

Integrating ecophysiology and plankton dynamics into projected maximum fisheries catch potential under climate change in the Northeast Atlantic

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Cheung, W. W. L., Dunne, J., Sarmiento, J. L., and Pauly, D. 2011. Integrating ecophysiology and plankton dynamics into projected maximum fisheries catch potential under climate change in the Northeast Atlantic. – ICES Journal of Marine Science, 68: 1008–1018.

Received 30 June 2010; accepted 3 January 2011; advance access publication 13 April 2011.

Previous global analyses projected shifts in species distributions and maximum fisheries catch potential across ocean basins by 2050 under the Special Report on Emission Scenarios (SRES) A1B. However, these studies did not account for the effects of changes in ocean biogeochemistry and phytoplankton community structure that affect fish and invertebrate distribution and productivity. This paper uses a dynamic bioclimatic envelope model that incorporates these factors to project distribution and maximum catch potential of 120 species of exploited demersal fish and invertebrates in the Northeast Atlantic. Using projections from the US National Oceanic and Atmospheric Administration's (NOAA) Geophysical Fluid Dynamics Laboratory Earth System Model (ESM2.1) under the SRES A1B, we project an average rate of distribution-centroid shift of 52 km decade⁻¹ northwards and 5.1 m decade⁻¹ deeper from 2005 to 2050. Ocean acidification and reduction in oxygen content reduce growth performance, increase the rate of range shift, and lower the estimated catch potentials (10-year average of 2050 relative to 2005) by 20–30% relative to simulations without considering these factors. Consideration of phytoplankton community structure may further reduce projected catch potentials by ~10%. These results highlight the sensitivity of marine ecosystems to biogeochemical changes and the need to incorporate likely hypotheses of their biological and ecological effects in assessing climate change impacts.

Keywords: biogeochemistry, climate change, fisheries catch, Northeast Atlantic, ocean acidification, oxygen, range shift.

Introduction

Climate change is causing biological and ecological changes in the ocean (Brierley and Kingsford, 2009). Specifically, changes in the physical (e.g. temperature, ocean current patterns) and biogeochemical (e.g. acidity, oxygen content, primary productivity, plankton community structure) conditions of the ocean result in changes in physiology, species distribution, phenology, and species assemblages (e.g. Edwards and Richardson, 2004; Richardson and Schoeman, 2004; Perry *et al.*, 2005; Hiddink and Hofstede, 2007; Rosa and Seibel, 2008; Pörtner, 2010). Such changes may be more rapid in future (IPCC, 2007). For example, projections from global circulation models (GCMs) suggest that surface temperature may increase by 0.6–4°C by 2090–2099 relative to 1980–1999 (IPCC, 2007). In addition, average surface water pH of the ocean has dropped by ~0.1 units since pre-industrial times and an increase in atmospheric CO₂ concentration to 800 ppmv may further reduce ocean pH by 0.3–0.4 units by 2100 (Caldeira and Wickett, 2003; Orr *et al.*, 2005). Increased temperature and ocean stratification may change the extent of oxygen minimum zones (e.g. Stramma *et al.*, 2010). Global ocean

primary production may change in the future, although current projections are uncertain. For example, Sarmiento *et al.* (2004) suggest that global primary production may increase by 0.7–8.1% by 2050 relative to 2005. Conversely, based on the output of four global coupled carbon cycle-climate models, Steinacher *et al.* (2010) suggest that global mean primary production may decrease by 2–20% by 2100 relative to preindustrial conditions, and there are large regional differences in all these simulations too. Although the period of the estimates reported in these two studies is different, the opposite trends in projected changes covering the similar period highlight the uncertainty of projection of the large-scale changes in primary productivity.

A major challenge to designing effective climate change adaptation strategies for marine ecosystems is to assess the impacts of different scenarios of potential changes in the ocean. Using a dynamic bioclimatic envelope model (Cheung *et al.*, 2008), Cheung *et al.* (2009) established that there might be a high rate of species invasion in high-latitude regions and local extinctions along the tropics by 2050 under the Special Report on Emission Scenario (SRES) A1B.

Furthermore, combining the projected range shift from Cheung *et al.* (2009) and future primary production (Sarmiento *et al.*, 2004), Cheung *et al.* (2010) predicted that potential fisheries catch may increase in the Arctic and Subarctic regions, but decrease in the tropics. Similarly, Hare *et al.* (2010) applied a fisheries stock assessment and spatial distribution model to study Atlantic croaker (*Micropogonias undulatus*) along the east coast of the United States and projected an increase in spawning biomass of 30–60% and a northward shift of 50–100 km of the distribution centre by 2100. However, these models mainly account for changes in physical conditions (e.g. temperature and current patterns), salinity, and primary production, without accounting for other important aspects of potential ocean biochemical changes, such as ocean acidification, expansion of oxygen minimum zones, or changes in phytoplankton community structure.

Recent theories and empirical evidence suggest that biogeochemical changes in the ocean may have large ecological impacts. Specifically, ocean acidification may have negative impacts on many organisms (Guinotte and Fabry, 2008; Doney *et al.*, 2009). However, current studies suggest that species' responses to more acidic water vary considerably and that the mechanisms of biological effects of ocean acidification and their long-term impacts are not fully understood (Dupont and Thorndyke, 2009; Melzner *et al.*, 2009). In addition, the expansion of oxygen minimum zones will directly affect the aerobic performance of marine organisms (Pörtner, 2010). For example, the aerobic scope of two coral reef fish, *Ostorhinchus doederleini* and *O. cyanosoma*, from the Great Barrier Reef was experimentally demonstrated to decline by 33 and 47% in acidified water relative to control water (Munday *et al.*, 2009a). The aerobic scope of marine ectotherms is related directly and positively to the scope for growth (Pauly, 2010). Finally, changes in ocean conditions not only affect the total primary productivity, but also the planktonic community structure (Richardson and Schoeman, 2004; Hays *et al.*, 2005), which is likely to have considerable implications for marine biodiversity and ecosystem services (Beaugrand *et al.*, 2010). Particularly, changes in phytoplankton size structure affect the amount of energy transferred to higher trophic levels. For instance, smaller phytoplanktonic cells are often grazed by small herbivorous microzooplankton, which in turn are preyed upon by larger planktonic consumers. The additional step in the food chain from primary production to large zooplankton may result in a less efficient transfer to a higher trophic level (fish).

In this study, we aim to assess the sensitivity of projected changes in the distribution and fisheries catch potential to biogeochemical changes in the ocean. We focus our study on the exploited demersal fish and invertebrates in the Northeast Atlantic Ocean (here defined as United Nations Food and Agriculture Organization Statistical Area 27), i.e. on the 120 most important species (99 fish and 21 invertebrates), contributing more than 95% of the average total catch in FAO Area 27 in the past two decades (www.seaaroundus.org). We apply a new version of the dynamic bioclimatic envelope model, with explicit considerations of the main physical and biogeochemical factors affecting the exploited demersal fish and invertebrates in the Northeast Atlantic. The model simulates changes in ecophysiology, life history, distribution, relative abundance, and potential catch of each studied species under scenarios of climate change. Specifically, we focus on evaluating the sensitivity of the projected changes in potential catch to some existing hypotheses of how

changes in ocean biogeochemistry may affect the marine ecosystems.

Methods

Model description

The model approach involve three stages: (i) predicting current species distribution; (ii) projecting future changes in distribution and relative abundance; and (iii) projecting future changes in potential catch.

Predicting current species distributions

The distribution map of each species in recent decades was derived from an algorithm of Close *et al.* (2006). This algorithm estimates the relative abundance of a species on a 30' latitude × 30' longitude grid of the world ocean. Input parameters for the model include the species' maximum and minimum depth limits, northern and southern latitudinal range limits, an index of association to major habitat types (seamounts, estuaries, inshore, offshore, continental shelf, continental slope, and the abyss), and known occurrence boundaries. The parameter values of each species, which are posted on the Sea Around Us Project website (<http://www.seaaroundus.org/topic/species/default.aspx>), were derived from data in online databases, mainly FishBase (www.fishbase.org) and SeaLifeBase (www.sealifebase.org). We applied this model to predict the distributions of relative abundance (normalized across the grid) of the 120 species of demersal fish and invertebrates. Figure 1 shows the distribution of species richness calculated using the predicted distribution of the 120 species considered here.

Projecting future species distributions

A new version of the dynamic bioclimatic envelope model was used to project future species distribution. First, the model simulated how changes in temperature, oxygen content (represented by O₂ concentration), and pH (represented by H⁺ concentration) would affect the growth of marine fish and invertebrates. The model algorithm was derived from the von Bertalanffy growth function (VBGF; von Bertalanffy, 1951). Therein, growth is viewed as the difference between two processes, i.e. growth = anabolism – catabolism, or

$$\frac{dB}{dt} = HW^a - kW, \quad (1)$$

where H and k are the coefficients for anabolism and catabolism, respectively. Anabolism scales with body weight (W) with an exponent $a < 1$, whereas catabolism scales linearly with W . Solving for $dB/dt = 0$, we obtained $H = kW_{\infty}^{1-a}$, where W_{∞} is the asymptotic weight.

Equation (1) can be illustrated by a “p-diagram” (Figure 2; Kolding *et al.*, 2008; Pauly, 2010). Figure 2 suggests that relative oxygen supply becomes increasingly limiting as fish grow, because of the lower rate of increase in respiratory surface (and hence oxygen supply) relative to that of increase in body size (and hence oxygen demand; Pauly, 1981, 2010). Therefore, body growth depends on the difference between available oxygen [aerobic scope; anabolic term in Equation (1)] and oxygen demand for maintenance [catabolic term in Equation (1)], with asymptotic weight being reached when the aerobic scope equals oxygen demand.

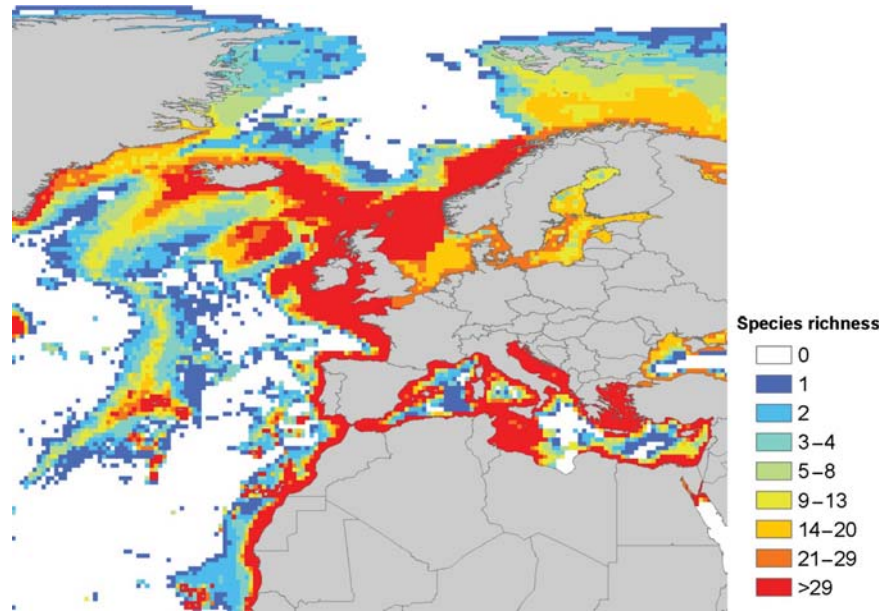


Figure 1. Current pattern of species richness of demersal fish and invertebrates in the Northeast Atlantic based on the distribution ranges of 120 major exploited species.

Equation (1) can be integrated into a generalized VBGF (Pauly, 1981):

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

Substituting $K = k(1-a)$ into Equation (2a), we have

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

where K is the von Bertalanffy growth parameter.

For simplification, we assume that $a = 0.7$, although empirical studies indicate that a generally varies from 0.50 to 0.95 between fish species (Pauly, 1981, 2010). Moreover, metabolism is temperature-dependent, aerobic scope depends on oxygen availability in water, and maintenance metabolism is affected by physiological stress (e.g. increased acidity). Therefore,

$$H \propto f(O_2)f_1(T), \quad (3)$$

and

$$k \propto f_2(T)f([H^+]). \quad (4)$$

Temperature effect on H and k follows the Arrhenius equation:

$$f_1(T) \propto e^{-j_1/T}, \quad (5a)$$

and

$$f_2(T) \propto e^{-j_2/T}, \quad (5b)$$

where $j = E_a/R$, with E_a and R the activation energy and the Boltzmann constant, respectively, whereas T is the temperature (in K). In addition, the aerobic scope of marine fish and

invertebrates decreases as temperature approaches their upper and lower temperature limits (Pörtner, 2010).

We set the values of j based on empirically estimated metabolic scaling exponents. A meta-analysis of the resting metabolic rate of teleosts suggests that the within-species Q_{10} of temperature ranges from 0.45 to 3.41, with a median of 2.4 (Clarke and Johnston, 1999). We assume that the resting metabolic rate represents metabolic demand for basic body functions and maintenance. Hence, we calculated a j_2 in the Arrhenius equation (5a) for catabolism that would result in the reported Q_{10} over the possible physiological temperature range (1–28°C) of ~ 8 . Given that anabolism is considered to be less temperature sensitive than catabolism (Perrin, 1995), and based on the fact that the slope of the regression between $\log(K)$ and $\log(W_\infty)$ among different populations of a species is ≈ 0.7 (Pauly, 2010), we estimated that j_1 should be ≈ 4.5 .

In this model, oxygen availability depends on dissolved oxygen (O_2), whereas physiological stress from ocean acidification depends on the concentration of the hydrogen ion (H^+). We incorporated two hypotheses of potential effects of changes in oxygen concentration and ocean acidification on growth of marine fish and invertebrates. For oxygen, we explored the hypothesis that oxygen supply to the fish body is reduced linearly with a reduction in oxygen concentration in the ocean from the current levels. Moreover, the model accounts for the hypothesis that increased acidity increases oxygen demand, for example, for ionic balance regulation or increased calcium carbonate formation. Some recent experimental studies suggest that the aerobic scope of marine fish and invertebrates could be affected by ocean acidification (Melzner et al., 2009). For example, an ~ 2.5 times increase in CO_2 concentration might cause an average of 33–47% reduction in the aerobic scope of two species of cardinal fish (family Apogonidae; Munday et al., 2009a). However, these might be among the coral reef fish that are most sensitive to acidification, because these species inhabit an environment without substantial changes in acidity, rendering them more

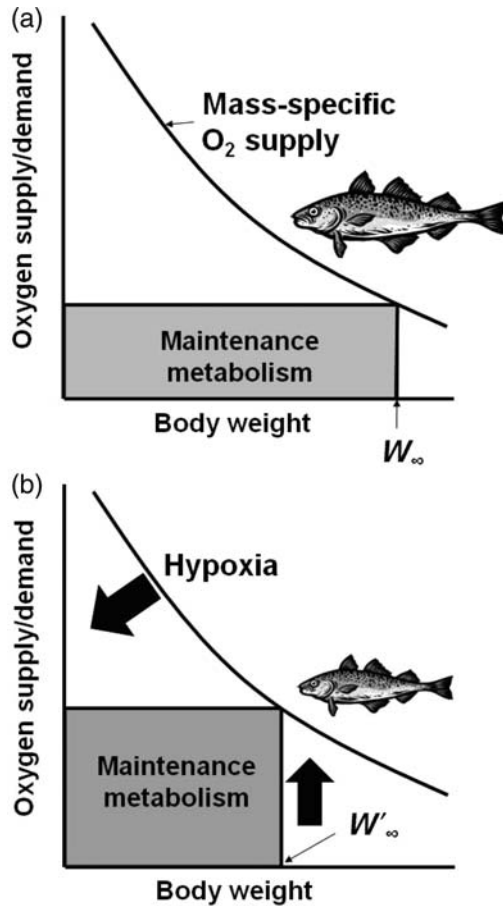


Figure 2. Two p-diagrams illustrating how (a) growth and maximum (i.e. asymptotic) size of fish depend on the balance between oxygen supply and demand; (b) factors that increase maintenance metabolism (e.g. increased temperature, physiological stress) or reduced oxygen supply (e.g. hypoxia) will reduce growth and asymptotic weight (from W_∞ to W'_∞). Oxygen supply scales allometrically with body mass, whereas oxygen demand (for maintenance metabolism) is directly proportional to body mass. Growth depends on the aerobic scope, i.e. on the difference between oxygen supply and demand curves. Asymptotic size is reached when oxygen supply is just enough to meet oxygen demand for basic body maintenance. Hence, increase in oxygen demand or decrease in oxygen supply will affect growth and asymptotic size.

sensitive to ocean acidification (Munday *et al.*, 2009a). In addition, sensitivity of physiological performances of marine fish and invertebrates appears to be highly variable between species and taxonomic groups (Melzner *et al.*, 2009). Existing knowledge does not allow us to predict accurately how sensitive fish and invertebrate species are to ocean acidification. To examine the potential effects of ocean acidification on species distributions and fisheries catch potential, we therefore developed the broad-brush scenarios of species' sensitivity to ocean acidification; including (i) oxygen demand of marine fish and invertebrates is insensitive to ocean acidification; (ii) oxygen demand increases by 15% when H^+ ion concentration in the ocean is doubled from current levels; and (iii) oxygen demand increases by 30% when H^+ ion concentration in the ocean is doubled from the current levels. We recognized that these scenarios are developed from limited information on physiological responses of marine organisms to ocean

acidification and that they do not account for the differential sensitivity to acidification between species. Nevertheless, we aim to demonstrate how impacts of ocean acidification, for different levels of sensitivity at the individual level (physiology), may yield impacts at the population and community level and on fisheries catch potential.

Therefore,

$$H = g[O_2]e^{-j_1/T}, \quad (6a)$$

and

$$k = h[H^+]e^{-j_2/T}. \quad (6b)$$

The coefficients g and h were derived from the average W_∞ , K , and environmental temperature (T_0) of the species reported in the literature:

$$g = \frac{W_\infty^{1-a}K}{[O_2]e^{-j_1/T_0}}, \quad (7a)$$

and

$$h = \frac{k/(1-a)}{[H^+]e^{-j_2/T_0}}, \quad (7b)$$

where $H = kW_\infty^{1-a}$ and $k = K/(1-a)$ [Equations (1) and (2)].

The model predicts changes in VBGF parameters according to changes in temperature, oxygen, and pH in the ocean relative to the initial conditions, as

$$W_\infty = \left(\frac{H}{k}\right)^{1/(1-a)}, \quad (8a)$$

and

$$K = k(1-a). \quad (8b)$$

Modelling population dynamics

Based on the computed VBGF parameters, the model determined the change in carrying capacity in each $30'$ latitude \times $30'$ longitude cell. Carrying capacity is expressed as a function of expected biomass per recruit and recruitment. Expected biomass per recruit was determined using a size-based population model. To parametrize this model, the natural mortality rate (M) was predicted from Pauly's empirical equation (Pauly, 1980):

$$\log M = 0.2107 - 0.0824 \log W_\infty + 0.6757 \log K + 0.4627 \log T', \quad (9)$$

where T' is the temperature in degrees Celsius.

The size-transition matrix (X), a matrix of probabilities of an individual growing from a particular body-size class to other size classes in a time-step (year), was computed from Quinn and Deriso (1999):

$$\theta_{y,r,l} = \exp \left[-\frac{(\bar{l}_l - [l_\infty(1 - e^{-K}) + \bar{l}_l e^{-K}])^2}{2\sigma^2} \right], \quad (10a)$$

and

$$X_{l,l} = \frac{\theta_{r,l}}{\sum_l \theta_{r,l}}, \quad (10b)$$

where l_∞ is the asymptotic length, l and l' the adjacent length classes, γ the age of the fish, and σ the variation in growth, which is assumed to have a coefficient of variation of 20% and is independent of length and age. Biomass per recruit (BPR) was calculated using

$$\text{BPR} = \sum_y \sum_l \bar{W}_l X_{l,l} e^{-M}, \quad (11)$$

where \bar{W} is the mean weight of length class l .

Many studies indicate that the ratio L_m/L_∞ is relatively constant within most families of fish (Beverton and Holt, 1959; Beverton, 1963; Mitani, 1970; Pauly, 1984; Binohlan and Froese, 2009), where L_m and L_∞ are the length at maturity and asymptotic length. In fact, the relationship between L_m and L_∞ can be re-expressed as:

$$\frac{Q_m}{Q_\infty} = \left(\frac{L_m}{L_\infty} \right)^{b(1-a)} \approx 0.714, \quad (12a)$$

where Q_m and Q_∞ are the mass-specific relative oxygen supply when the fish reaches sexual maturation and asymptotic size, respectively (Pauly, 1984). The exponents a and b for the anabolic term in Equation (1) and the length–weight relationship are defined as previously. Pauly (1984) established that the ratio of Q_m to Q_∞ is ~ 1.4 . Rearranging Equation (12a), we have

$$L_m = L_\infty (0.714)^{1/[b(1-a)]}. \quad (12b)$$

Assuming knife-edge recruitment at L_m , the model calculated spawning biomass per recruit (SPR) from:

$$\text{SPR} = \sum_y \sum_l \bar{W}_l X_{l,l} \text{mat} e^{-M} \begin{cases} \text{if } L_l < L_m, \text{ mat} = 0 \\ \text{if } L_l \geq L_m, \text{ mat} = 1. \end{cases} \quad (13)$$

Total larval production is directly proportional to SPR.

Initial relative recruitment strength (R) was calculated using the initial relative abundance (A , normalized across the $30' \times 30'$ degree resolution grid) and calculated biomass per recruit in each cell, as $\text{BPR} = cA/R$, where c is a constant that scales from relative abundance to absolute abundance. Hence, $R = cA/\text{BPR}$ and $A = \text{BPR} R/c$.

The model identified the “environmental preference profiles” of the 120 species, defined by seawater temperature (bottom and surface), depth, salinity, distance from sea ice, and habitat types. Preference profiles are defined as the suitability of each of these environmental conditions to each species, with suitability calculated by overlaying environmental data (2001–2010) with maps of relative abundance of the species (Cheung et al., 2009). For example, for each species, the model calculated a temperature preference profile for the adult and prerecruit phases, based on the relative abundance and the computed recruitment strength of the species. Sea surface temperature was used for temperature preference profiles for the prerecruit phase, whereas bottom temperature was applied to preference profiles for the adult demersal species.

Change in species' carrying capacity (A_∞) in each spatial cell was dependent on its calculated theoretical relative abundance and environmental preferences. Carrying capacity is assumed to vary positively with habitat suitability of each spatial cell and habitat suitability depends on the species' preference profiles to the environmental conditions in each cell. The final carrying capacity of a cell is therefore calculated as the product of the habitat suitability of all the environmental conditions considered in the model.

The model simulated changes in relative abundance of a species by

$$\frac{dA_i}{dt} = \sum_{j=1}^N G_i + L_{ji} + I_{ji}, \quad (14)$$

where A_i is the relative abundance of a $30' \times 30'$ cell i , G the intrinsic population growth, and L_{ji} and I_{ji} the settled larvae and net migrated adults from surrounding cells (j), respectively.

Intrinsic growth is modelled by a logistic equation:

$$G_i = rA_i \left(1 - \frac{A_i}{A_{\infty,i}} \right), \quad (15)$$

where r is the intrinsic rate of population increase. The model explicitly represents larval dispersal through ocean currents with an advection–diffusion–reaction model (see Cheung et al., 2008, 2009, for details).

Therefore, changes in ocean conditions are transformed by the model into changes in life history, growth, carrying capacity, population growth, net migration, and, hence, relative abundance of a species, in each cell it occupies. Given the projected changes in ocean conditions from the ocean–atmosphere–coupled GCM under climate change scenarios, the model simulates the annual changes in the distribution of relative abundance of each species on the global $30' \times 30'$ grid.

We determined the rates of range shift of the 120 species in the Northeast Atlantic Ocean from 2001 to 2055. For each simulation year, we calculated the latitudinal and depth centroids of distribution of each species, expressed as the average latitude and depth of the centre of each spatial cell weighted by the relative abundance of the species in the cell in the Northeast Atlantic, respectively. Bathymetry data were based on mean depth in each $30 \times 30'$ cell calculated using the ETOPO1 Global Relief Model (<http://www.ngdc.noaa.gov/mgg/global/global.html>).

Scenarios of biogeochemical changes in the ocean

Our scenario of ocean conditions is based on outputs from the prototype Earth System Model (ESM2.1) developed at the Geophysical Fluid Dynamics Laboratory (GFDL) of the US National Oceanic and Atmospheric Administration (NOAA; Dunne et al., 2005, 2007). The scenario considered here is the SRES A1B, which assume CO_2 concentration at 720 ppm in 2100. The original resolution of the outputs from the coupled model is 1° at latitudes higher than 30°N and 30°S , with the resolution becoming finer towards the equator. We interpolated the physical variables from the coupled model with a resolution of $30'$ in latitude and longitude, using the nearest neighbour method, thus avoiding making complicated assumptions about the relationship between the coarser-resolution model outputs and their downscaled values. Ocean condition fields used included

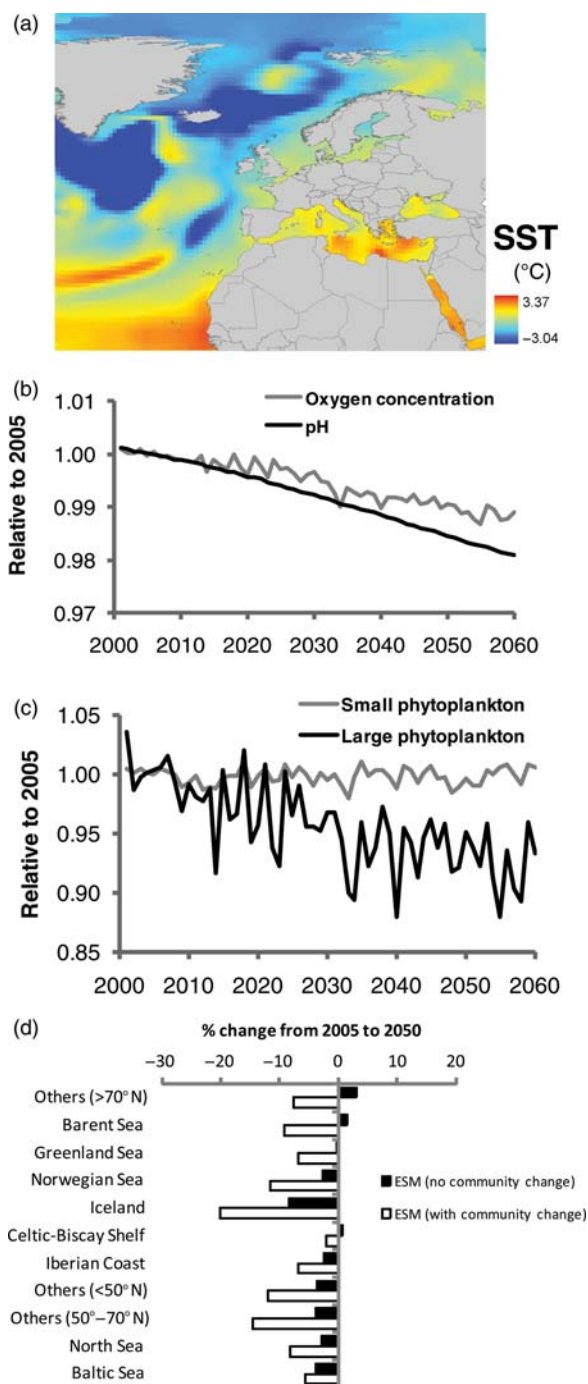


Figure 3. Changes in physical and biogeochemical conditions of the ocean predicted from ESM2.1: (a) map of sea surface temperature anomalies between 2005 and 2050 (10-year average), (b) changes in average pH and oxygen concentration, (c) changes in the production of small and large phytoplankton in the Northeast Atlantic, and (d) changes in primary production by LMEs.

sea surface and bottom temperature, sea ice concentration, surface advection, surface and bottom oxygen and hydrogen ion concentration, salinity, and small and large phytoplankton production (Figure 3).

Three scenarios of predicted primary production were tested in the model. The first and the second scenarios of primary

production data were based on outputs from ESM2.1, whereas the third set was based on the empirical models. The first scenario assumes that small and large phytoplankton cells contribute equally to fish production. The second scenario assumes that a food chain based on small phytoplankton cells is less efficient at transferring energy to fish groups (because of the longer trophic path length) than a food chain based on large phytoplankton cells. Specifically, we assumed that, on average, small phytoplankton cells must be consumed by an additional trophic level before (a fraction of) their embodied energy became available to higher trophic level groups. In addition, we assumed that the transfer efficiency between trophic levels is 10%, as demonstrated by Pauly and Christensen (1995) to be applicable to a wide range of marine ecosystems. The third scenario was based on primary production calculated using published empirical models and algorithms (Behrenfeld and Falkowski, 1997; Carr, 2002; Sarmiento *et al.*, 2004). Sarmiento *et al.* (2004) detailed how these algorithms were applied to project future primary production. All estimated values of annual average primary productivity from the years 2001–2055 are scaled onto a 30' latitude \times 30' longitude grid of the world ocean (Figure 3).

Projected changes in fisheries catch potential

We simulated changes in maximum catch potential based on the methods of Cheung *et al.* (2010). For each studied species, changes in maximum catch potential were calculated based on changes in species distributions and primary productivity. First, we projected how the distribution of the 120 species of demersal marine fish and invertebrates would shift under the climate change scenario by applying the model used in this paper to simulate changes in the distribution of relative abundance on the 30' \times 30' grid from 2005 to 2050. Second, we calculated changes in primary production within the distribution range of the species. We then applied the empirical method of Cheung *et al.* (2010) to calculate the projected changes in catch potential in each 30' \times 30' cell. We also calculated how total maximum fisheries catch potential of the studied species within the large marine ecosystems (LMEs) of the Northeast Atlantic Ocean changes by 2050 relative to 2005 (10-year average). We conducted separate analyses for simulations with and without consideration of ocean biogeochemical effects.

Results

Our model predicted changes in life-history characteristics consistent with empirically estimated growth parameters (Figure 4). It predicted growth parameters over the environmental temperature range (5th and 95th percentiles of the water temperature within the predicted distribution range) of each of the 120 studied species. The plot between predicted K and L_{∞} is similar to the plot using growth parameters reported in the published literature for 2015 fish species (available from FishBase: www.fishbase.org; Pauly, 1998). The predicted intraspecific changes are also consistent with observations, as illustrated in the example of Atlantic cod (Figure 4).

When future scenarios of changes in biogeochemistry were considered, growth performance of many of the studied species was projected to decrease, relative to the scenario that growth was affected only by temperature (Figure 5). Therefore, ocean acidification and hypoxia result in a decrease in slope of the log–log plot between K and asymptotic size. In other words, the consideration of increase in oxygen demand or reduce in supply

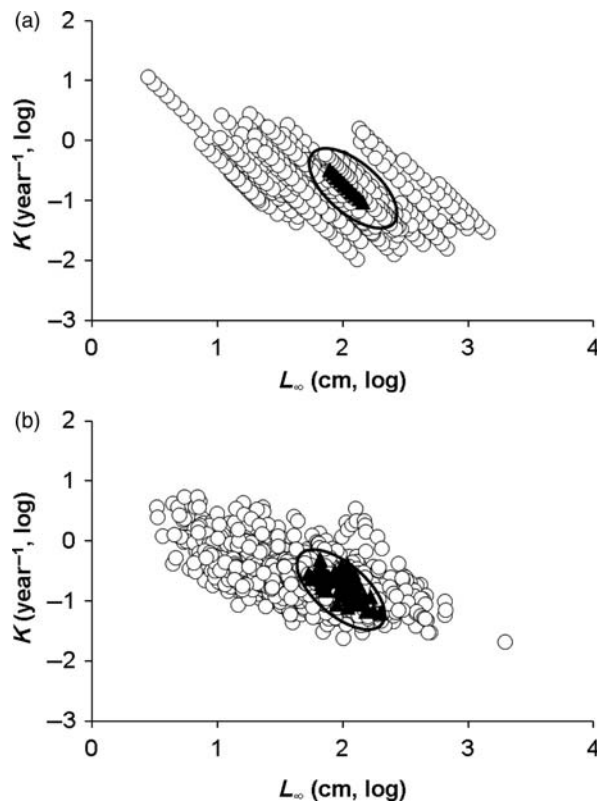


Figure 4. Plot of $\log K$ against $\log L_{\infty}$ of (a) 120 demersal fish over the 5th and 95th percentile of their predicted habitat temperature (as predicted from the dynamic bioclimate envelope model); and (b) published empirical estimates of VBGF of 2015 fish (available from FishBase). The black triangles in (a) and (b) represent predictions and estimates for different Atlantic cod populations. Using Atlantic cod as an example, the predicted slope between $\log K$ and $\log L_{\infty}$ not significantly different ($p < 0.05$) from the slope calculated using observed $\log K$ and $\log L_{\infty}$ (Taylor, 1958).

from ocean acidification and hypoxia, in addition to temperature increase, caused the model to predict a reduction in W_{∞} that does not correspond to as large an increase in K as predicted from considering temperature only.

Our model predicted that distributions of most of the 120 studied fish and invertebrates will shift northwards (Figure 6). With the considerations of physical and biogeochemical factors, the centroids of species distribution (calculated using the average latitude and depth of the centre of each spatial cell weighted by the relative abundance of the species in the cell in the Northeast Atlantic) shifted at an average rate of $52.1 \text{ km decade}^{-1}$ towards the north and $5.1 \text{ m decade}^{-1}$ towards deeper water between 2005 and 2050, under the scenario of high physiological sensitivity to ocean acidification (i.e. 30% reduction in oxygen demand as the H^+ ion concentration in the ocean doubles). When the model was run with the scenarios of physical changes only (without acidity, oxygen, and phytoplankton community structure), the latitudinal and depth centroids of the distributions were predicted to shift at a slower rate of an average of 45.5 and $4.3 \text{ m decade}^{-1}$, respectively.

With the projected changes in the distribution of relative abundance and primary production, the total maximum catch potential may change substantially in the Northeast Atlantic region (Figure 7). If we exclude the changes in oxygen content and pH

in the analysis, maximum catch potential increases in the LMEs of the Subarctic (Barents Sea, Greenland Sea, Norwegian Sea, Iceland LMEs, and other regions above 70°N) by up to 80% from 2005 to 2050 (10-year average; Figure 7). Catch potentials in the lower latitude LMEs (Celtic-Biscay Shelf, North Sea, Baltic, and other regions south of 70°N) by 2050 relative to 2005 (10-year average) remained relatively unaffected.

When all biogeochemical factors were considered, the projected maximum catch potential in 2050 declined substantially (Figure 7). Under the scenario of high physiological sensitivity to ocean acidification, relative increases in catch potential from 2005 to 2050 in the Barents Sea LME and Greenland Sea decreased from ~ 70 and 40% (without O_2 and pH) to around 35 and 10% (with all biogeochemical factors), respectively. Moreover, changes in catch potential became negative in the other LMEs in the Northeast Atlantic. Particularly, catch potentials were projected to decrease by up to 30% in the Celtic-Biscay Shelf, Iberian Coast, North Sea, and Baltic Sea by 2050. Moreover, the change in maximum catch potential is sensitive to the scenario of physiological sensitivity to ocean acidification. The scenario of intermediate sensitivity to ocean acidification resulted in an intermediate level of changes in maximum catch potential approximately mid-way between the high sensitivity and no sensitivity scenarios (Figure 7).

The projected changes in maximum catch potential were moderately sensitive to primary production predicted from different methods (Figure 8). Without consideration of changes in oxygen content and pH, projected changes in catch potential were largest when total primary production in ESM2.1 was considered. When the relative contribution of different phytoplankton cell size was examined, percentage changes in catch potential from 2005 to 2050 declined by $10\text{--}20\%$. Projected changes in catch potential using primary production predicted from empirical models (documented in Sarmiento *et al.*, 2004) were intermediate relative to the other two sets of predictions.

Discussion

Future changes in species distributions and maximum catch potential in the Northeast Atlantic may be strongly affected by changes in oxygen content, acidity, and phytoplankton community structure in the ocean. Without consideration of these factors, the model projected poleward movement of species distributions and gains in catch potential that are consistent with previous studies (Cheung *et al.*, 2009, 2010). The projected deepening of species distribution is moderately higher than the observed rate in the North Sea from the 1980s to 2000s ($3.1 \text{ m decade}^{-1}$; Dulvy *et al.*, 2008), which is reasonable, given that the projected future rates of change in temperature and other ocean conditions are higher than the historical rates under the climate change scenario considered in this study. However, this study suggests that the projected impacts of climate change on species distribution and maximum catch potential were underestimated when biogeochemical factors were not considered. Specifically, in the model, ocean acidification and reduction in oxygen level reduced the aerobic scope for growth and, hence, maximum catch potential of most species in the region. Such an effect was particularly apparent at the edge of distribution ranges, where the temperature was close to the tolerance limits of the species, and the fish consequently exhibited a limited aerobic scope. This also explained the increase in the projected rate of range shift when ocean acidification and changes in oxygen content were considered. In addition, energy transferred from primary production to higher trophic levels may decline when

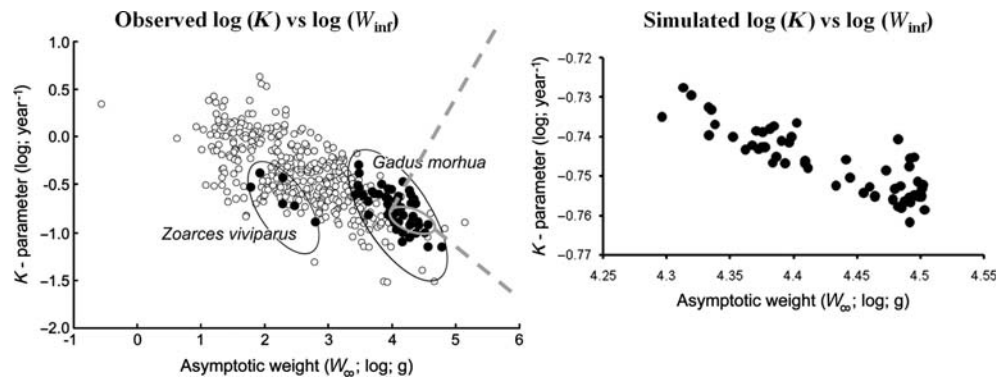


Figure 5. Comparing the observed changes in growth parameters (left) with simulated changes from the dynamic bioclimate envelope model under future scenarios of changes in ocean biogeochemistry and physical conditions (right). The slope of the plot on the right is less steep than observed (left panel).

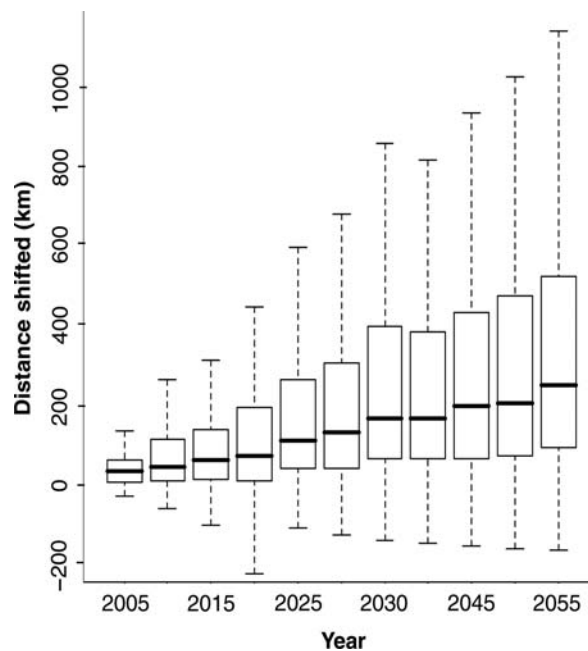


Figure 6. Projected mean rate of shift in latitudinal centroids of the 120 studied demersal fish and invertebrates under a scenario that considers both physical and biogeochemical factors (including acidity, oxygen, and phytoplankton community structure). In this scenario, the physiological sensitivity to acidification and oxygen is high. The black bars represent the median values, whereas the boundary of the box represents the 25th and 75th percentiles. When biogeochemical factors are not considered, the projected rate of range shift declines from a median of 52 km decade⁻¹ to 45 km decade⁻¹ by 2050.

the phytoplankton communities shift towards smaller size in future. Indeed, consideration of these factors reversed the sign of catch potential changes in some intermediate regions, such as the North Sea and Baltic Sea, whereas in low-latitude areas, considerations of these factors intensified negative trends. This will largely affect the expected impacts and adaptation costs of countries in the Northeast Atlantic region to climate change and may have large implications for planning for climate change-adaptation policies (World Bank, 2009; Sumaila and Cheung, 2010).

We acknowledge that the magnitude of changes projected by the model is uncertain. First, the model projections were affected by uncertainties about the projected physical and biogeochemical conditions (e.g. IPCC, 2007; Friedrichs *et al.*, 2009). We used projections from one model ensemble member from ESM2.1; consequently, our study results may be affected by the errors or biases in this particular set of model outputs (Stock *et al.*, 2010). Future extension of this study will explore the sensitivity of projected ecological changes between different climate model and ESM2.1 and between different ensemble members of a model, allowing the exploration of the sensitivity of our projections to different projections of physical and biogeochemical changes. Second, the underlying biological hypothesis, represented by the model structure and input biological and ecological parameters, may be uncertain. Specifically, we assumed that growth and maximum body size in marine fish and invertebrates are determined primarily by availability of oxygen; the latter is related partly to the availability of respiratory surfaces. Although this hypothesis is supported by abundant evidence (Pauly, 2010), it has not been considered before. Conversely, the simulated variations in growth parameters between and within species match with empirical observations; this provides some support to the model in representing growth of marine fish and invertebrates. Moreover, although parameter uncertainty may render predictions at individual species level inaccurate, the large sample size and taxonomic and geographic coverage of our study allowed us to detect the signals of changes that may otherwise be distorted by uncertainties. We did not account for interactions between species (e.g. effects of changes in prey availability and predation pressure on growth, population dynamics, and distribution) and with human activities (e.g. fishing). An analysis using a trophodynamic model suggests that trophic interactions may significantly affect the relative abundance of animals in a region, although the direction of changes is consistent with projections from the bioclimatic envelope model (Ainsworth *et al.*, 2011). In future, interspecific linkages could be incorporated to test the effects of trophic interactions on model projections. In addition, our model did not account for potential genetic changes as an adaptation to the changing environmental conditions. Evolutionary processes may affect species' environmental tolerance, range shift, and extinction under environmental changes (Davis *et al.*, 2005). For example, evolutionary mechanisms might select for genes that can facilitate range movement (Parmesan, 2006). Conversely, the limited

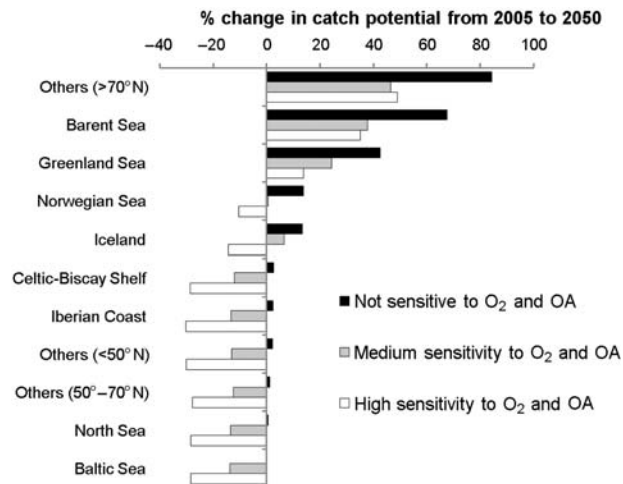


Figure 7. Projected changes in maximum catch potential between 2005 and 2050 (10-year average) in the LMEs in the Northeast Atlantic with high sensitivity (open bar), medium sensitivity (grey bar), and insensitive (black bar) to changes in oxygen content and pH.

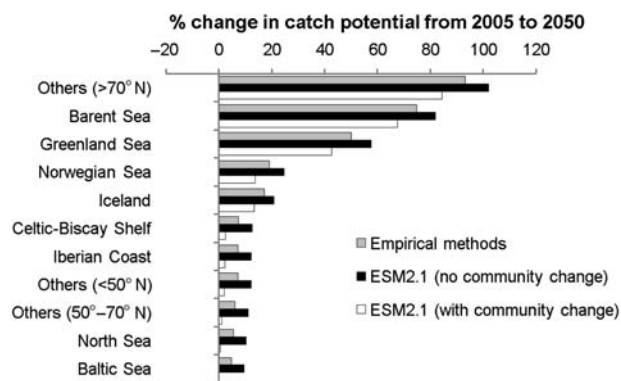


Figure 8. Projected changes in maximum catch potential between 2005 and 2050 (10-year average) in the LMEs in the Northeast Atlantic under three different primary production projections: (grey) empirical models as documented in Sarmiento *et al.* (2004); (black) total primary production from ESM2.1; (white) from ESM2.1, but considering phytoplankton cell size.

evidence available suggests that absolute tolerances to climate change will not evolve fast enough for a distribution range to be conserved (Etterson and Shaw, 2001; Jump and Peñuelas, 2005; Parmesan, 2006). Additional empirical evidence is needed before we could determine the potential effects of evolutionary changes under climate change.

The new version of the dynamic bioclimate envelope model presented in this paper is an attempt to fill a number of gaps in the approaches to project climate change effects on species distributions. The model allowed testing of the potential effects of projected future changes in physical and biogeochemical conditions of the ocean. With explicit representation of ecophysiological effects, the model took explicit account of the phenotypic plasticity of fish to changes in environmental conditions, through changes in body size, growth, and life history. This provides explicit linkages between climate change effects on growth, life history, and population dynamics of marine fish and invertebrates, thus accounting for the potential impacts from individual animals to population

and community levels. This is a considerable advance over the conventional bioclimatic envelope model (Elith and Leathwick, 2009). Projections from this model may be treated as alternative hypotheses of potential climate change impacts on biodiversity and fisheries catch potential in the Northeast Atlantic. Comparison with projections from other models with different complexity, structure, assumptions, and input data could increase the robustness of the projections and should be carried out in the future (Morin and Thuiller, 2009).

The model can be used to test different hypotheses of how climate change may affect marine organisms through changes in physical and biogeochemical conditions of the ocean. Currently, a range of hypotheses on the biological and ecological effects of ocean acidification on marine fish and invertebrates has been proposed with equivocal empirical evidence (Guinotte and Fabry, 2008; Wood *et al.*, 2008; Dupont and Thorndyke, 2009; Gooding *et al.*, 2009; Munday *et al.*, 2009a, b). For example, some studies suggest that ocean acidification may increase energy expenditure on growth or body regulation (Munday *et al.*, 2009a; Pörtner, 2010), whereas others established direct increases in the mortality of marine fish from impaired body function (Munday *et al.*, 2009b). Although this study assessed only one of such hypotheses (effects on energy expenditure), the model could be modified easily to test the sensitivity of species distributions and maximum catch potential to different hypotheses of impacts.

In summary, we demonstrate that consideration of ocean acidification, changes in oxygen content, and phytoplankton community structure may reduce strongly the projected maximum catch potential in the Northeast Atlantic. This may have large implications for planning climate change-adaptation strategies in the region. This also highlights the need to increase our understanding of these impacts and to conduct interdisciplinary research across climate and ocean sciences, physiology, ecology, fisheries, economics, and social science. In future, the study could be extended to address a number of knowledge gaps in the study of climate change impacts on fish and fisheries. Particularly, the model could be applied to assess the sensitivity of future marine biodiversity and fisheries catch potential to different hypotheses about the ecological effects of ocean biogeochemical changes. In addition, based on historical changes in ocean condition, the model can be applied to generate hindcasts of changes in major marine fish and invertebrates, presenting hypotheses of climate change influences on these species in the past.

Acknowledgements

We thank A. Karpechko for his advice on regridding ocean data, A. Atanacio for help with the graphics, and S. Jennings for commenting on an early draft of the manuscript. WWLC was partly supported by the Seedcorn Fund provided by the Centre for Environment, Fisheries and Aquaculture Science. The *Sea Around Us* project, a scientific collaboration between the University of British Columbia and The Pew Environmental Group, provided the species distribution ranges used in this study and funding to DP. JS was supported by the Carbon Mitigation Initiative (CMI) project at Princeton University, sponsored by BP and Ford Motor Company.

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