Shrinking of fishes exacerbates impacts of global ocean changes on marine ecosystems

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Changes in temperature, oxygen content and other ocean biogeochemical properties directly affect the ecophysiology of marine water-breathing organisms[1-3]. Previous studies suggest that the most prominent biological responses are changes in distribution[4-6], phenology[7,8] and productivity[9]. Both theory and empirical observations also support the hypothesis that warming and reduced oxygen will reduce body size of marine fishes[10-12]. However, the extent to which such changes would exacerbate the impacts of climate and ocean changes on global marine ecosystems remains unexplored. Here, we employ a model to examine the integrated biological responses of over 600 species of marine fishes due to changes in distribution, abundance and body size. The model has an explicit representation of ecophysiology, dispersal, distribution, and population dynamics[3]. We show that assemblage-averaged maximum body weight is expected to shrink by 14–24% globally from 2000 to 2050 under a high-emission scenario. About half of this shrinkage is due to change in distribution and abundance, the remainder to changes in physiology. The tropical and intermediate latitudinal areas will be heavily impacted, with an average reduction of more than 20%. Our results provide a new dimension to understanding the integrated impacts of climate change on marine ecosystems.

Global climate and ocean changes resulting from anthropogenic greenhouse-gas emissions are currently affecting and expected to continue to affect marine organisms[1-11]. These impacts are fundamentally linked to the close relationship between ocean conditions and the ecophysiology of marine organisms, notably water-breathing ectotherms[1,2,13]. However, previous studies focus largely on the implication of thermal tolerance and limitations of other environmental factors for the distribution range of these organisms[4-6]. Few studies have assessed the integrated responses of changes in ecophysiology, distribution and their effects on key characteristics of marine biota such as body size.

The size of aquatic water-breathers is strongly affected by temperature, oxygen level and other factors such as resource availability[2,14]. Specifically, the maximum body weight (W_∞) of marine fishes and invertebrates is fundamentally limited by the balance between energy demand and supply, where W_∞ is reached when energy demand = energy supply (thus net growth = 0). This can be expressed by the function that is commonly used to describe growth of fishes[15]:

$$\frac{dW}{dt} = HW^a - kW \tag{1}$$

where dW/dt is growth in body weight, H and k are the coefficients for anabolism and catabolism, respectively, and a describes the allometric scaling of energy input. A growth function is obtained by integrating equation (1):

$$W_t = W_\infty[1 - e^{-K(t-t_0)}]^{1/(1-a)} \tag{2}$$

where W_t and W_∞ are weight at age t and asymptotic weight, respectively; K is the growth parameter that represents the rate of approaching W_∞ through growth.

Oxygen is one of the key ingredients for body growth. Ample theoretical and empirical evidence suggests that the capacity for growth is limited by oxygen in aquatic water-breathing ectotherms and oxygen-limitation is one of the fundamental mechanisms determining biological responses of fish to environmental changes, from cellular to organismal levels[1,2]. Assuming that other resources for growth are constant, the anabolic term can be expressed as a function of oxygen supply. The catabolic term represents only the pre-oxidative phase of the breakdown of body materials. This phase mainly involves structural loss and hydrolization of protein without coupling with energy-providing exergonic reactions (see ref. 2 for details). The subsequent oxidative phase, which is included in the first term of equation (1), involves break-down of amino acids, is exergonic and requires oxygen. Applying equation (1) and previously estimated growth parameters, ocean conditions and published metabolic parameters of fishes, we calculated W_∞ and K of marine fishes under scenarios of future water temperature and oxygen level (see Methods and Supplementary Information). We also examine the sensitivity of the calculated values to the key parameters on the model (Supplementary Information).

We accounted for the effects of species distribution shifts in mediating the ecophysiological responses of individual marine fishes to environmental changes and their linkages to community-level changes (Fig. 1). Marine fishes are observed and projected to shift their distributions and abundance as temperature, primary productivity and other ocean conditions change[3-6,9,16]. These will mediate the effects of such changes on the metabolism and body weight of the organisms. Here, we modelled the integrated changes in ecophysiology and distribution of 610 species of exploited marine demersal fishes around the world using the Dynamic Bioclimate Envelope model (DBEM; see Supplementary Information and ref. 3). DBEM simulates changes in the relative abundance and spatial distribution of the marine population on a global grid by accounting for the organisms' ecophysiology, preferences and tolerances to environmental conditions, adult movement and

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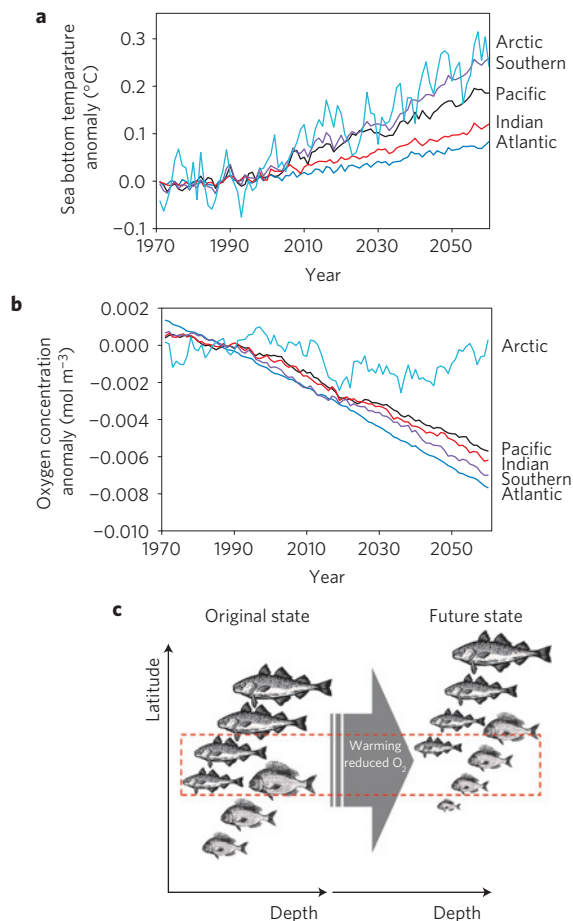
Figure 1 | Projected changes in ocean conditions and the expected biological responses of fish communities in terms of distribution and body size. a, Projected changes in sea bottom temperature. **b**, Dissolved oxygen concentration. Anomalies in temperature and oxygen are average projections from GFDL ESM2.1 and IPSL-CM4-LOOP relative to the average 1971–2000 values under the SRES a2 scenario. **c**, Schematic illustrating the expected changes in body size at individual and assemblage levels in a specific region (area enclosed by dashed red line). It is hypothesized that under warming and reduced oxygen levels, the fish at a particular location will have smaller body weight. Together with the invasion/increased abundance of smaller-bodied species and local extinction/decreased abundance of larger-bodied species, mean maximum body weight is expected to lower at the assemblage level.

larval dispersal, and population dynamics. Applying the model to simulate historical (1959–2004) changes in species distributions and comparing the results with available observations on range and abundance shifts (in the Bering Sea and around the UK) show that results from DBEM agree significantly ($P < 0.01$) with these observations (Supplementary Fig. S3). This provides empirical support that the DBEM has skill in predicting shifts in distribution range and changes in community structure under changes in oceanographic conditions.

We calculated changes in individual- and community-level average (geometric mean) maximum body weight of fishes in the global ocean driven by predicted physical and chemical conditions from two IPCC-class earth system models: NOAA's GFDL ESM 2.1 and IPSL-CM4-LOOP under the SRES A2 scenario (Fig. 1, see Supplementary Information). We then calculated the changes in average maximum body weight for individual fish in a population and for fish assemblage from year 2000 (average from 1991 to 2010) to 2050 (average from 2041 to 2060; see Methods).

Overall, the ocean is projected to become warmer and less oxygenated under the SRES A2 scenario[17]. Because demersal fishes spend most of their time near the bottom layers of the ocean, sea bottom temperature and oxygen content are more representative of the environmental conditions that demersal fishes experience. Averaged across the two earth system models, sea bottom temperature in the large marine ecosystems in the Pacific, Atlantic, Indian, Southern and Arctic oceans are projected to increase at average rates of 0.029, 0.012, 0.017, 0.038 and 0.037 °C decade^{-1} respectively between 2000 and 2050, whereas oxygen content is predicted to decrease at average rates of 0.8, 1.1, 0.9, 0.9 and 0.1 mmol m^{-3} decade^{-1} (Fig. 1 and Supplementary Fig. S5).

Although the projected rate of change in environmental temperature and oxygen content seems to be small, the resulting changes in maximum body size are unexpectedly large (Fig. 2). This study predicts that the current (1991–2010) assemblage-averaged W_∞ is smallest in the tropics and approximately five and two times larger in the northern and southern temperate regions, respectively (Fig. 2a). Overall, assemblage-averaged W_∞ is projected to decrease by 14–24% from 2001 to 2050 (20-year average) or 2.8–4.8% decade^{-1} (Fig. 2b). The projected decrease is largest in the Indian Ocean (24%), followed by the Atlantic Ocean (20%) and Pacific Ocean (14%; see Supplementary Fig. S4 for the delineation of ocean basins). Across latitudinal zones, changes in assemblage-averaged W_∞ in the tropics are predicted to be large, with an average reduction of around 20% from 2001 to 2050 (20-year average; Fig. 2b). The magnitude of change is similar in the temperate regions (∼30°–60° N/S). In areas where the model projected a decrease in assemblage-averaged W_∞, there is a generally high level of agreement (coefficient of variation <20%) in the projections generated from using the two different earth system models (Fig. 2c).

Focusing on individual W_∞ within each fish population, our study shows that most (>75%) of the studied populations are expected to experience a reduction of their W_∞ of 5–39%, with a median of 10% in all ocean basins (Fig. 3). As a result of the higher rates of warming and reduction in oxygen content, the magnitude of decrease in individual W_∞ is larger for fishes in the Pacific and Southern oceans, followed by those in the Atlantic, Indian and Arctic oceans (Fig. 3).

Overall, each of the two factors—changes in individual W_∞ and species composition—contributes around half of the projected body weight shrinkage at the assemblage-level. Out of the 20% average assemblage-level shrinkages by 2050, around 10% is explained by the individual-level shrinkages from increased oxygen demand and reduced oxygen supply, because of the projected warming and reduced oxygen content (Fig. 1). Also, our model projects that distributions of most fish populations are expected to shift poleward at a median rate of around 27.5–36.4 km decade^{-1} by 2050 relative to 2000 under the SRES A2 scenario (Supplementary Fig. S6 and Methods). As assemblage-averaged maximum body weight in the lower latitude region is smaller than that in the higher latitude regions (Fig. 2a), the model shows that a poleward shift of the fish community explains another half of the projected shrinkage of assemblage-level maximum body weight by 2050.

This study requires a number of assumptions and simplifications to represent and project long-term changes in the complex biological and earth systems, and is thus subject to several sources of uncertainty. First, there are uncertainties associated with projections of climate and ocean conditions. We attempted to address this by using outputs from two earth system models and identifying area of agreement between models. Our projected global trends are robust to outputs from the two earth system models. However, future studies should include outputs from more earth system models to investigate how different models affect the projected patterns of body size changes. Second, in
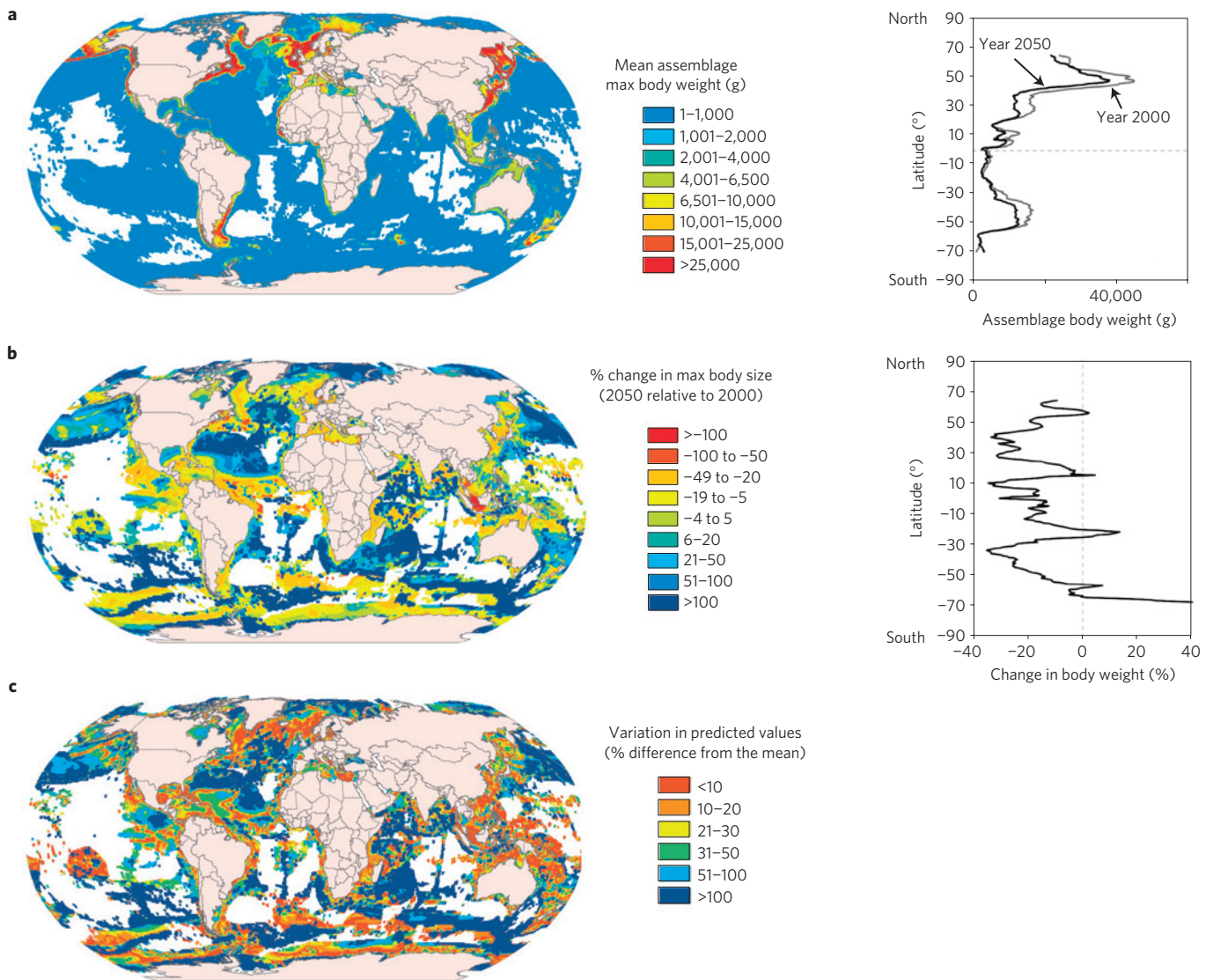
Figure 2 | Predicted mean assemblage maximum body weight (*g*) and its changes from 2000 to 2050 (20-year average) under the SRES A2 scenario. **a–c**, The mean and variation of projections from simulations driven by GFDL ESM2.1 and IPSL-CM4-LOOP are presented. White areas on the maps represent no data. **a**, Maximum body weight in 1991–2010 is predicted from the Dynamic Bioclimate Envelope Model (left, see Methods). Latitudinal average of mean assemblage maximum body weight in the global ocean in 1991–2010 and 2041–2060 (right). **b**, The projected percentage changes in mean assemblage maximum body weight between 2000 and 2050 (left) and latitudinal change in average mean assemblage maximum body weight in the global ocean between 2000 and 2050 (right). **c**, Level of variation in predictions driven by the two earth system models. Areas of agreement between models (coefficient of variation <20%) are indicated in red and orange. The data are filtered with a 5-degree running mean across the latitudinal averages.

modelling the ecophysiology, relative abundance and distribution of the fish species, the DBEM does not address factors such as an organism's capacity to adapt to environmental changes through phenotypic and evolutionary changes[3,6]. Although consideration of such factors may reduce species' sensitivity to environmental changes, there is currently little evidence that fishes would adapt to compensate completely for warming. In contrast, increasing empirical evidence supports that warming has led to reduction in body size across foodwebs[10–12]; there is also ample evidence for climate-induced shifts in distribution[4,5]. Moreover, comparing the observed relationship between intra-specific differences in maximum body size at different locations or different time-periods, we show that the predictions from our model are within the range of reported values and are more conservative in projecting shrinking of fishes under warming (Fig. 4). Examples of observed decreases in community-level body size under warming are also available from freshwater fishes in lakes[18].

Sensitivity analysis of key parameters in the growth and metabolic scaling models suggest moderate sensitivity of the results to extreme parameter values, but particularly high sensitivity to an extremely high value (0.95) of the scaling coefficient (*a* in equation (3)), which may result in a considerably larger reduction in maximum body size (Supplementary Fig. S7). On the other hand, the use of alternative parameter values does not alter the direction of change. Also, our comparisons with empirical data and sensitivity analysis suggest that the rate of shrinking of maximum body size projected here is likely to be conservative. Our analysis did not explicitly account for trophic interactions, which may affect both the growth and distribution of marine biota[19]. Specifically, the widespread changes in assemblage-level body size structure suggest that climate and ocean changes are expected to cause considerable modification of foodweb dynamics. In particular, predator and prey relationship across marine ecosystems are strongly dependent on mass[20]. For example, the prey size of Atlantic cod (*Gadus*
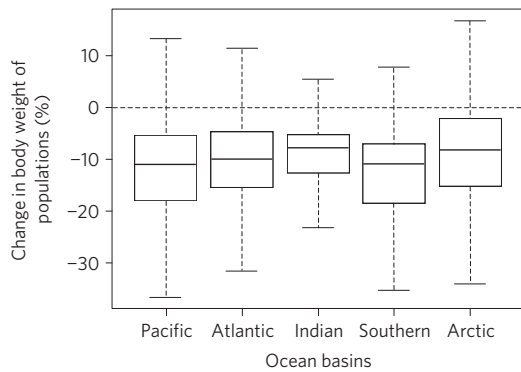
Figure 3 | Change in individual-level maximum body size of fishes in different ocean basins from 2000 (averages of 1991–2010) to 2050 (averages of 2041–2060). The thick black lines represent median values, the upper and lower boundaries of the box represents 75 and 25 percentiles and the vertical dotted lines represent upper and lower limits.

morhua) in the North Sea is significantly related to the size of this predator[21]. Moreover, maximum body weight, with temperature being a covariate, is significantly and positively related to size at maturity[22], but negatively correlated with natural mortality rate[23] and food consumption rate[24]. These are key factors determining trophic interactions[25]. Furthermore, food availability, which is assumed here to remain unlimited as fish's maximum body size decreases and distribution shifts, will change as ocean productivity or abundance of prey changes. We did not investigate the potential effects of interactions between climate change and other human stressors, such as overfishing, habitat destruction and pollution, on species' biological responses.

Despite these uncertainties, this study is the first-ever attempt to use models to examine the integrated effects of changes in species distribution, population abundance, and individual- and assemblage-level W_∞ induced by climate and ocean changes on marine ecosystems. Assumptions and simplifications of the complex biological system underlying this study are inevitable if we are to make steps toward a better understanding of the effects of global change on marine biota. Such a study, however, provides the foundation for future work, incorporating other mechanisms and factors, and ultimately improving our ability to assess the effects of climate change on biological systems.

This study indicates that the consequences of failing to curtail greenhouse-gas emissions on marine ecosystems are likely to be larger than previously expected. It has been recognized that warming will increase the metabolic rate of terrestrial ectotherms globally across taxonomic groups[26]. Here, we demonstrate that the effects of warming on metabolic rate extend to fishes in the ocean. Furthermore, the results suggest that oxygen-limited growth in aquatic water-breathing animals and species' range shift will translate, given their physiological responses to warming and changes in oxygen level, into a reduction in individual- and assemblage-level body size. We demonstrate that such a widespread decrease in W_∞ exacerbates the impacts of distribution and abundance change on marine ecosystems. Previous studies identified that the tropics will suffer most from a high rate of local extinction and reduction in maximum catch potential, whereas higher latitude regions, such as the northern temperate regions, may gain[9]. This study shows that both the tropics and temperate regions will also be impacted by reduction in body size. Other human impacts, such as overfishing and pollution, are likely to further exacerbate such impacts[27]. Consequently, these changes are expected to have large implications for trophic interactions, ecosystem functions, fisheries and global protein supply.
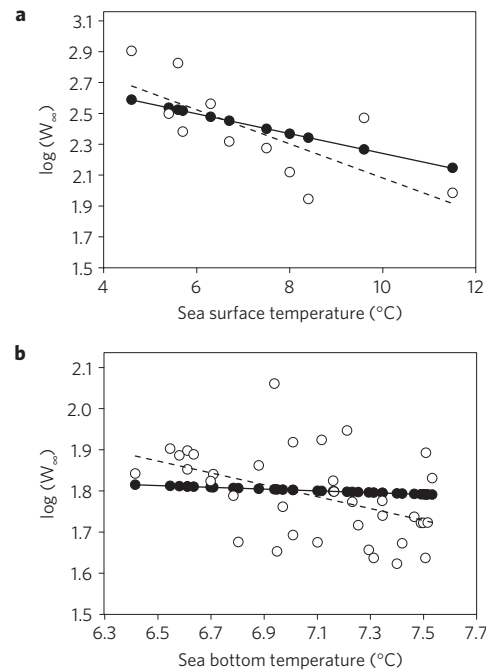

Figure 4 | Comparison of relationship between maximum body size (W_∞) and habitat temperature predicted from the growth model presented in this study (filled dots, solid line) and observations (open dots, broken line). a, Maximum body weight for Atlantic cod (*Gadus morhua*) in the North Atlantic based on growth parameters estimated from body size-at-age data from populations in different locations in ref. 28, and **b**, maximum body weight for North Sea haddock (*Melanogrammus aeglefinus*) (based on growth parameters in ref. 11.) The slopes of the best fit lines from linear regression for both datasets are significant ($p < 0.05$). In both cases, the predicted changes in maximum body weight (log) over temperature are more conservative than the observed changes.

Methods

Predicting changes in individual-level maximum body weight. For simplification, the study assumes $a = 0.7$ (equation (2)), although it varies from 0.5 to 0.95 between fish species[2]. Solving for $dW/dt = 0$ in equation (1), we obtain:

$$W_\infty = \left(\frac{H}{k}\right)^{1/(1-a)} \qquad (3)$$

H and k can be expressed as a function of temperature through the Arrhenius equation. To represent the limitation of capacity for growth by oxygen in fishes, H is also expressed as a function of dissolved oxygen in water (see Methods in Supplementary Information). Thus, H is directly proportional to O_2, whereas both H and k are proportional to $e^{-j/T}$ and $e^{-i/T}$, respectively, with the exponential term representing the Boltzmann factor. The growth parameter K (equation (2)) can be expressed as $k(1-a)$; therefore $\log(W_\infty)$ and $\log(K)$ should be negatively and linearly related, and $\log(K)$ is negatively related to the inverse of temperature ($1/T$; see Supplementary Fig. S1).

In this study, we assume that food availability remains constant and in optimal supply so that it is not limiting maximum body size across space now and in the future. On the other hand, the consumption rate of fishes increases with temperature and correlates strongly with W_∞ and K (Supplementary Fig. S1). Also, oxygen is required to convert food into metabolically available energy. Thus, we expect that fishes' response to any climate change-related changes in food availability through alteration of maximum body size would be similar to those through oxygen-limitation.

The theoretical relationship between temperature, K and W_∞ is clearly demonstrated from empirical analysis of fish's growth parameters. Such analysis show significant intra-specific relationships between $\log(W_\infty)$ and $\log(K)$ (see ref. 2), and between $\log(K)$ and water temperature (for example, refs 28–30). These provide the empirical basis for applying this model to predict changes in W_∞ and K under changing temperature.

We obtained averaged values of i and j for marine fishes based on published estimates of Q_{10} of basal metabolic rate of fishes with respect to temperature, W_∞ and von Bertalanffy growth parameter K (see Supplementary Information

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and ref. 3). Thus, given known estimates of W_∞, K, sea water temperature and oxygen content of the habitat and their changes over time, we applied equation (3) to predict changes in W_∞ as a result of changes in ocean conditions for fish populations. Moreover, changes in fish distributions were modelled by the Dynamic Bioclimate Envelope Model (see Supplementary Information). We initialized the models using predicted current (average of 1970–2000) species distribution[6], and published parameter values for the growth and metabolic models (ref. 3 and see Supplementary Information). This model predicted changes in life-history characteristics that are consistent with empirically estimated growth parameters (that is, W_∞ and K; see ref. 3 and Supplementary Fig. S2). We also examine the sensitivity of the results to the key parameters in equation (3) on the simulation (Supplementary Information).

Calculation of mean assemblage-level body weight. We calculated the mean (geometric) assemblage-level body weight from the predicted distribution and maximum body weight of the modelled fish species. We identified species that were predicted to occur in each $30'$ latitude $\times 30'$ longitude cell. We then calculated the mean (geometric) predicted maximum body weight in each cell weighted by the predicted relative abundance of each species, the area of the grid cells, and their historically observed maximum catch. Fish body weights range over several orders of magnitude, thus the geometric mean provides a better representation of the relative changes in body weight across the size spectrum of the assemblage. The historical maximum catch (C) was used as a proxy of the current level biomass of each species in the ocean, which was calculated from time-series catch data (1950 to the present) obtained from the United Nations Food and Agriculture Organization (FAO) and processed by the *Sea Around Us* project (www.seaaroundus.org). For each species, we calculated the average maximum catch from the mean of the five highest annual catches across the time-series. The mean assemblage-level body weight (W') at cell i was then calculated from:

$$\log(W_i') = \frac{\sum_{j=1}^{n} \log(W_{\infty,i,j}) \times Abd_{i,j} \times C_j}{\sum_{j=1}^{n} Abd_{i,j} \times C_j}$$

where $W_{\infty,i,j}$ is the maximum body weight of species j. The projected future level of biomass was calculated by multiplying C by the predicted relative abundance (Abd) from the DBEM under climate and ocean changes. The values of W_i' are calculated for each year from 1971 to 2060.

Calculation of latitudinal centroid shift. The latitudinal centroid (LC) of each species was calculated from:

$$LC = \frac{\sum_{i=1}^{n} Lat_i \times Abd_i}{\sum_{i=1}^{n} Abd_i}$$

where Lat_i is the latitude of the centre of the spatial cell (i), Abd is the predicted relative abundance in the cell (corrected by area of the grid cells), and n is the total number of cells. The range shift was then calculated from the difference between the latitudinal centroid of the projected and reference years. Shift in distance (kilometre) was then calculated from:

$$\text{Distance shift} = \cos^{-1} \times \left[\sin\left(Lat_m \times \frac{\pi}{180}\right) \times \sin\left(Lat_n \times \frac{\pi}{180}\right) \right.$$
$$\left. + \cos\left(Lat_m \times \frac{\pi}{180}\right) \times \cos\left(Lat_n \times \frac{\pi}{180}\right) \right] \times 6378.2$$

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Author contributions

W.W.L.C. and D.P. designed the study. W.W.L.C. conducted the analysis and wrote the manuscript. J.L.S., J.D. and T.L.F. provided and prepared the outputs from the Earth System Models. R.W. provided the global catch data. V.W.Y.L. prepared the current species distributions. M.L.D.P. extracted the distributional and growth parameters from FishBase. All authors reviewed and commented on the manuscript.

Additional information

Supplementary information is available in the online version of the paper. Reprints and permissions information is available online at www.nature.com/reprints. Correspondence and requests for materials should be addressed to W.W.L.C.

Competing financial interests

The authors declare no competing financial interests.