4)$$

Where n is the species richness in the current period (2001–2005) and $n_{i,y}^I$ and $n_{i,y}^E$ are the number of species invading and going locally extinct in cell i and year y , respectively. Resulting data were averaged latitudinally to explore the impact of any projected changes in species richness, invasion, and local extinction on the global latitudinal pattern of marine biodiversity.

Projections from the three SDMs were then combined to depict the locations of hotspots of agreement between different model outputs. First, changes in species richness, invasion, and local extinction intensity were averaged across modelling procedures. Then, the extent of agreement (Jones *et al.*, 2013b) between models for a particular level of invasion or local extinction intensity was calculated. Areas with good agreement between modelling procedures were located in the following way. First of all, specific levels of local extinction and invasion intensity were chosen according to the distribution of intensity values predicted from each model. They were (i) 1%, (ii) 20%, and (iii) 40% for invasion intensity and (i) 1%, (ii) 20%, and (iii) 60% for extinction intensity. We then assessed how the models agreed in predicting invasion or local extinction at or above a particular intensity level. Predictions of local extinction or invasion intensity were then converted into binary maps, allocating values at or above a particular threshold to 1 and values below to 0 in each $0.5^\circ \text{ lat} \times 0.5^\circ \text{ long}$ grid cell. To examine where hotspots of different level of biodiversity impacts might coincide with areas of maximum agreement across models, the three binary predictions were then summed to give an index of agreement from 0 to 3. Thus, while 0 indicates that no model predicts above a specified percentage of local extinction or invasion, a value of 3 indicates maximum agreement at or above the specified level of biodiversity impact. Furthermore, we assessed the level of agreement between models in predicting invasion and local extinction in species' most suitable habitats. To do this, binary maps were calculated after applying a 0.7 percentile threshold to restrict each species' distribution using a high threshold of potential occurrence. This

threshold was chosen as one of a set of thresholds applied in a sensitivity analysis (outlined below).

Sensitivity analysis

The sensitivity of the projected species' distributions to restriction using a minimum presence threshold was examined. As there is currently no consensus on the most suitable method for applying thresholds (Nenzén and Araújo, 2011), to test the effect of this procedure on results obtained and conclusions drawn, a set of contrasting thresholds was selected and results from each compared (Jones *et al.*, 2012). The use of increasingly larger threshold values restricted projected occurrence to areas of increasing relative habitat suitability. The extent to which results are robust to threshold setting was thus assessed by comparing outputs obtained using the following set of threshold cut-offs: (i) the minimum relative habitat suitability value at a species occurrence datapoint (minimum presence point threshold), and the fixed threshold at the (ii) 0.1, (iii) 0.5, and (iv) 0.7 percentiles for each prediction. Predictive values of relative habitat suitability below the threshold value obtained for each species were set to 0.

Results

Applying the three models to simulate historical (1959–2004) changes in species distributions in the Bering Sea allowed projected model results to be compared with observations of species' range shift at a community level (Supplementary Figure S1). Annual changes in modelled hindcast climate data are shown to compare well with observed data (Supplementary Figure S2). However, all three SDMs have a tendency to overestimate poleward latitudinal shifts at a community level, in particular for the upper extremes of the projections, where species are predicted as shifting the furthest. This is highlighted by the differences in projected decadal latitudinal shifts between modelled and observational data at a community level (Supplementary Figure S1). Maxent (difference at: median latitudinal shift = 4.2 km decade⁻¹, at 25th percentile = 3.0 km decade⁻¹, at 75th percentile = 8.0 km decade⁻¹, $n = 20$) and the

DBEM (differences at median latitudinal shift = 4.1 km decade⁻¹, at 25th percentile = 3.1 km decade⁻¹, at 75th percentile = 8.5 km decade⁻¹, $n = 20$) are shown to simulate the community level response more accurately than AquaMaps (differences at median latitudinal shift = 33.3 km decade⁻¹, at 25th percentile = 23.1 km decade⁻¹, at 75th percentile = 36.7 km decade⁻¹, $n = 20$).

Climate-induced range shifts

Applying the multi-model procedure to a set of 802 globally distributed marine species predicted that 93% of species would show poleward shifts in latitudinal centroid between 2000 and 2059 under a low emissions climate change scenario, and 97% under a high emissions climate change scenario. Overall, the median rate of latitudinal poleward centroid shift was predicted at 15.5 km decade⁻¹ under RCP 2.6, with a minimum and maximum range of -92 to 286 km decade⁻¹ (Figure 1a). Projected shifts increased significantly under RCP 8.5, with a median of 25.6 km decade⁻¹, ranging between -75 and 282 km decade⁻¹ (paired Wilcoxon's test, $p < 0.05$, using species within SDM as replicates). The differences in shifts between pelagic and demersal species were found to be significant when modelled using the DBEM or AquaMaps models and environmental data representing RCP 2.6 (Figure 1b; two-sample Wilcoxon's test, $p < 0.05$, using species as replicates). However, except DBEM and AquaMaps modelling pelagic species under RCP 2.6, the differences between species' latitudinal shifts predicted using different SDMs were significantly different (paired Wilcoxon's test, $p < 0.05$, $n = 802$ spp.).

Change in species richness

The latitudinal pattern of species richness for the set of species modelled here in the current period is shown in Figure 2. Projecting species' distributions under climate change predicts altered patterns of global species richness by 2050. High intensities of species invasions are projected to occur in higher latitude regions, such as the Arctic Ocean, South Pacific, and South Atlantic Oceans

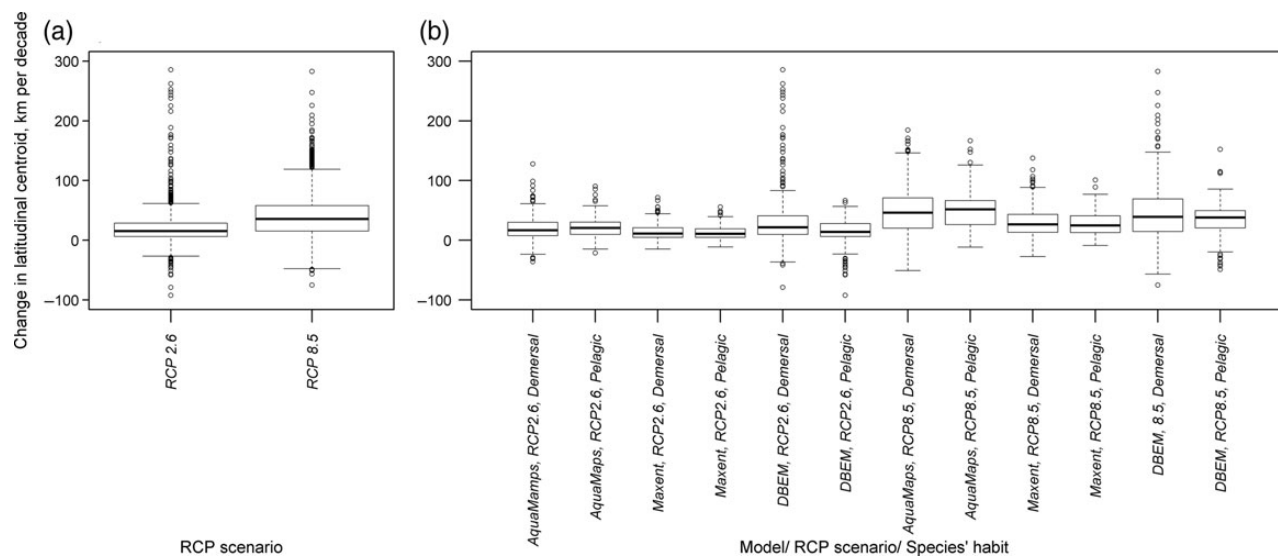


Figure 1. Projected changes in latitudinal centroid in kilometre per decade (averaged between 1970 and 2060) (a) for each RCP scenario across all species and SDM models and (b) for demersal and pelagic species for each SDM model and RCP scenario. The thick horizontal lines represent median values, while lower and upper boundaries of the box represent the upper and lower quartiles of the data, and the whiskers the most extreme data points no greater than 1.5 times the inter-quartile range from the box. Points more extreme than this range are represented as open circles.

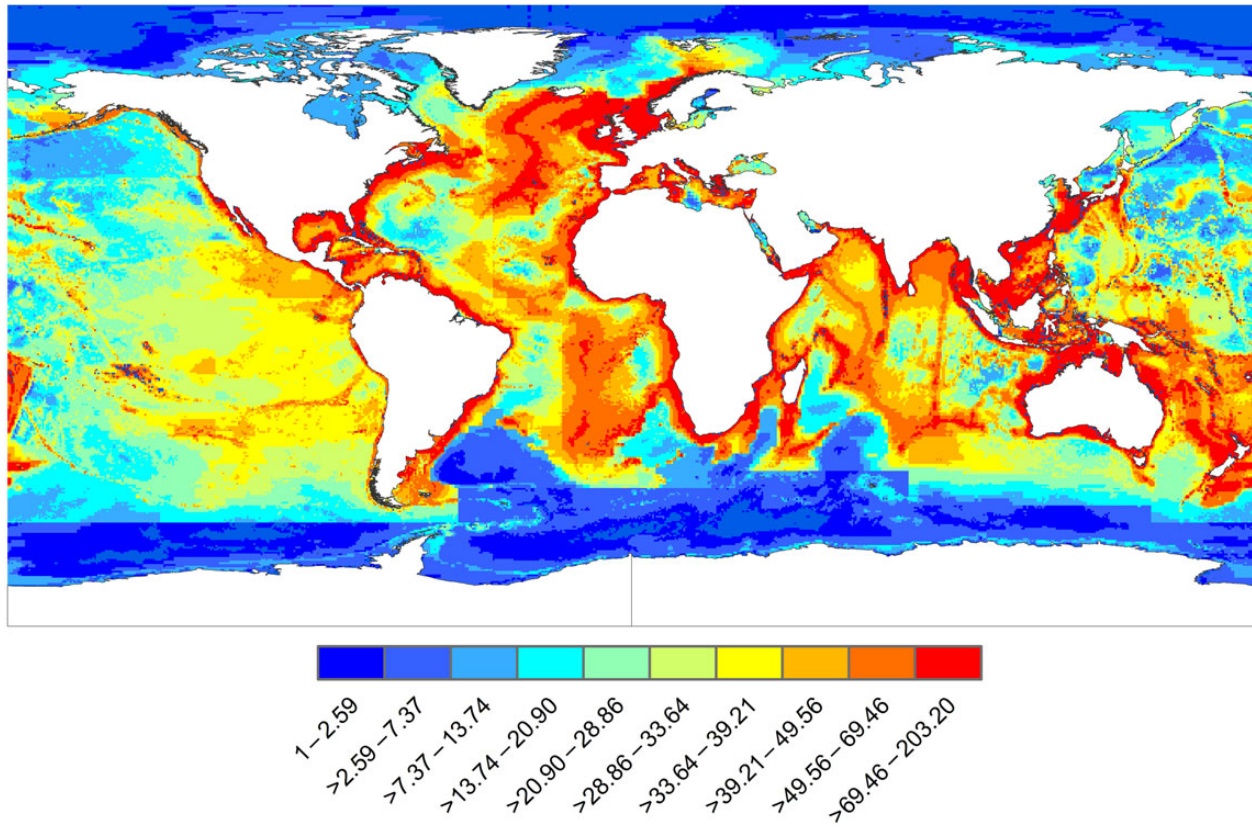


Figure 2. Species richness averaged across SDMs for the current period (1991–2010).

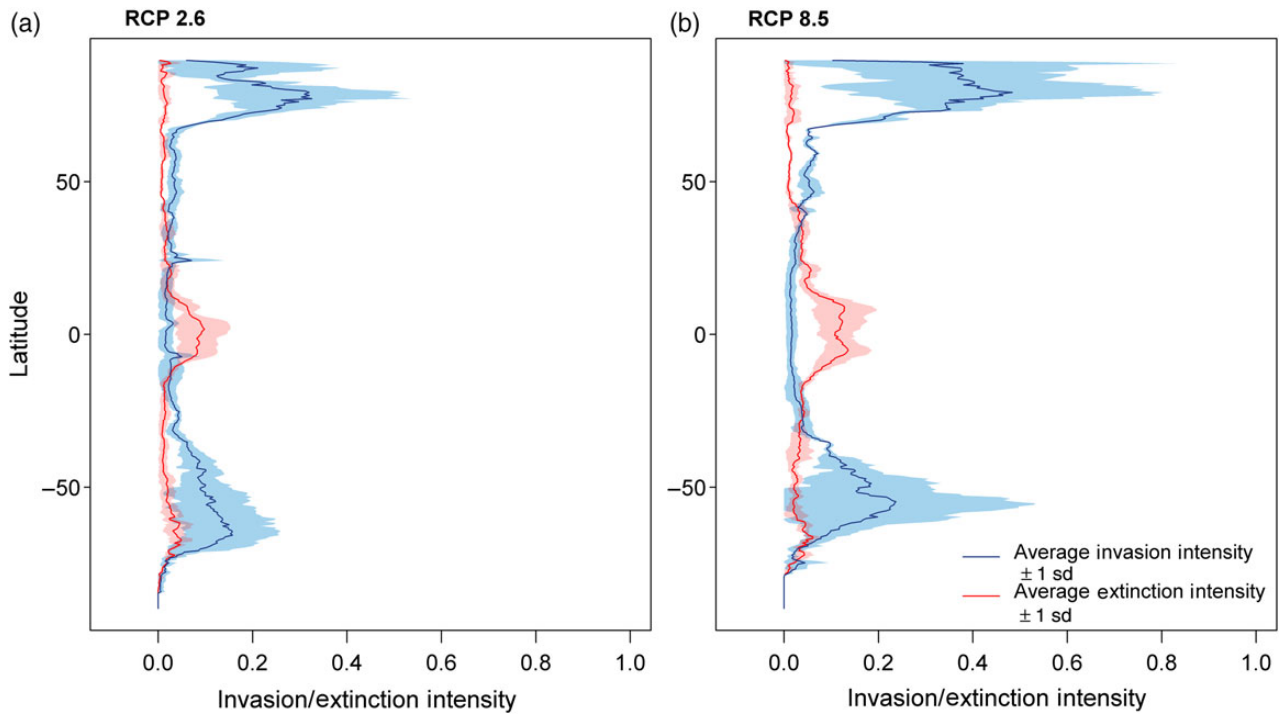


Figure 3. Latitudinal average of invasion and local extinction intensities per 0.5° latitude between 2000 and 2050 under climate change scenarios (a) RCP 2.6. and (b) RCP 8.5. The shaded area represents confidence intervals at 1 standard deviation (s.d.).

(Figure 3). While global average latitudinal invasion intensity is predicted to be 6% of the initial species richness for RCP 2.6, this increases to 15% at latitudes $>60^\circ$ north, and 10% between 40 and 60° S (the Southern Ocean), but decreases to only 2% in equatorial regions (10° – 10° N). Under the high emissions scenario, invasion intensity remains low in the Equatorial regions (at 8%) but increases to 26% in the Arctic Ocean ($>60^\circ$ N).

Contrasting the latitudinal pattern of invasion intensity, hotspots of local extinction intensity are concentrated in lower latitude regions around the equator. Local extinction intensities measure 8% between 10° and 10° S compared with 2% globally, with estimates increasing to 12 and 4%, respectively, under RCP 8.5. Although the magnitudes of species invasion and local extinction intensities are higher in RCP 8.5 than those in RCP 2.6, the patterns of species invasions and local extinctions are similar between the two scenarios. The variation in invasion intensity is also highest in the Southern Ocean in both scenarios, highlighting relatively higher uncertainty of the projections in this region.

Presenting predicted changes as the total numbers of species invading or going locally extinct per degree latitude shows that, while species invasions continue to be more common at the poles, there are regionally fewer species invading than those going locally extinct in equatorial regions (Figure 4). Specifically, in tropical regions between 10° N and 10° S, our study predicted an average of 6.5 species becoming locally extinct per 0.5° latitude compared with 1.4 species per 0.5° latitude globally under RCP 8.5. Average invasions were predicted to be 2.0 species per 0.5° latitude in the Arctic Ocean, 1.5 species per 0.5° latitude in the Southern Ocean, and 1.3 species per 0.5° latitude globally.

The degree of geographic variation in projected species local extinction varies between SDM (Supplementary Figure S3). For example, total numbers of projected local extinction by latitude are most concentrated in the lower latitudes using the DBEM (an

average of nine species per 0.5° latitude at 10° N– 0° S compared with one averaged globally), whereas Maxent predicts the most even distribution of local extinctions (average of three species per degree of latitude at 10° N– 10° S compared with one averaged globally).

Model agreement

Predicted local extinction hotspots with high agreement (i.e. all three models) between SDMs are concentrated in tropical oceans. Under the high emissions scenario, areas that are predicted to experience $\geq 20\%$ local extinction using all three distribution models are relatively rare and mostly located in the tropical Pacific Ocean (Figure 5a). When agreement between two or more SDMs (instead of only three) was considered, the hotspots of $\geq 20\%$ local extinction spread throughout the tropical regions on the central and eastern Pacific, extended towards Malaysia and into the central Indian Ocean and the Gulf of Guinea. When a more restricted threshold for species occurrence was applied (occurrence of the species was included when habitat suitability values ≥ 0.7 percentile for each species), the areas of high agreement of $\geq 20\%$ local extinction are more extensive, in particular expanding into the equatorial regions of major oceans, including the central Indian and Atlantic Oceans and the East Pacific (Supplementary Figure S4).

Conversely, high agreement in hotspots of $\geq 30\%$ invasion intensity was projected to occur in the northern Barents Sea, Greenland Sea, Bering Sea, and East Siberian Sea in the Arctic (Figure 5b). When species invasions are restricted to the new occurrence of species in the most suitable areas (habitat suitability ≥ 0.7), the invasion hotspots in the Arctic Ocean generally move coastward, in particular in the Barents and Greenland Seas (Supplementary Figure S5). Although small, localized patches of invasion intensity $\geq 20\%$ are predicted to occur in the Southern Ocean and North Pacific, these areas are more extensive when assessing areas of

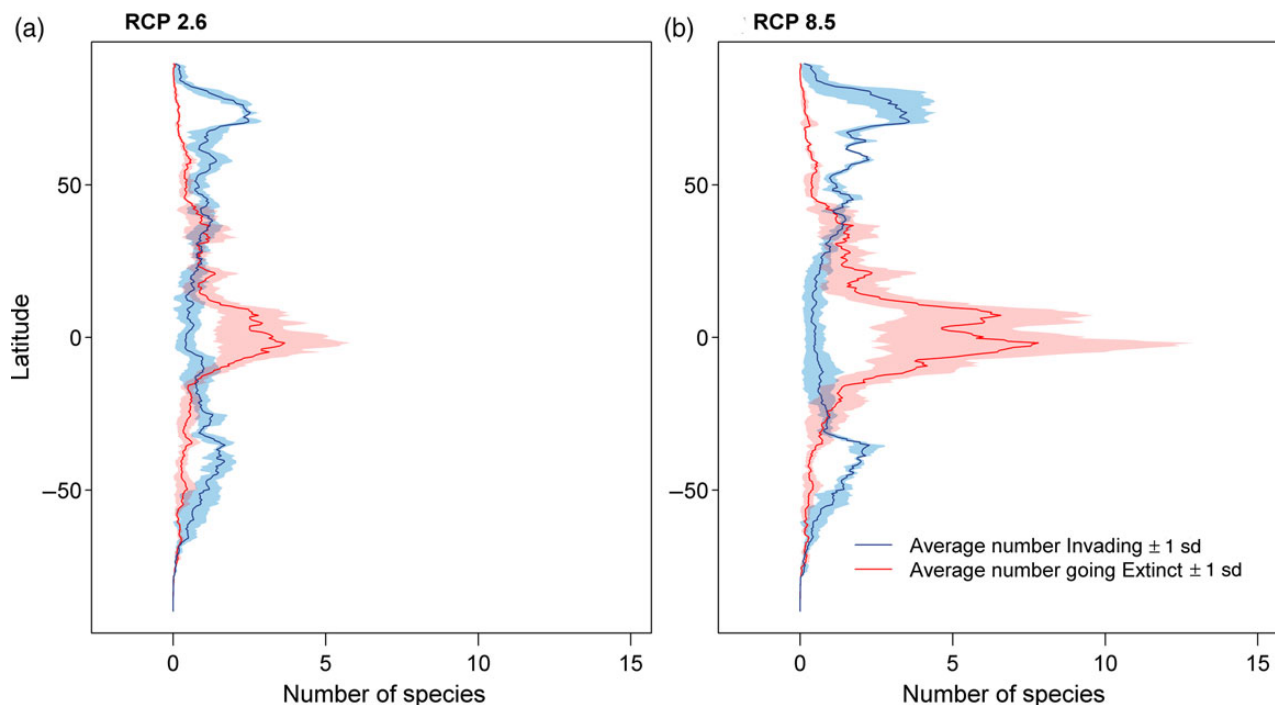


Figure 4. Latitudinal average of total number of species predicted to invade and go locally extinct per 0.5° latitude between 2000 and 2050 under climate change scenarios (a) RCP 2.6 and (b) RCP 8.5. The shaded area represents confidence intervals at 1 standard deviation (s.d.).

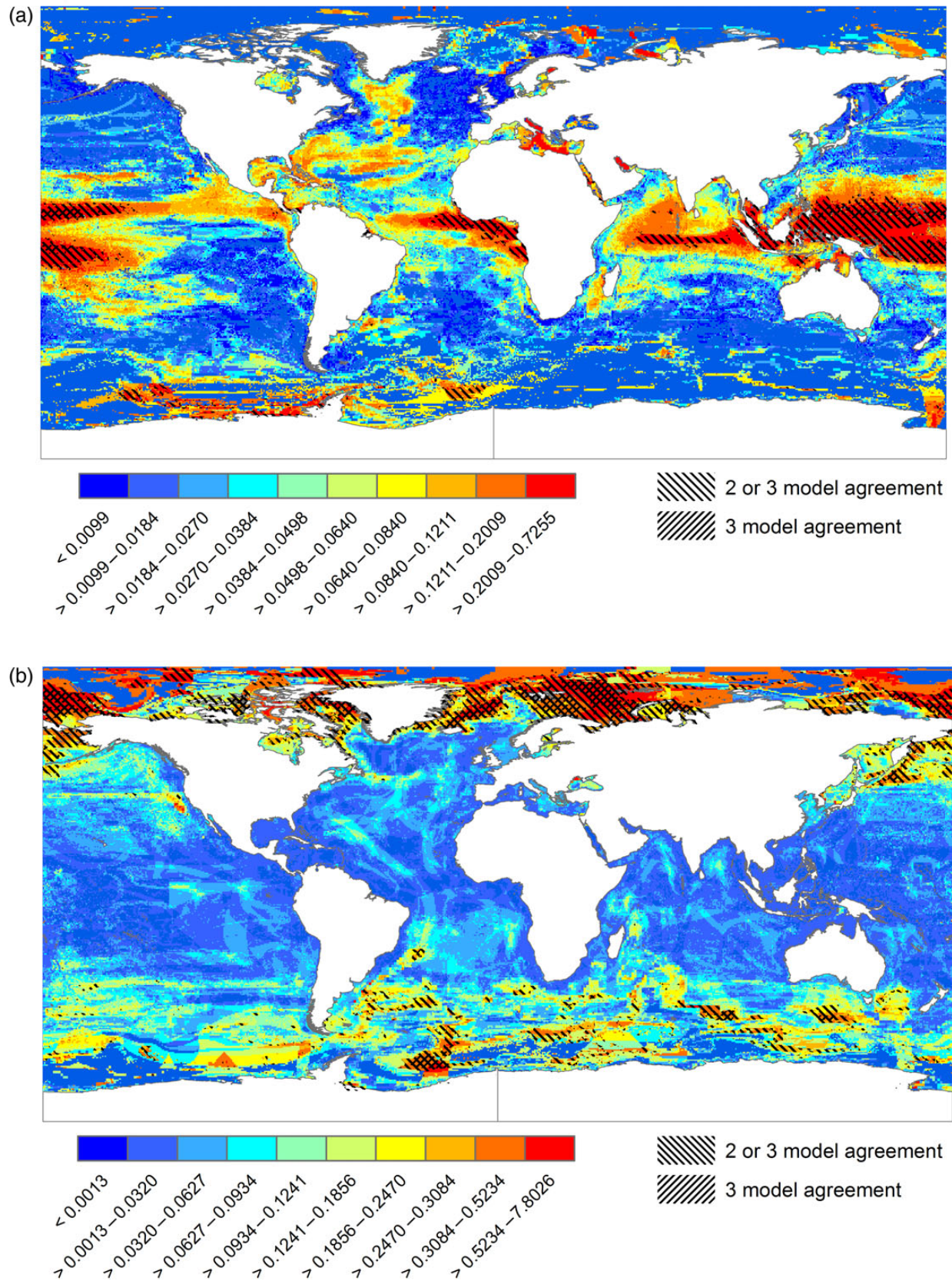


Figure 5. Hotspots of (a) local extinction and (b) invasion intensity of 20% of more, between 2000 and 2050 averaged across AquaMaps, Maxent, and the DBEM under scenario RCP 8.5 and using the minimum presence point threshold, the minimum relative habitat suitability at a species occurrence data-point. Shading shows areas of high (3 models) and moderate (2 models) agreement.

moderate agreement (two or more models). Under the RCP 2.6 scenario, hotspots of agreement show similar patterns of distribution but are more localized (Figure 5b).

Sensitivity analysis

Projected patterns of species richness in 2000 and 2050 varied only slightly with different habitat suitability thresholds (Supplementary Figure S6), while the variation between richness calculated using different SDMs was greater using the fixed thresholds (0.1, 0.5, and 0.7). Restricting species distributions to only those most suitable areas resulted in an overall decrease in richness across latitudes. The general patterns of local extinction and invasion intensity were not sensitive to the threshold applied, although the magnitude of projected changes averaged for each 0.5° latitude, and their variations across SDMs increase as more restrictive thresholds are applied (Supplementary Figure S7).

Discussion

This study shows a general signal of potential future climate change impacts on biodiversity that is robust to characteristics of the modelling procedures. Previous analyses using the same set of SDMs that were applied here advocate the need for a multi-model approach, thereby encompassing uncertainties due to differences in validated modelling methodologies and algorithms (Jones *et al.*, 2012, 2013a). The multi-model approach allows us to assess the uncertainties associated with the lack of knowledge surrounding many marine organisms and their responses to change. Particularly, the skills of different modelling approaches may vary between species and regions. In our case study of historical changes in the Bering Sea, the DBEM and Maxent are shown to be slightly more accurate in simulating the community level response to climate change (mean percentile differences = 7.0 and 6.7, respectively). Such difference between SDMs may be attributed to the ability of Maxent to weight variables, while no weighting of variables was applied in AquaMaps, or further variations in modelling parameterizations and characteristics (Jones *et al.*, 2012). This overestimation of latitudinal shifts in the Bering Sea may cause AquaMaps to bias the multi-model average. However, this study only allows comparison at a regional scale within a relatively small climatic gradient. Undertaking similar assessments within tropical, temperate, and polar regions would allow the capability of all models to project range shifts to be more comprehensively assessed. Global scale comparisons would also allow the overestimation of the highest observed distribution shifts by all models to be more adequately assessed. Furthermore, we do not know whether species at different latitudes vary in their relative sensitivities to change in particular climate variables, or whether the SDMs vary in their ability to reflect this sensitivity. Until data can be obtained to undertake this global scale assessment, using a set of SDMs enables us to bracket uncertainties in exploring the response of marine organisms to climate change at a global scale, reducing the potential bias from applying a single model. This is particularly important when applying a generalized approach to many species.

Latitudinal shifts

This study predicts that large numbers of commercially targeted marine fish and invertebrates will exhibit poleward shifts in distribution, agreeing with distribution shifts observed for marine species in the last few decades (Stebbing *et al.*, 2002; Macleod *et al.*, 2005; Perry *et al.*, 2005; Simpson *et al.*, 2011; Poloczanska *et al.*, 2013). For example, six species in the North Sea were found to exhibit

boundary shifts in relation to climate and time at a rate of 22 km decade⁻¹ (Perry *et al.*, 2005). Although this shift is similar to that projected using a high emissions climate change scenario (RCP 8.5), this is consistent with the relatively shallow depth and thus higher rates of warming in the North Sea relative to the global average. There is variation, however, between rates of shift projected here and those obtained from a meta-analysis of 1 735 marine responses (Poloczanska *et al.*, 2013), which found the leading, trailing edge, and centre of marine species' ranges to be shifting at a rate of 30.6 ± 5.2 km decade⁻¹. This higher rate of range shift is likely due to the inclusion of shifts of range edge, as well as the set of species examined. The species used in this study are predominantly commercially exploited species. Because these are also, in general, wide-ranging, extinctions are concentrated in the tropics, with fewer local extinctions in sub-Arctic regions. This study supports the higher rates of latitudinal shift in the marine environment than on land that have been observed (Parmesan and Yohe, 2003) and predicted elsewhere using a single SDM (Cheung *et al.*, 2009), likely due to higher velocities of climate change (Burrows *et al.*, 2011) and lower constraints on dispersal in the sea. However, it should also be noted that, as mentioned above, comparing results with observations in the Bering Sea indicated a slight overestimation in projecting latitudinal shifts. While the extent of this difference might vary with species and region, the uncertainties in projections should be considered.

Changing patterns of species richness

Projected species' distribution shifts will likely affect global latitudinal patterns of biodiversity, with the greatest levels of change in species richness predicted to be at the poles and tropics, which will become hotspots of invasions and local extinctions, respectively. This supports the hypothesis that the intensity of climate change impacts will vary geographically, consistent with the distribution of climate change impacts on land (Sala, 2000) and predictions of faster rates of warming near the equator and poles than the global average (IPCC, 2013). In addition, results are consistent with the theory proposing that the response of biodiversity to changing environmental variables, such as temperature, will depend not only on the magnitude of change but also on the physiological sensitivity of organisms to change (Pörtner and Peck, 2010; Scott and Johnston, 2012) and the position of that change within an organism's characteristic tolerance limits. For example, species in tropical and polar regions have narrower thermal tolerances and live closer to their tolerance limits than those in temperate regions (Deutsch *et al.*, 2008). Furthermore, the strongest ocean warming signal is predicted to be in subtropical and tropical regions, with SST data used in this study projecting warming between 1951 and 2069 by 0.98°C in the Arctic Ocean (>60°N), compared with a 2.08°C increase around the equator (10°S–10°N) and a 1.36°C global average SST increase, under RCP 8.5 (GFDL ESM 2.1). Therefore, in addition to tropical species exhibiting high sensitivities to environmental change, the high level of exposure to warming in these areas increases their vulnerabilities and the likelihood of high local extinction intensities in tropical regions. This overall vulnerability in the tropics, and the relatively shallow depths of seas surrounding Indonesia, explain the hotspot of extinction in this area.

Conversely, it has been suggested that species living in thermally stable environments have reduced acclimatory ability (Portner *et al.*, 2000; Nguyen *et al.*, 2011). In polar regions, for example, this might be caused by cold-adaptation, which has led to fewer red blood cells, oxygen-binding proteins (Nikinmaa, 2002), and enzymes that

are particularly sensitive to temperature (Portner *et al.*, 2000). In addition to pronounced increases in surface waters near the equator, future projections of ocean warming are characterized by heat uptake in the deep Southern Ocean at the end of the century (IPCC, 2013). This combined exposure and organism sensitivity to exposure at their upper thermal limit likely explains the areas of local extinction projected there, although the total numbers of local extinctions are shown to be relatively small. For other polar species, warming temperatures will reduce the likelihood that organisms will be exposed to their lower thermal limits, therefore allowing increases in both numbers and extent of populations previously at the edges of the lower thermal range. In addition, melting sea ice will open up habitats in the high latitude reaches of their ranges, leading to the projected increases in species richness predicted here, as indicated by the higher invasion intensity. The greater prevalence of invasion in the Arctic than the Antarctic is likely due to the greater rate of warming in this area (0.98°C compared with 0.72°C increase in SST and 0.60°C compared with 0.24°C in SBT, respectively). Furthermore, the higher invasion intensity in the Arctic Ocean may reflect the closer distance of the Arctic to other land masses. For example, if a species is restricted to coastal regions for feeding or spawning, dispersal towards the Antarctic may be restricted, despite seemingly favourable habitat. As an environmental layer indicating the presence of critical habitat, such as shelf regions required for spawning, was not available, depth was here used as a proxy.

As estimates of invasion and local extinction intensity indicate the percentage loss or gain in species per 0.5° latitude × 0.5° longitude grid cell, the initial species richness in an area contributes to the perceived relative levels of change and biodiversity impact. As the species set assessed in this study was weighted to exploited species, and data were more scarce in certain regions (such as the Southern Ocean) than others (such as the Northeast Atlantic), local invasions at the poles may appear relatively common simply because fewer species are being projected there. For this reason, total numbers of species invading and going extinct were also assessed. However, a small number of species in regions such as the Southern Ocean also attributes high levels of uncertainty to projecting general patterns of biodiversity change. For example, the projected low levels of extinction might be misleading if resulting from changes in a couple of key species. It would thus be beneficial to extend this work as data become available, exploring how warming Polar Waters might impact the distributions and persistence of cold-adapted species.

Exploring how areas predicted to be hotspots of change in species richness coincide with agreement between models allows an assessment of how robust particular scenarios of change are to aspects of the modelling procedure. This may be interpreted as the risk posed by climate change to different geographic areas (Jones *et al.*, 2013b); those areas showing both relatively high levels of extinction, for example, and agreement in a level of extinction or higher, may be described as being areas at high risk of climate change impacts. The level at which agreement of change is cut off (here 20%) may then be altered to further explore the geographic localization of particular levels of local extinction, or invasion, intensity. However, the analyses carried out here aimed to make projections of future patterns of species richness, local extinction, and invasion intensity. They were thus limited in their scope to estimate factors such as when local extinction might lead a particular species' range to decrease below a minimum viable size, or when a change in community structure

in a particular area might lead to loss of species or traits vital to ecosystem function.

There are also limitations and uncertainties associated with the approaches applied here that should be considered when extending analyses and interpreting or applying model projections, for example, to inform conservation priorities or management plans. Variability and uncertainty will, for example, be introduced into the modelling procedure through variations in the data used to train and project a model as well as the SDM itself (Jones *et al.*, 2013a). Although the multi-model approach attempts to partly assess structural uncertainty of the models and incorporate this variability, input data may also affect model accuracy and interpretation through the inherent assumptions of species distribution modelling. For example, SDMs assume that species are in pseudo-equilibrium with their environment, and that occurrence data used represent the entire ecological niche of a species (Svenning and Skov, 2004; Guisan and Thuiller, 2005). In reality, if these data only reflect a subset of a species' true niche space due to the impact of, for example, adaptation, species interactions, and dispersal on a species' distribution, both the estimated climatic envelope, and the way that it might be projected to estimate a potential current or future distribution, may be inaccurate (Soberón, 2007; Jiménez-Valverde *et al.*, 2008; Warren, 2012). However, it has been suggested that marine ectotherms conform more closely to their thermal tolerance limits than terrestrial species and are more likely to fulfil their potential latitudinal ranges (Sunday *et al.*, 2012). To overcome, as far as possible, the problem of temporally changing realized climatic space and its implication for estimating a species' potential current and future distributions, all available valid occurrence data on each species were included to obtain as near as possible an estimate of a species' absolute tolerance limits and climatic envelope. Even if a species' exact climatic niche is known, however, further inaccuracies may be introduced into estimates of species' future potential distributions if biotic interactions, which are not taken into account by the models, prevent a species occupying otherwise suitable habitat (Araújo and Luoto, 2007). As a recent study using the DBEM found projections of species distribution shifts changed little following inclusion of competitive interactions (Fernandes *et al.*, 2013), it may be the case that the parameterizations of the model, such as the inclusion of natural mortality, may already account for some of the effects of trophic interactions. However, further work would benefit from exploring predator–prey interactions, and how they might change or limit responses to climate change and projected range shifts. For commercially targeted marine species, realized responses to climate change may further be influenced by the impacts of fisheries (Planque *et al.*, 2010). The interaction of fishing pressure, and its impacts on the demographic structure of a population, and the integrity of breeding grounds and habitat, with stock reactions to environmental change may thus have implications for the accuracy of future distribution predictions. For example, if north and south regions of the North Sea are home to different abundances of particular commercial species due to higher rates of fishing mortality in the south, rather than a causal difference in habitat suitability, predictions based on the assessment of habitat suitability may be incorrect, with consequences for any management plans and conservation actions they might inform (Dulvy *et al.*, 2008). In addition, species in the North Sea have been observed to be adapting to increasing temperatures through a shift in depth (Dulvy *et al.*, 2008). Depth and SBT were here included as predictor variables, thereby accounting for the influence of depth in determining habitat suitability.

However, allowing species to adapt by shifting their distribution to deeper, cooler waters and thereby potentially reducing predicted latitudinal shifts in distribution would require data on projected temperature changes throughout the water column, which is not currently available over a global extent. Developments have been made, however, in the three-dimensional modelling of marine species' distributions (Bentlage *et al.*, 2013). Thus, although the multi-model ensemble approach provides a way for broadly assessing the impact of climate change on species for which knowledge and data may be scarce, the challenge in their development would seem to be the incorporation of the influence of changing climate and the changing distributions and abundances of species with which they interact. However, their improvement and continued validation and assessment with observed data and knowledge of species biology and ecology that might impact the realization of predicted range shifts remain important.

There are also uncertainties in the climate data input into the SDM procedure. Although the world's continental shelf regions and coastal waters account for most known marine biodiversity (Mora *et al.*, 2008), modelling continental shelf seas presents particular difficulties in climate modelling as the present generation of climate models does not have sufficient resolution to resolve the shelf topography and many of the processes that influence primary production in the shelf sea ecosystem (such as run-off, seasonal stratification, tides, and nutrient recycling; Ådlandsvik, 2008; Holt *et al.*, 2009). For example, Holt *et al.* (2010) used a regional model to predict that the climate change effects on the Northwest continental shelf would be very different from those in the open ocean over the next 100 years (Holt *et al.*, 2010). However, these predictions still contained unexplored uncertainty and differed from those made using a regional climate model by Ådlandsvik (2008). Exploring the sensitivity of projected changes in biodiversity in coastal regions to downscaled data and regional climate models may therefore be useful, although an ensemble of regional models may be needed to enable a reliable assessment of the effects of future climate change in shelf seas, and the uncertainties involved.

Although model outputs here reflect species-specific environmental tolerance limits, and results are consistent with regional differences in vulnerability due to alternative physiologies, differences between species in traits that might impact their overall response to climate change, or adaptability, have not themselves been accounted for. Species may, however, vary considerably in the extent to which changes in their biophysical niche space impact their local, or overall, extinction risk due to particular life history characteristics, or traits (Foden *et al.*, 2013; Garcia *et al.*, 2014). For example, if a species exhibits narrower thermal tolerances or has highly specific habitat requirements at particular life cycle stages that have not been accounted for in these modelling approaches, the impact of climate change on a particular species may be underestimated (Petitgas *et al.*, 2013). There may also be interactions between the impact of fisheries on species' traits and abundances and their response to climate change. For example, both fisheries and warming waters are thought to have caused the decline in sandeel in UK waters (Pinnegar *et al.*, 2012). Developments are also being made in linking impacts from these two sources in species distribution modelling. However, given the lack of knowledge frequent for marine species, this study provides a first step in indicating key areas where further vulnerability assessment on a set of species, for which there are sufficient data, would be beneficial. For example, these might be in regions predicted to experience high levels of extinction intensity, or those that show medium risk

from climate change, but which have high economic or social dependence on fisheries. Future studies will also account for the uncertainties associated with the projections of ocean conditions by applying different Earth System Model outputs to the SDMs.

Conclusions

This study is the first to apply a multi-model SDM approach to assess the potential impact of climate change on marine biodiversity at a global scale. Using generalized approaches to elucidate the averaged signal of response in latitudinal patterns of species richness gave average results consistent with previous observations and empirical projections of a trend for poleward shifts in species' distributions and altered patterns of biodiversity under climate change. Analyses presented here allow the identification of hotspots of biodiversity impacts, with hotspots of local extinction intensity occurring mostly notably in the tropical Pacific ocean, and hotspots of invasion occurring in Arctic regions such as the Barents Sea, East Siberian Sea, and Greenland Sea. In addition, we indicate where identified hotspots of change, and the extent of change, are robust within the multi-model approach, coinciding with high levels of agreement. This study therefore expands on previous global assessments of climate change impact by providing an initial framework to incorporate particular aspects of projection uncertainty and depict the risks to biodiversity of climate change in the oceans.

Supplementary data

Supplementary material is available at the *ICESJMS* online version of the manuscript.

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