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Projecting global marine biodiversity impacts under climate change scenarios

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Abstract

Climate change can impact the pattern of marine biodiversity through changes in species' distributions. However, global studies on climate change impacts on ocean biodiversity have not been performed so far. Our paper aims to investigate the global patterns of such impacts by projecting the distributional ranges of a sample of 1066 exploited marine fish and invertebrates for 2050 using a newly developed dynamic bioclimate envelope model. Our projections show that climate change may lead to numerous local extinction in the sub-polar regions, the tropics and semi-enclosed seas. Simultaneously, species invasion is projected to be most intense in the Arctic and the Southern Ocean. Together, they result in dramatic species turnovers of over 60% of the present biodiversity, implying ecological disturbances that potentially disrupt ecosystem services. Our projections can be viewed as a set of hypothesis for future analytical and empirical studies.

Keywords Bioclimate envelope, climate change impact, global marine biodiversity, niche-based model, species turnover

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Introduction

Climate change is an important factor in determining the past and future distributions of biodiversity (Peterson *et al.* 2002; Parmesan and Yohe 2003; Root *et al.* 2003; Thomas *et al.* 2004a,b; Rosenzweig *et al.* 2008). In the ocean, the pattern of marine species richness, notably for fish and invertebrates, is strongly related to environmental factors (Macpherson 2002). Also, observations and theory suggest that marine species respond to ocean warming by shifting their latitudinal range (e.g. Perry *et al.* 2005; Parmesan 2006; Hiddink and Hofstede 2008; Mueter & Litzow 2008) and depth range (Dulvy *et al.* 2008). Such species responses may lead to local extinction and invasions, resulting in changes in the pattern of marine species richness. For example, in the North Sea, species richness of fish fauna increased from 1985 to 2006 which was related to large-scale biogeographical patterns and climate change (Hiddink and Hofstede 2008). Overall, changes in pattern of species richness may disrupt marine biodiversity and ecosystems, and impact commercial fisheries (Roessig *et al.* 2004; Worm *et al.* 2006; Cheung *et al.* 2008b). Here, local extinction refers to a species ceasing to exist in an area although it still exists elsewhere (e.g., Peterson *et al.* 2002; Dulvy *et al.* 2003), while invasion refers to the expansion of a species into an area not previously occupied by it (Rahel and Olden 2008).

Previous attempts to investigate climate change effects on marine species dealt with limited taxa and on specific regions (Table 1). A review of recent literature on quantitative analysis of the effect of anthropogenic climate change on community assemblages or distributional range of marine fish and invertebrates shows that the majority of the reviewed papers focus on a regional scale (e.g. North Sea, coast of Britain and California). Most of the regional studies took place in North Atlantic, Northeast Pacific and the Mediterranean. The few (two reviewed papers) studies on ocean basin scale (North Atlantic Ocean) and global scale focus on limited taxa (Calanoid copepod and Skipjack tuna, respectively) (Table 1). The lack of large-scale study that encompasses a wide array of marine species is in contrast to the situation prevailing in the terrestrial realm (e.g. Peterson *et al.* 2002; Thomas *et al.* 2004a; Deutsch *et al.* 2008). Particularly, climate change impacts on marine biodiversity are likely to intensify in the future, with the intensity of impacts differing geographically according to changes in ocean conditions and sensitivity of the species (Roessig *et al.* 2004; Harley *et al.* 2006; Munday *et al.* 2008). Thus, a global perspective on the impact of climate change on a wide range of marine species is urgently needed to obtain a more complete picture of the climate change problem; this is the primary objective of this paper.

Bioclimate envelope models, alternatively called environmental niche models, have been widely used to predict distributions of plants and animals (e.g. Peterson *et al.* 2002; Thomas *et al.* 2004a; Thuiller *et al.* 2005; Arájo *et al.* 2006). A bioclimate envelope can be defined as a set of physical and biological conditions that are suitable to a given species. Thus, shifts in species distributions can be predicted by evaluating changes in bioclimate envelopes under climate change scenarios. Despite its wide application in projecting climate change effects on species distributions, predictions from bioclimate envelope models are often sensitive to model assumptions and uncertainties (Pearson and Dawson 2003; Thuiller 2004; Lawler *et al.* 2006; Pearson *et al.* 2006). These include the lack of considerations of biotic interactions, evolutionary change and species dispersal, and the assumption that the observed distributions are in equilibrium with their environment (e.g. Pearson and Dawson 2003; Guisan and Thuiller 2005). On the other hand, bioclimate envelope modelling is among the few available quantitative tools to predict potential ecological changes resulting from shifts in species distributions (Botkin *et al.* 2007). Validation of selected bioclimate envelope models suggests that predictions can agree reasonably well with observations (e.g. Araújo *et al.* 2005). Moreover, the approach can be improved by incorporating critical processes such as dispersal and population dynamics (Guisan and Thuiller 2005; Cheung *et al.* 2008a). Thus, projections from such models are valuable in generating hypotheses for future studies and providing guidance for policy making (Hannah *et al.* 2002; Peterson *et al.* 2002; Araújo *et al.* 2005). The approach can provide a first approximation of the general pattern of climate change impact on biodiversity (Thomas *et al.* 2004a,b).

In this paper, we predict global patterns of local extinction, invasion and their combined effects on species turnover for the year 2050 relative to year 2003 by projecting future ranges of a sample of 1066 exploited marine fish and invertebrate species under climate change scenarios. Species local extinction, invasion and turnover are considered

Table 1 Review of recent literature on quantitative analysis of the effect of anthropogenic climate change on the distribution and abundance of marine fish and invertebrates.

Study region	Time period	Studied taxa	Results summary
Global	Future scenarios	Skipjack tuna (*Katsuwonus pelamis*)	Doubling atmospheric CO_2 concentration results in significant large-scale changes of skipjack habitat in the equatorial Pacific, with overall extension of favourable habitat throughout the tropical ocean[1]
North Atlantic Ocean and European shelf seas	1960–1999	Calanoid copepod assemblages	Species richness of southern and pseudo-oceanic temperate species has increased by 10° of latitude while richness of colder-temperate, subarctic and arctic species has decreased in the north[2]
North Sea	1925–2004	> 300 fish spp.	Species having southern biogeographic affinities increased in abundance since the mid-1990s[3]
	1977–2001	36 spp. of demersal fish	Centers of distribution of 15 out of 66 spp. shifted in relation to warming, with 13 spp. of them shifting northward. Range boundaries of 10 out of 12 spp. shifted with warming[4]
	1977–2003	118 taxa of fish, with six taxa of multispecies groups	Increases in species richness of fish fauna, which are shown to be related to large-scale biogeographical patterns and climate change[5]
	1977–2002	Atlantic Cod (*Gadus Morhua*)	Decrease in spatial extent of optimal habitat[6]
	Future scenarios (2000–2050)	Atlantic Cod (*Gadus Morhua*)	Ocean warming may increase the rate of decline of cod population in the North Sea[7]
The coast of Norway and the Svalbard archipelago	Between 1977, 1994 and 2002	Blue mussel (*Mytilus edulis*)	Expansion of range from the Norwegian mainland to the Svalbard archipelago, with distribution range extended northward by 1000 km to Bear Island and then Isfjorden on Svalbard island[8,9]
Intertidal shore, Britain and Ireland	1950s, 1980s and 2002-2004	33 spp. of intertidal flora and fauna	North and north-eastern range extensions of some southern species including *Osilinus lineatus* and *Gibbula umbilicalis*[10,11]
Intertidal shore, Ireland	Between 1958 and 2003	27 spp. of rocky intertidal species	A northern species and an introduced species increased in abundance while five northern, one southern and four broadly distributed species decreased in abundance. Robust conclusions about species fluctuations and anthropogenic effects cannot be drawn[12]
English Channel and Bristol Channel	1913–2002	72 taxa and 81 spp. of marine fish from English Channel and Bristol Channel, respectively	Climate change had strong effects on community composition[13]
Western English Channel	Between the 1920s and 1980s	Zooplanktons and intertidal invertebrates	Increase in abundance and extension of distributional ranges of warm water species during periods of warming and *vice versa* for cold-water species. The opposite was observed during period of cooling. Observed latitudinal shifts were up to 120 miles (193 km) in 70 years (≈ 28 km decade^{-1}). With a rise in mean temperature of 2 °C in 50 years. Future range shifts was extrapolated to be about 65–130 km decade^{-1} [14]
Intertidal shore, Portugal	Between the 1950s and 2003–2005	An intertidal gastropod *Patella rustica*	Bridging of a historical distribution gap on the northern Portuguese coast[15]

Table 1 Continued.

Study region	Time period	Studied taxa	Results summary
List Tidal Basin, Wadden Sea	1984–2006	Mesozooplankton	Extended copepod season and higher copepod abundance[16]
Marine caves, north-western Mediterranean	From the 1970s to 1998–2003	Two endemic spp. of tolerance) cave mysids: *Hemimysis speluncola* and *H. margalefi*.	Reduction in abundance and distribution of *H. speluncola* (having lower temperature tolerance during warming) and replacement by *H. margalefi* (having higher temperature tolerance)[17]
Northwest Atlantic Ocean	1967–1990	36 spp. of fish and squid	Changes in mean latitude of occurrence for 12 of 36 species can be significantly explained by variations in water temperature[18]
Newfoundland, Northwest Atlantic	1505–2004	Atlantic cod (*Gadus morhua*)	Climate affects population productivity[19]
Continental shelf, northeastern USA	1963–future scenarios	Atlantic cod (*Gadus morhua*)	Distribution of cod is strongly influenced by temperature. Warming leads to loss of thermal habitat particularly in the southern range and reduces survival during early life stages offsetting increases in growth with warmer temperature[20]
Continental shelf, Bering Sea	1982–2006	46 fish and invertebrate taxa	Community-wide northward distribution shifts. Invasion of subarctic fauna resulted in increase in biomass, species richness and average trophic level in area that was formerly covered by seasonal sea-ice. Centers of distribution of forty taxa shifted northward by an average of 34 km (SD = 56 km)[21]
Pacific Grove, California	Between 1931–1933 and 1993–1996	62 spp. of rocky intertidal macroinvertebrates	10 of 11 southern spp. increased in abundance, five of seven spp. decreased in abundance, and cosmopolitan spp. showed a weak trend toward decreases (12 spp. increased, 16 spp. decreased)[22]
Monterey Bay, California	Between the 1930s and the 1990s	>130 spp.	Increase in the abundance of southern species of gastropods, anthozoans and barnacles and decrease in abundance of northern anthozoan and limpet species with no apparent trend for species with cosmopolitan distribution[23]
Rocky intertidal shore, California	The late 1970s/early 1980s–2000s	An intertidal gastropod *Kelletia kelletii*	Northward shift of the northern range edge[24]
	Between 1921–1931 and 1983–1993	45 spp. of intertidal invertebrates	Eight of nine southern species increased in abundance, five of eight northern species decreased in abundance and no trend for cosmopolitan species[25]
Intertidal shore, Chile	Between 1962 and 1998–2000	10 intertidal spp.	Eight of 10 species did not show expansion of southern distributional endpoint; on average, species showed small and non-significant contractions, with low rates of decadal change (0.18° latitude decade^{-1})[26]

[1]Loukos *et al.* (2003). [2]Beaugrand *et al.* (2002); [3]Beare *et al.* (2004); [4]Perry *et al.* (2005); [5]Hiddink and Hofstede (2008); [6]Blanchard *et al.* (2005); [7]Clark *et al.* (2003); [8]Weslawski *et al.* (1997); [9]Berge *et al.* (2005); [10]Mieszkowska *et al.* (2007); [11]Mieszkowska *et al.* (2006); [12]Simkanin *et al.* (2005); [13]Genner *et al.* (2004); [14]Southward *et al.* (1995); [15]Lima *et al.* (2006); [16]Martens & Beusekom (2008); [17]Chevaldonné & Lejeusnu (2003); [18]Murawski (1993); [19]Rose (2004); [20]Fogarty *et al.* (2008); [21]Mueter & Litzow (2008); [22]Sagarin *et al.* (1999); [23]Barry *et al.* (1995); [24]Zacherl *et al.* (2003); [25]Barry *et al.* (1995); [26]Rivadeneira & Fernández (2005).

Table 2 List of environmental variables and the sources of data that the dynamic bioclimate envelope model accounts for in projecting the future distributions of marine fish and invertebrate.

Environmental variables	Sources
Sea surface and bottom temperature	NOAA's GFDL CM 2.1 (Delworth *et al.* 2006)
Salinity	NOAA's GFDL CM 2.1 (Delworth *et al.* 2006)
Sea ice cover	NOAA's GFDL CM 2.1 (Delworth *et al.* 2006)
Ocean advection	NOAA's GFDL CM 2.1 (Delworth *et al.* 2006)
Bathymetry	*Sea Around Us* Project
Coral reef	UNEP World Conservation Monitoring Centre
Estuary	(Alder 2003)
Seamounts	(Kitchingman and Lai 2004)
Coastal upwelling	Secondarily derived from SST. See Xie and Hsieh (1995) for the algorithm used.

as a good measure of biodiversity and ecosystem perturbation (Peterson *et al.* 2002; Thuiller 2004). We employ a generic dynamic bioclimate envelope model for marine fish and invertebrates that incorporates population and dispersal dynamics to project future species distributions under climate change (for details, see Cheung *et al.* 2008a). Using this model, we project the global rate of shift of marine species distributions and illustrate the potential future hotspots of climate change impacts on marine biodiversity.

Methodology

Sample of marine fish and invertebrates

Our study included a total of 1066 exploited marine fish (836 spp.) and invertebrate species (230 spp.). These species were all relatively abundant, as they included only those reported as being fished by at least one member country of the Food and Agriculture Organization of the United Nations (FAO). These species are generally better-studied than non-exploited species and their basic biological and distributional data are available. This also weighted our sample of marine biodiversity towards the species contributing most to marine metazoan biomass.

The current distributions of the 1066 species of marine fish and invertebrates, representing the average pattern of relative abundance in recent decades (i.e. 1980–2000), were produced using an algorithm developed by the Sea Around Us Project (see Close *et al.* 2006; Cheung *et al.* 2008a). This algorithm predicts probability of occurrence of a species on a 30′ lat. × 30′ long. grid based on the species' depth range, latitudinal range and broad known occurrence regions. The distributions were further refined by assigning habitat preferences to each species, such as affinity to shelf (inner, outer), estuaries and coral reefs. Such information was mainly obtained from FishBase (http://www.fishbase.org) for fish and SeaLifeBase for other taxa (http://www.sealifebase.org); both databases contain key information on the latitudinal and depth distribution of the animals in question, and on their occurrence in various parts of the world ocean. The distribution maps are available at http://www.seaaroundus.org, along with their habitat preferences and other parameters used in their construction. Fig. 1a presents an example of a map of predicted current distribution for the Small yellow croaker (*Larimichthys polyactis*, Sciaenidae).

Dynamic bioclimate envelope model

We used a modelling approach that integrates population dynamics with a bioclimate envelope model to project future distributions of the 1066 species. This approach is a modified version of the dynamic bioclimate envelope model developed by Cheung *et al.* (2008a). This model predicts a species' range (on a 30′ lat. by 30′ long. grid of the world ocean) based on the association between the modelled distributions and environmental variables. The algorithm of the model is detailed in Cheung *et al.* (2008a). Basically, the model inferred preference profiles, defined as the suitability of different environmental conditions to each species, from its predicted current distribution. Preference profiles were calculated by overlaying environmental data (from 1980 to 2000) with maps of relative abundance of the species on a 30′ × 30′ grid (Fig. 1). We assume that the predicted current distributions realistically depict the environmental condition preferred by the species. Thus, the degree of preference and association to the environmental condition was represented by the relative abundance of the species over the habitat with such condition,

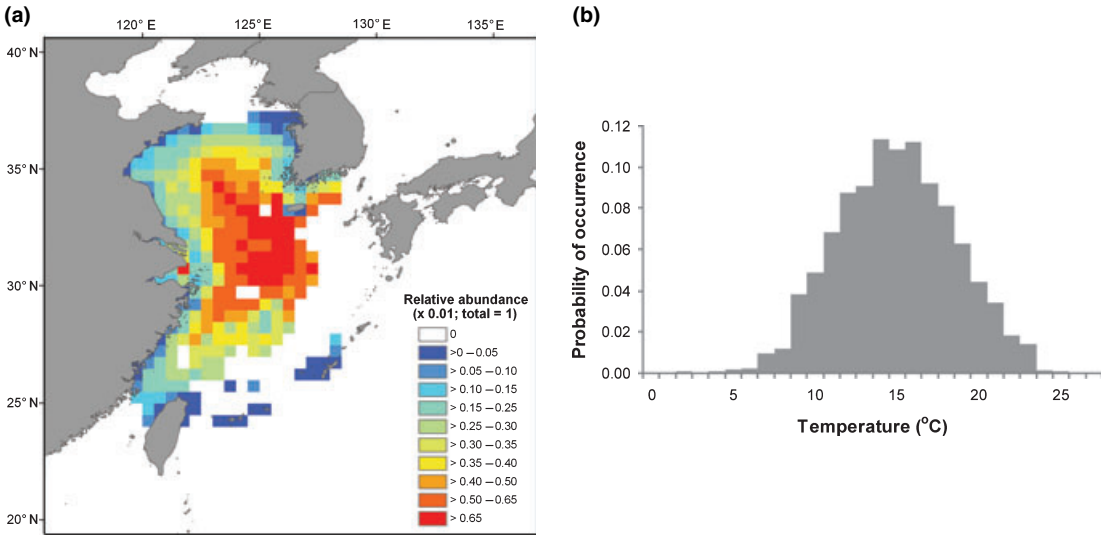

Figure 1 (a) Predicted current distribution of the small yellow croaker (*Larimichthys polyactis*) on a 30′ lat. × 30′ long. grid (area of a cell along the equator ≈ 3,090 km^2) and (b) the temperature preference profile inferred from overlaying the distribution map with spatial sea water temperature data.

including sea surface and bottom temperature, coastal upwelling, salinity, distance from sea-ice and habitat types (coral reef, estuaries and seamounts) (Table 2). For example, temperature preference profiles were calculated from annual sea bottom temperature for demersal species and from seasonal average (summer and winter) sea surface temperatures (SST) for pelagic species. An example of the temperature preference profile of Small yellow croaker calculated from its distribution map and sea bottom temperature data is shown in Fig. 1.

In modelling future ranges, our model simulated changes in relative abundance using a logistic population growth model (for details, see Cheung *et al.* 2008a). Essentially, the model assumes that spatial and temporal dynamics of a population are determined by their intrinsic population growth, larval dispersal and adult migration:

$$\frac{dA_i}{dt} = \sum_{j=1}^{N} G_i + L_{ji} + I_{ji} \qquad (1)$$

where A_i is the relative abundance of a 30′ × 30′ cell i, G is the intrinsic population growth, and L_{ji} and I_{ji} are settled larvae and net migrated adults from surrounding cells j, respectively. Intrinsic population growth was determined by the population growth rate and carrying capacity of the species:

$$G_i = r \cdot A_i \cdot \left(1 - \frac{A_i}{KC_i}\right) \qquad (2)$$

where r is the intrinsic rate of population increase, A_i and KC_i are the relative abundance and population carrying capacity at cell i, respectively. We assume that carrying capacity varies positively with habitat suitability of each 30′ × 30′ cell to the species in question. Habitat suitability is dependent on the species' preference profiles to the environmental conditions of each cell. Thus, as environmental conditions in a cell (e.g. temperature, ice-coverage) become more suitable for an animal, carrying capacity is assumed to increase. The final value in carrying capacity of a cell was calculated from the product of the habitat suitability of all the environmental conditions considered in the model.

The model explicitly represents larval dispersal and movement of adult animals according to ocean conditions. In the model, migration consists of larval dispersal and migration of adults. Specifically, dispersal pattern of larvae was assumed to follow ocean current which was explicitly modelled by an advection–diffusion-reaction model (Gaylord and Gaines 2000). The distance and direction of larval dispersal are a function of the predicted pelagic larval duration (based on an empirical equation, O'Connor *et al.* 2007). Moreover, animals are assumed to migrate along the calculated gradient of habitat suitability. Thus, changes in habitat

suitability in each cell, determined by ocean conditions, lead to changes in the species' carrying capacity, population growth, net migration, and thus, relative abundance in each cell. However, as with most bioclimate envelope models, this model does not explicitly account for changes in predation pressure and food availability (Pearson and Dawson 2003).

Climate change scenarios

We included three climate scenarios representing high-, medium- and low- range greenhouse gas emissions with climate projections generated by the Geophysical Fluid Dynamics Laboratory of the U.S. National Oceanic and Atmospheric Administration (GFDL's CM 2.1) (Delworth *et al.* 2006). The three climate scenarios included: the 720 ppm stabilization experiment (Special Report on Emissions Scenarios, or SRES, A1B), the 550 ppm stabilization experiment (SRES B1) and the committed climate change experiment (commit), representing the high-, mid- and low- range climate change (Delworth *et al.* 2006). The A1B scenario describes a world of very rapid economic growth, low population growth, rapid introduction of new and more efficient technologies, and moderate use of resources with a balanced use of technologies. The B1 scenario describes a world with low population growth, rapid change to an information and service economy. As cleaner technology is used and less reliance is placed on natural resources in this scenario, there will be a drastic reduction in carbon dioxide from the present. In the 'commit' scenario, the climate forcing agents were stabilized at the end of 20th century levels for the 100 year duration of this experiment. Scenarios of higher future greenhouse gas emissions from a more fossil fuel intensive society are included in the IPCC assessment (e.g. SRES A1F; IPCC 2007), but are not applied here.

Physical variables obtained from the GFDL's CM 2.1 include sea temperature, sea ice coverage, salinity and advection under different climate change scenarios. The original resolution of the outputs from the coupled model is 1° at latitudes higher than 30° north and south, with the meridional resolution becoming progressively finer towards the equator. Also, the model uses a tripolar (1°) grid north of 65° latitude, with poles located in Canada and Siberia. Making the resolution of the physical variable complementary to our species distribution data, we regridded the spatial cells to a regular grid. Then, we interpolated the physical variables with resolution of 30′ in latitude and longitude using Inverse Distance Weighted (IDW) method. Based on these data, we calculated the minimum distance from sea ice and strength of coastal upwelling; both are factors that determine future species distributions.

Climate change impact on biodiversity

Since invasion to and extinction from an area (collectively called species turnover) can affect biodiversity, community structure and ecosystem functions (Sala *et al.* 2000; Stachowicz *et al.* 2002; Genner *et al.* 2004; Hooper *et al.* 2005), we calculated the average frequency of invasion and local extinction events in each 30′ × 30′ cell from 2040 to 2060 relative to the average of 2001 to 2005 to identify hotspots of climate change induced impacts for 2050. Firstly, we calculated the current species richness in each 30′ × 30′ cell by overlaying distribution maps of all the 1066 sampled species (Fig. 2a). The resulted latitudinal pattern of species richness (Fig. 2b) mimics the empirically observed pattern for marine fish and invertebrates (Macpherson 2002). Then, using the dynamic bioclimate envelope model, we projected the change in

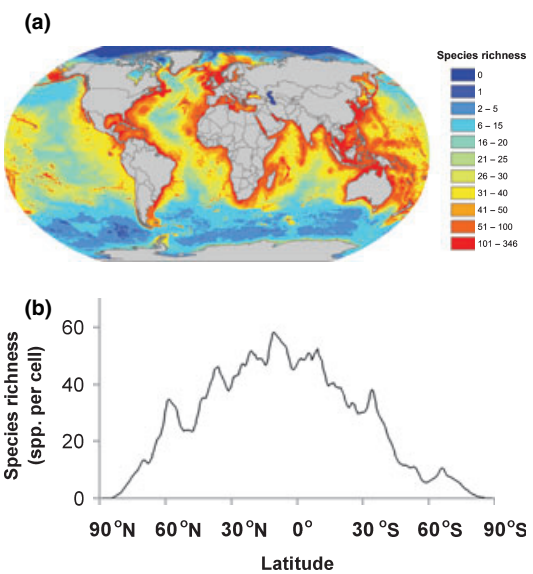

Figure 2 Distribution of species richness (1066 species of fish and invertebrates): (a) on a 30′ × 30′ grid and (b) averaged across latitude (smoothed by a running mean over 2°lat.).

distributions of the 1066 species of marine fish and invertebrates under the high-, medium- and low- climate change scenarios. We calculated the number of newly occurring species (invasion) and the number of locally extinct species in each cell. As the species distribution maps available for analysis were not evenly distributed, but concentrated on continental shelves and around islands in non-polar regions (Fig. 2), we standardized the number of invading or locally extinct species in each cell by the initial species richness (number of species) to calculate invasion intensity (I) and local extinction intensity (E):

$$I_{i,y} = \frac{n^{\mathrm{I}}_{i,y}}{n_i} \tag{3}$$

$$E_{i,y} = \frac{n^{\mathrm{E}}_{i,y}}{n_i} \tag{4}$$

where $n^{\mathrm{I}}_{i,y}$ and $n^{\mathrm{E}}_{i,y}$ represent the number of invading and locally extinct species, respectively, in cell i and year y; n is the initial species richness (mean of 2001 to 2005) measured by the number of species with positive relative abundance in each cell. Thus, turnover, invasion and local extinction intensities were expressed as a proportion to the initial species richness in each spatial cell. To minimize the effect of inter-annual variability of the climate projection, projections for 2050 were represented by the average from 2040 to 2060. In addition, we calculated the zonal (latitudinal) average of species invasion and local extinction across all climate scenarios to reveal the latitudinal patterns of climate change impact on marine biodiversity. Zonal results were also presented by ocean basins.

Given that shifts in distribution ranges are a signature of climate change effects (Parmesan and Yohe 2003; Root *et al.* 2003), we predicted the average magnitude of range-shifting of the 1066 species by 2050 (mean of 2040–2060) relative to the mean of 2001–2005. Based on the results from the dynamic bioclimate envelope model, we calculated the median poleward shift in distribution centroids and higher latitude boundaries (e.g. northern boundary in the Northern Hemisphere) of each species. Distribution centroid (C) is calculated from:

$$C = \frac{\sum_{i=1}^{N} A_i \cdot \mathrm{Lat}_i}{\sum_{i=1}^{N} A_i} \tag{5}$$

where A_i and Lat_i is the relative abundance and mean latitude of each 30′ × 30′ cell i and N is total number of cells with $A > 0$. We compared our projected poleward shift of species' ranges with observed range-shifts reported in the published literature.

Results

Our model predicted general patterns of species invasion and local extinction across all the climate scenarios examined here (Fig. 3). High intensity of species invasion was predicted to be concentrated in high latitude regions, specifically the Arctic and the Southern Ocean (Fig. 3a). These areas correspond to the marginal sea ice and sub-polar biomes as defined by the oceanographic features categorized by Sarmiento *et al.* (2004). This bioregional classification system parallels the system proposed

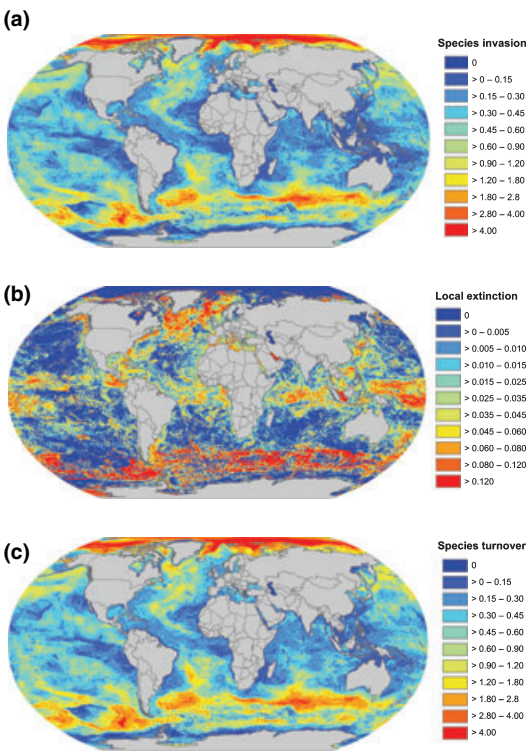

Figure 3 Predicted distribution of biodiversity impact due to warming-induced range shifts in marine metazoans. Biodiversity impact is expressed in terms of: (a) invasion intensity; (b) local extinction intensity and (c) species turnover for the 1066 species of fish and invertebrates in 2050 relative to the mean of 2001–2005 (high-range climate change scenario). Intensity is express as proportional to the initial species richness in each 30′ × 30′ cell.

by Longhurst (2006), as both schemes identify marine provinces from oceanographic features. Local extinctions were predicted to be most common in the tropics, the Southern Ocean, the north Atlantic, the northeast Pacific coast and in semi-enclosed seas such as the Mediterranean, the Red Sea and the Persian Gulf (Fig. 3b). Species turnover, which accounts for invading and locally extinct species, was predicted to be highest in the Arctic and the sub-polar region of the Southern Ocean (Fig. 3c). The pattern of species turnover was generally dominated by species invasion. On the other hand, although the relative rate of species turnover decreases towards the equator, the absolute number of species turning over is high in the tropics (Fig. 3a, b).

The global zonal averages across climate scenarios showed distinct peaks of invasion and local extinction intensity in various latitudinal zones (Fig. 4). Globally, the average projected mean invasion intensity for 2040–2060 relative to 2001 - 2005 and under the three climate scenarios was 55% of the initial species richness. Mean invasion intensity in high latitude regions such as the Arctic (> 60°N) and around the Southern Ocean (40°–60°S) were nearly 5.5 and 2 times the global average, respectively, while at the equator, mean invasion was less than half of the global average (Fig. 4). Global average local extinction rate was 3% of the initial species richness. However, local extinction intensity was higher in the tropics (between 30°N and 30°S) and in the sub-polar biomes (Sarmiento *et al.* 2004) where the mean local extinction intensity was 4% and 7%, respectively. Separating the species into pelagic and demersal groups, the pelagic system shows considerably higher invasion intensity than the demersal system while the patterns of species invasion, local extinction and turnover are generally similar between the pelagic and benthic realms. The low initial species richness largely contributes to the high biodiversity impact in the Polar regions.

Zonal average patterns of invasion and local extinction intensity between ocean basins (Pacific, Atlantic and Indian Oceans) are generally consistent with the global pattern (Fig. 4e–j). However, in the Atlantic and Indian Oceans, local extinction intensity is high in the sub-tropical region in the Northern Hemisphere (around 30°N) – a result of the high local extinction intensity in the semi-enclosed seas including the Mediterranean Sea and Red Sea. On the contrary, local extinction intensity in similar region in the Pacific Ocean is around the global average intensity.

Climate change-induced range shift

Overall, distribution centroids and poleward range boundaries of most of our studied species were predicted to shift poleward under climate change (Fig. 5). Between 2001 - 2005 and 2040 - 2060, with the high-range projected climate change, the range limits shift poleward by a median of 291 km (25th to 75th percentiles = 61–747 km) with 83% of the species (887 spp.) showing positive poleward shift. Specifically, range limits were projected to shift poleward by a median of 600 km for pelagic species (n = 209) and 223 km for demersal species (n = 857) under the high-range scenario. Therefore, although the overall direction of shift was the same for pelagic and demersal species, the pelagic group had a significantly higher rate of range shift ($P < 0.001$, Mann–Whitney test) than the demersal group. This may be expected, given the higher dispersal ability pelagic species have in our model, and the faster rate of warming near the surface where pelagic species were usually found. Moreover, the level of range shift was significantly lower under the low-range projected climate change ($P < 0.001$, Mann–Whitney test), which results in a median shift in range of 223 km (25th to 75th percentiles = 33–596 km with 79% of species (835 spp.) showing positive pole-ward shift between 2001–2005 and 2040–2060. Similarly, for the centre of the species' range, the median shifts were 79 km (25th to 75th percentiles = 24–179 km) and 44 km (25th to 75th percentiles = 11–100 km) under the high- and low-range climate change scenarios, respectively. Overall, our projected global median rate of shifting of range limits across climate change scenarios for marine fish and invertebrates is 45–59 km per decade.

Our projected rate of range shift generally agrees with expectations from observed rates of shift of marine fish in recent decades (Fig. 5, Table 1). Under the low-range climate change scenario (i.e. greenhouse gas emission maintained at the year 2000 level), our projected rate of range-shift for demersal fishes was within the range of observed rates for demersal fishes in the North Sea (Perry *et al.* 2005) that showed poleward shifts in range over the past three decades (Fig. 5). However, under a high-range climate change scenario, the projected range-shift was two times higher than the

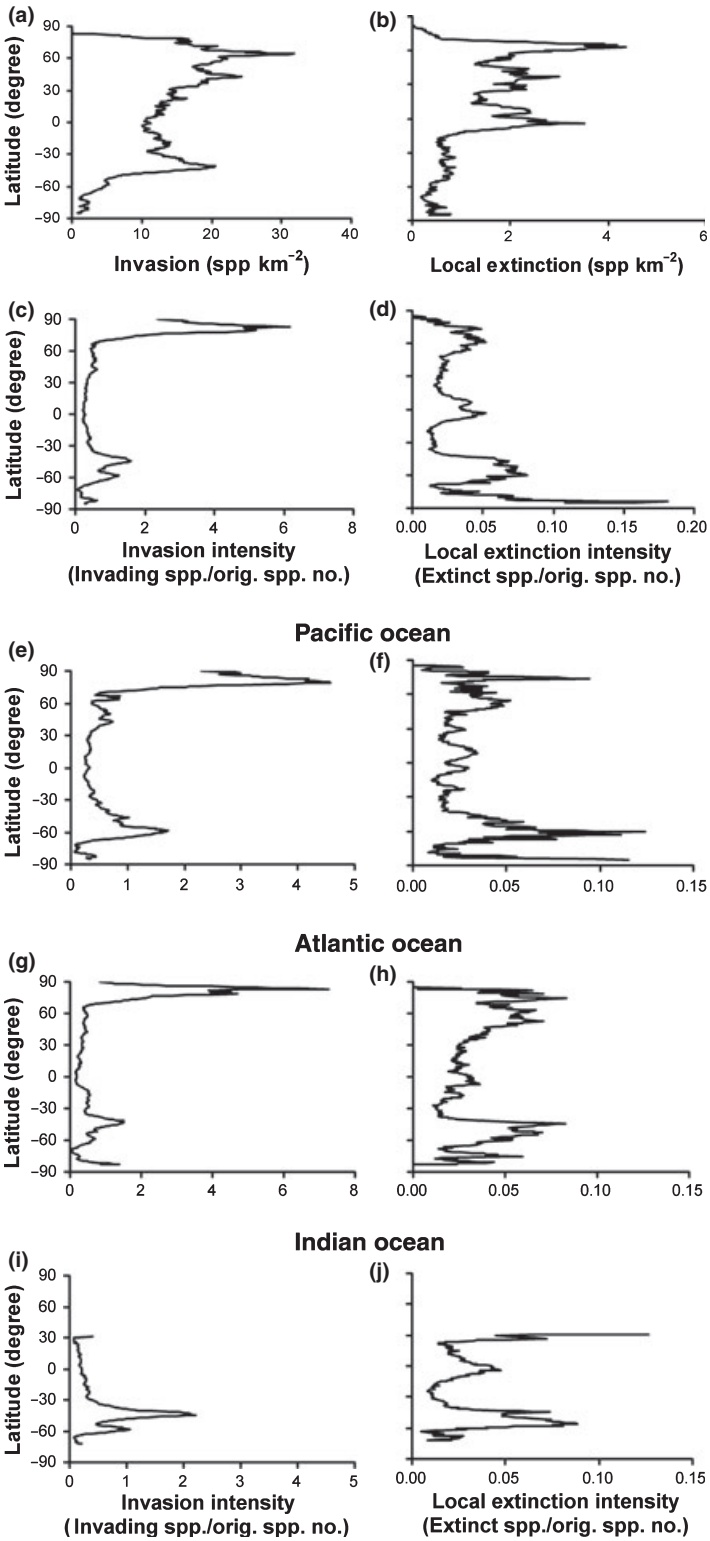

Figure 4 Projected zonal average invasion and local extinction by 30′ latitude across the high, medium and low-range climate scenarios between 2001 to 2005 and 2040 to 2060. (a, b) Global average number of invading and locally extinct species per unit area, respectively; (c, d) Global average invasion intensity measured by the number of invading and locally extinct species relative to the initial species richness from 2001 to 2005; (e,f) Average invasion and local extinction intensity in Pacific Ocean; (g,h) Average invasion and local extinction intensity in Atlantic Ocean; (i,j) Average invasion and local extinction intensity in Atlantic Ocean. Northern and southern hemispheres are distinguished by positive and negative latitudinal values, respectively.

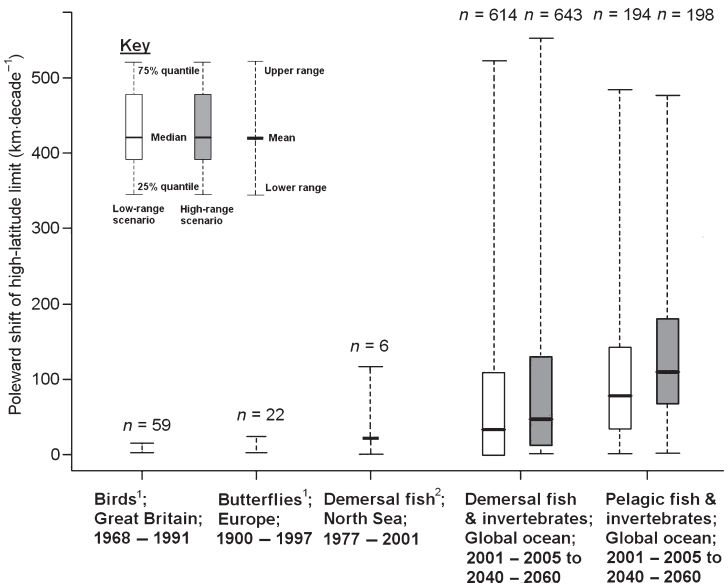

Figure 5 Comparison between the past observed rate of poleward shift of high-latitude limit of birds, butterflies and North Sea demersal fish from the present study. The area and time covered by the studies are noted in the horizontal axis. Projection from the high-range (grey box) and low-range (white box) climate scenarios are included. Data with positive shifts are displayed only. 1 – Parmesan and Yohe (2003); 2 – Perry *et al.* (2005).

previously observed rate. Moreover, similar to previous observed rate of range shift of mobile marine ectotherms, our overall projected range shift rate was an order of magnitude higher than terrestrial animals such as birds and butterflies (Fig. 5), which have moved on average 6.1 km decade^{-1} (Parmesan and Yohe 2003).

Discussion

In this paper, we show that biodiversity in the high latitude regions is likely to be highly sensitive to climate change. This agrees well with theory and observations. Latitudinal pattern of species richness of marine fish and invertebrates shows a plateau of around 40°N–30°S and declines towards the Poles (Fig. 2b, Macpherson 2002). Generally, distributions of marine ectotherms tend to extend poleward as global ocean warms up, leading to high invasion intensity and overall increases in species richness in high latitude (> 40°N and > 30°S) regions. This is also in agreement with the climate change-related increase in species richness of fish fauna in the North Sea observed in recent decades (Hiddink and Hofstede 2008).

The high sensitivity of polar species to temperature change renders the polar regions particularly susceptible to climate change biodiversity impact. Polar species generally have temperature limits that are 2–4 times narrower than lower latitude species (Somero and DeVries 1967; Peck *et al.* 2004). Therefore, in our model, increasing temperature led to the retreat of low-latitude range boundaries of polar species. This resulted in bands of high local extinction intensity in the sub-polar regions of the north Atlantic and the Southern Ocean. Simultaneously, the poleward expansion (invasion) of species' high-latitude range, compounded with the lower species richness in higher latitude, resulted in high invasion intensity in the polar region. These predictions, which agree with the eco-physiology of animals (Pörtner *et al.* 2007; Tewksbury *et al.* 2008), suggest that marine communities at the extreme ends of the environmental temperature spectrum are especially at risk from climate change. Particularly, the expansion of poleward range of species in the polar region is limited by the availability of suitable habitats. Thus, retractions of the equator-ward range lead to range contraction, which further increases the impact on individual population and biodiversity.

Biodiversity in tropical regions is likely to be impacted by higher rate of local extinction. Tropical marine poikilotherms tend to have a thermal tolerance (defined by the upper and lower lethal temperature limits of a species) close to the maximum temperature of their habitat (Pörtner and Knust 2007; Tewksbury *et al.* 2008), rendering them highly sensitive to increase in sea water temperature. Thus, generally, these animals were projected to move to colder habitats in higher latitude when tropical water temperature increases, leading to local extinction in the tropical regions.

Our analysis did not consider the potential implications of climate change impact on habitat-forming organisms such as coral reef. For example, warming is predicted to increase the frequency and scale of coral bleaching and mortality (e.g. Donner *et al.* 2005) which may affect coral reef species (Munday *et al.* 2008). Thus, our projected rate of local extinction in the tropics is considered conservative.

The interactions between geography and species' dispersal patterns strongly affected our predicted climate impact on marine biodiversity. In semi-enclosed seas, the dispersal of many species was limited by land boundaries. In addition, sea bottom temperature and SST of semi-enclosed seas were projected to increase at a faster rate than temperatures in the adjacent open seas, causing more local extinctions and range-shifting in these semi-enclosed water bodies. For example, local extinction intensity is high along the southern coast of the Mediterranean while many species invade the Ligurian and Adriatic Seas in the north; the latter pattern agrees with empirical evidence (Bianchi and Morri 2000). Moreover, limited by the availability of suitable habitats for coastal and continental shelf species, invasion was predicted to concentrate around the poleward tips of continental margin, such as coastal South Africa and Tasmania in southeastern Australia. Furthermore, since modelled sea ice around Antarctica did not show as strong a declining trend as the Arctic (IPCC 2007), invasions of non-polar species into the Antarctic was limited by the availability of ice-free habitats.

Overall, we did not find a rate of global extinction of marine species that is comparable to the high rate of extinction (15–37%) predicted for terrestrial organisms (Thomas *et al.* 2004a,b). A possible reason is that marine species may have higher dispersal ability than terrestrial organisms as suggested from our predicted rate of range-shift and empirical comparison of dispersal ability between marine and terrestrial organisms (Kinlan and Gaines 2003). Thus, marine fish and invertebrates are more capable of finding suitable habitats as climate changes. On the other hand, climate change may reinforce the impacts from other human disturbance (e.g. fishing) on marine organisms (Rose 2004; Brander 2008), increasing their vulnerability to extinction (Walther *et al.* 2002). In the future, our modelling approach may be extended to incorporate other human disturbance to address this question.

Key uncertainties

To project the distributional shift of over a thousand species of fish and invertebrate across the world ocean, we made a number of key assumptions and approximations. Firstly, the current distribution maps may be uncertain, affecting both the inferred species' habitat preferences and distribution shifts. Secondly, accurate estimates of population and dispersal parameters were not available; thus we estimated their values using indirect methods (see Cheung *et al.* 2008a). Thirdly, distribution shifts may be influenced by synergistic effects between species or anthropogenic factors that were not captured in our model (e.g. fishing) (Davis *et al.* 1998; Harley *et al.* 2006; Hsieh *et al.* 2008). Moreover, the effects of changes in ocean chemistry (e.g. ocean acidification) was not considered, although it was predicted to have negative impacts on fishes, invertebrates and habitats such as coral reefs (Orr *et al.* 2005; Harley *et al.* 2006; Hoegh-Guldberg *et al.* 2007). Species' genotypic or phenotypic adaptations to the changing temperature were not considered (Pearson and Dawson 2003). In addition, because we only considered climate scenarios generated from one coupled atmosphere and ocean model (NOAA's GFDL), variability between projections from different models may affect our results (Araújo and New 2007).

Despite these uncertainties, the general pattern of climate change impact on marine biodiversity projected from our study is likely valid. Sensitivity analysis of major parameters showed that the direction of our projections is robust to the uncertainty of these parameters (Cheung *et al.* 2008a). Key aggregate features of our results (e.g. annual rate of latitudinal shift) correspond to the available field estimates. Also, there is little theoretical or experimental evidence that absolute tolerances to climate change of a species will evolve sufficiently to conserve its distribution range (Etterson and Shaw 2001; Hoegh-Guldberg *et al.* 2002; Donner *et al.* 2005; Jump and Peñuelas 2005; Parmesan 2006). Also, physiological compensation to changing temperature in aquatic ectotherms is far from complete (Pörtner *et al.* 2007). Empirical evidence suggests that evolutionary processes and adaptations are not an alternative to range movements but operate synergistically by modulating the magnitude and dynamics of range-shift (Parmesan 2006). Specifically, some species may evolve to increase its

dispersal ability and adaptability to new habitats (Thomas *et al.* 2001). Thus, our projected rates of species invasion and poleward range movement may be considered conservative while the importance of thermal adaptation, which may only affect our projected rate of local extinction, is more uncertain. Moreover, while predictions at individual species level may be inaccurate, the large sample size and taxonomic and geographic coverage of our study allows us to detect signals of changes that may otherwise be distorted by the uncertainties. Furthermore, projections calculated from 5-years and 20-years averages of the simulated results are qualitatively the same, suggesting the robustness of our projections to inter-annual variability of the climate predictions. Thus, our projections can at least be used as a 'null' hypothesis of climate change impact on marine biodiversity (Peterson *et al.* 2002).

Potential implications and future directions

We have shown that climate change may alter species diversity and community structure of marine ectotherms. Combining these results with the findings from studies focusing on terrestrial biomes, we illustrated that the pattern of climate change impact on biodiversity, particularly the high potential impact in high latitude and the tropics, is likely to be consistent between land and ocean across the globe. Similar to the terrestrial biomes (Sala *et al.* 2000), marine biodiversity is simultaneously impacted by a range of human activities such as over-fishing, habitat destruction and pollution (Pauly *et al.* 2002; Dulvy *et al.* 2003; Lotze *et al.* 2006; Worm *et al.* 2006). Climate change may add to and amplify these impacts on marine biodiversity (Walther *et al.* 2002). Changes in distributions and community structure of marine species may affect fishing activities and have socio-economic impacts on vulnerable coastal communities (Allison *et al.* 2009). These highlight the urgency to minimize greenhouse gas emissions and human-induced global warming and develop marine conservation strategies that account for the potential impact of climate change. Specifically, we also need to reduce other anthropogenic impacts such as over-exploitation and habitat destruction to restore the capacity of marine organisms and ecosystems to adapt to environmental changes (Brander 2008).

We consider that the global analysis presented in this paper is a first step towards developing marine conservation policy in the face of climate change. The global analysis of climate change on marine biodiversity helps identify the potential sensitivity of different species, regions, and fisheries to climate change impacts. Such global picture is also effective in building consensus and initiating actions among nations, societies and stakeholders to address the problem. Simultaneously, the result and approach presented here can be applied to project climate change-induced biodiversity impacts at regional and local scales. Thus, the next step is to obtain physical and biological data in finer resolution a regional scale studies, particularly on areas that are of high sensitivity to climate change. Our model for global analysis can then be downscaled to improve understanding of potential climate change impacts at finer spatial and temporal scale. The results can help design management systems and develop indicators and monitoring programme. Moreover, empirical data from local and regional studies can be synthesized to compare and validate our model. This approach to designing conservation plan that incorporates the climate change factor is currently being tested in the Western Australian region (J. Meeuwig, University of Western Australia, personal communication).

In summary, this study provides the first quantitative projection of the patterns of climate change impact on marine biodiversity at the global scale. This should give policy makers, the scientific community and public a picture of the potential scale of the problem. We show that the global pattern of climate change impact on marine biodiversity is consistent to those in the terrestrial biomes. Because of the complexity and scale of the problems and processes involved, the magnitude of our projections is uncertain. The results can be used as a null hypothesis for developing future theoretical and empirical studies.

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