

CHAPTER 8

GLOBAL-SCALE RESPONSES AND VULNERABILITY OF MARINE SPECIES AND FISHERIES TO CLIMATE CHANGE¹

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Of the various ways humans affect marine ecosystems, climate change may be the most insidious and unrecognized. In fact, even if they believe that it is occurring, most people think climate change is going to affect us later, and thus there is no real urgency. As we show below, however, climate change has already begun to affect us in multiple ways, including through effects on the oceans and marine fisheries. This chapter is thus devoted to documenting some of the work through which scattered observations on the effect of climate change on marine organisms were generalized and, in the process, the first global maps of observed and predicted climate change impacts on marine biodiversity and fisheries were produced, thus complementing work performed in the terrestrial realm.

Climate change affects ocean properties including water temperature, oxygen level, and acidity. According to the Intergovernmental Panel on Climate Change (IPCC) 5th Assessment Report (AR5), there is compelling evidence that the heat content and the stratification of the ocean have been increasing in the twentieth century, while sea-ice and pH have been decreasing, and that these trends can be

expected to continue in the next century under the climate change scenarios considered by the IPCC (2014). Also, available evidence indicates that climate change is expected to result in expansion of oxygen minimum zones, changes in primary productivity, changes in ocean circulation patterns, sea level rises, and increase in extreme weather events.

Marine fishery catches consist almost solely of fishes and invertebrates that are biologically sensitive to changes in temperature, oxygen level, and other ocean conditions; thus we expect that fisheries are being affected by climate change (CC) and ocean acidification (OA). In the ocean, physiological performance of aquatic and marine water-breathing organisms is strongly dependent on temperature and oxygen (Pauly 1981, 2010; Pörtner 2010). Because of the higher viscosity of water and because dissolved oxygen occurs in water in lower concentration than in the atmosphere, it is energetically costly for water-breathing organisms to obtain oxygen for respiration from water (Pauly 1981, 2010). Thus, changes in oxygen supply and demand are expected to have large implications for respiration and other body functions of fishes and invertebrates (i.e., water-breathing ectotherms). Although low oxygen tolerance thresholds vary across species and life stages, they tend to be highest for large water-breathing ectotherms. When temperature becomes either too high or too low, oxygen supply capacity decreases relative to oxygen demand and thus limits metabolism.

The ranges between the lowest and highest temperatures that are tolerated by organisms are generally consistent with the variability of environmental temperatures they are generally exposed to and can change during their life cycles. Also, smaller individuals are more heat tolerant than large ones, in line with observations of declining animal body sizes in warming oceans (Daufresne et al. 2009). Increases in CO₂ in the ocean may also have direct and indirect effects on growth, reproduction, and survivorship of fishes and invertebrates, particularly those that form calcium carbonate exoskeleton (Kroeker et al. 2013).

An understanding of the physiological sensitivity and responses to ocean temperature, oxygen, acidity, and other water properties allows us to develop hypotheses about how climate change and ocean acidification will affect exploited fish stocks and fisheries. These hypotheses include the following:

- Given ocean warming, fishes and invertebrates will be shifting their distributions, mainly to higher latitude and deeper water to maintain their thermal niche.
- In nontropical systems, warmer-water species will increase their contribution to local catches.
- Maximum body size of fishes will decrease as the oceans become warmer and less oxygenated.
- Global marine catches will decline, particularly in the tropics.

To examine these hypotheses at the global scale, we conducted a series of empirical and theoretical studies that made use of species' distribution ranges (see chapter 4) and spatially explicit global catch data from the *Sea Around Us* (see chapter 5) to evaluate the effects of climate change and ocean acidification on the distribution of exploited species, the species composition of catches, and projected fisheries catch potential.

As a conceptually first step (though one taken last in the sequence of studies described below), the signature of the effects of ocean temperature change on species composition of fisheries catches was studied, using a newly

developed metric called mean temperature of the catch (MTC). The second step was to develop a species distribution model, called the dynamic bioclimate envelope model (DBEM), that predicts changes in the distribution ranges of exploited marine species and the patterns of species richness in response to changing ocean conditions. Once developed, the DBEM was modified so as to progressively account for an increasing number of features, such as the population dynamics of the species included, their dispersal modes, interactions with other species, association with different habitats, oxygen requirements, and resistance to low pH. The third step was to use macroecological theory to derive the theoretical relationship between net primary production (NPP), biogeography, and fisheries catch potential and to express that relationship in a single empirical equation. Then, with projected changes in NPP and species distributions combined, future changes in distribution of fisheries catch potential and the maximum body size of exploited species could be projected. Finally, by use of the DBEM and basic principles of geometry and physiology, the effects of ocean warming and deoxygenation on the maximum body size of exploited fishes could be projected.

Mean Temperature of the Catch

Marine fishes and invertebrates exhibit physiological thermal tolerances that constrain them to live within a certain range of temperatures. Thus, for example, the seasonal migration of fishes up and down along the coast of northwest Africa tracks the seasonal temperature oscillations along that same coast (figure 8.1). Similarly, as the oceans warm up, fishes and invertebrates have to shift their distributions in order to maintain themselves in habitats with their preferred temperature. This results (at locations outside of the tropics) in changes in species composition, as the taxa increase in abundance that are adapted to warmer waters. For example, warming in the eastern Mediterranean (i.e., in Greece) caused a reduction of bearded horse mussel *Modiolus*

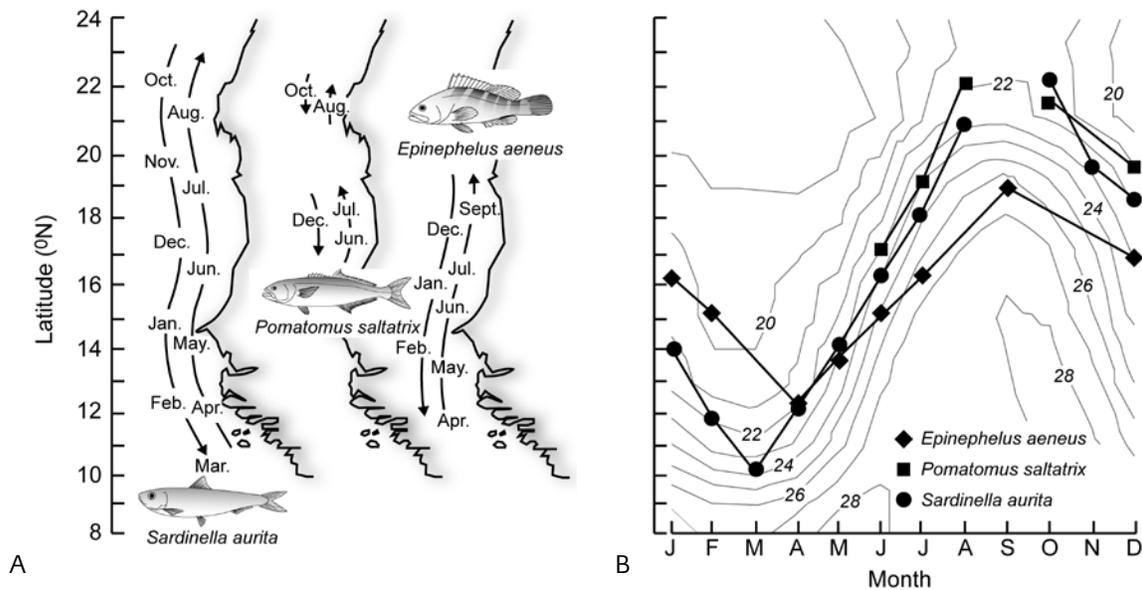


Figure 8.1. Seasonal latitudinal migrations of some northwest African fishes. (A) Summary of information on the occurrence in space (latitude) and time (month) of 3 species, *Sardinella aurita*, *Pomatomus saltator*, and *Epinephelus aeneus* (from Boëly et al. 1978, 1979; Champagnat and Domain 1978; Barry-Gérard 1994). (B) Same as in (A) but plotted against mean monthly temperature. Data from the Comprehensive Ocean–Atmosphere Data Set (COADS). The seasonal migrations result in the 3 species remaining in approximately the same temperature range (and hence having the same oxygen consumption) throughout the year. (Adapted from Pauly 1994.)

barbatus (Katsikatsou et al. 2011) and the establishment of the noxious silver-cheeked toadfish *Lagocephalus sceleratus*, a Red Sea or “Lessepsian” migrant (Kasapidis et al. 2007). Shifted species distribution ranges follow temperature clines from high to low, reflecting a lateral gradient at the basin scale (Pinsky et al. 2013; Poloczanska et al. 2013) or a vertical temperature gradient to deeper waters (Dulvy et al. 2008; Pauly 2010). However, the implications of such responses for global fisheries to ocean warming had not been empirically demonstrated.

The newly developed index, the MTC, shows that global catches are increasingly dominated by warmer-water species (Cheung et al. 2013c). The MTC is the weighted average of the preferred temperatures of the various fish and invertebrate species in the catch. The preferred temperature of each species (which is expected to be fairly stable in evolutionary time for most taxa) was predicted from overlaying the current distribution of the species, as mapped using the approach described in chapter 4 and sea surface temperature (SST). Therein, species that are distributed in warmer

waters will have higher preferred temperature and vice versa. Thus, for example, if the catch of a small country in the temperate zone is increasingly dominated by warmer-water species, its MTC would increase.

Using the *Sea Around Us* catch data, the MTC was calculated for all the Large Marine Ecosystems (LMEs) of the world from 1970 to 2006. After the effects of fishing and large-scale oceanographic variability were accounted for, global MTC increased at a rate of 0.19°C per decade between 1970 and 2006, and nontropical MTC increased at a rate of 0.23°C per decade. In tropical areas, MTC increased initially because of the reduction in the proportion of subtropical species catches but subsequently stabilized as scope for further “tropicalization” of communities became limited (figure 8.2). By showing that changes in MTC are significantly related to changes in SST across LMEs, Cheung et al. (2013c) showed conclusively that ocean warming has already affected global fisheries catch composition in the past four decades. This is now being verified at smaller scales (Keskin and Pauly 2014; Tsikliras and Stergiou 2014).

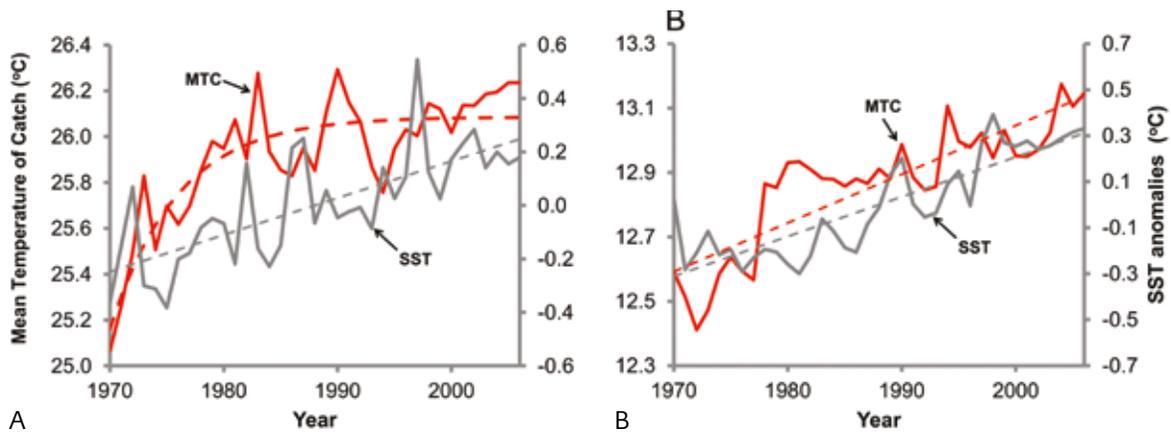


Figure 8.2. Observed trends in mean temperature of the catch (MTC) and sea surface temperature (SST) from (A) tropical and (B) nontropical Large Marine Ecosystems. (Adapted from Cheung et al. 2013c.)

Projecting Distribution Shifts of Exploited Species

Given that changes in the composition of fisheries catches are probably being driven by warming-induced biogeographic shifts, the next step was to investigate whether exploited species would continue to shift their biogeography in the future under climate change and how this would affect composition of the exploited species.

A DBEM was developed to project future distribution of more than 1,000 exploited fishes and invertebrates globally. The DBEM, described in Cheung et al. (2008b, 2009) and later in Cheung et al. (2011) and Fernandes et al. (2013), predicts a species' range (on a grid of about 180,000 cells of 30' latitude by 30' longitude representing the world ocean) based on the association between the modeled distributions and environmental variables. The current distribution of a taxon is predicted using a method developed by the *Sea Around Us* and described in chapter 4. Comparison with other species distribution modeling approaches that allow prediction of distributions for all the exploited species show that the DBEM performs equally well in terms of test statistics with observed occurrence data, for example, receiver operating characteristics (Jones et al. 2012). The DBEM infers preference profiles, defined as the suitability of different environmental conditions to the species covered, from their predicted current distributions, assuming that species' current

distributions match their environmental preference. Distinguishing features of the DBEM relative to other species distribution models include the explicit representation of spatial population dynamics (Cheung et al. 2008b), ecophysiology (Cheung et al. 2011) and, in a new version of DBEM, trophic interactions (Fernandes et al. 2013).

We applied the DBEM to project future distributions of 1,066 species of exploited fishes and invertebrates under climate change scenarios developed by the IPCC. These species include the overwhelming majority of the taxa whose population is large enough to generate catches that are reported at the species level in the global fisheries statistics of the Food and Agriculture Organization of the United Nations (FAO) and thus represent a very large sample of marine macrofauna. The rate of range shift and the intensity of species invasion and local extinction in the global ocean by 2050 relative to the 2000s were then calculated.

The resulting projections show that climate change leads, overall, to range shifts to higher latitude and deeper waters (figure 8.3), although some species display range shift in opposite directions as they follow local rather than large-scale climate change gradients (Cheung et al. 2009; Pinsky et al. 2013). Thus, numerous local extinctions in the subpolar regions, the tropics, and semienclosed seas can be expected. Simultaneously, species invasions are projected to be most frequent in the Arctic and the Southern Ocean. Jointly,

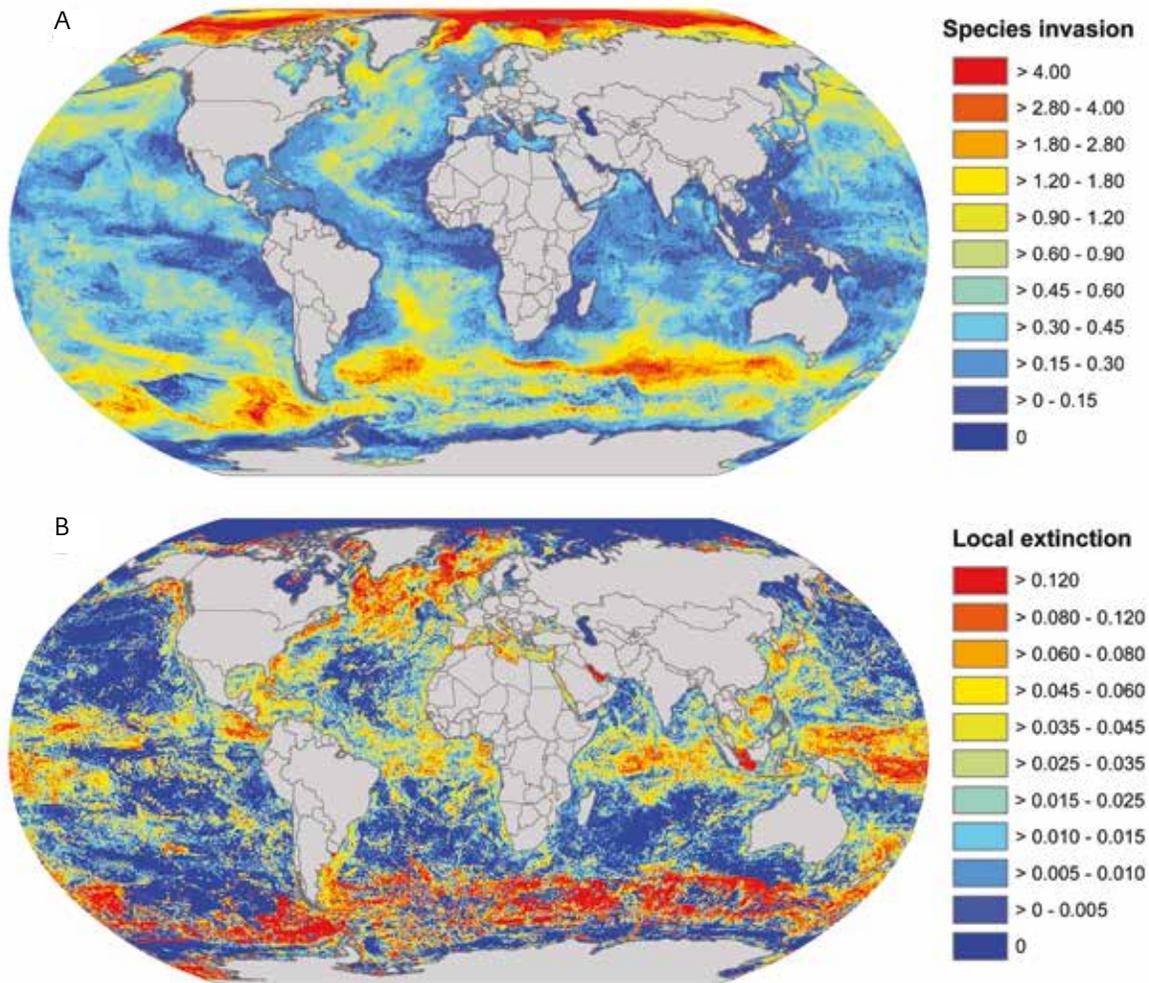


Figure 8.3. Projected intensity of (A) species invasion and (B) local extinctions by 2050 relative to 2000 (10-year average) under the IPCC Special Report on Emission Scenarios (SRES) A1B scenario. (Adapted from Cheung et al. 2009.)

these results, which are robust to the selection of species distribution models (Jones and Cheung 2015), suggest a dramatic turnover of current marine biodiversity, implying ecological disturbances that will massively disrupt the provision of ecosystem services. Moreover, these results support the hypothesis that the observed pattern of changes in species composition of catches, as indicated by the MTC introduced above, will continue in the future.

Relationship between NPP and Maximum Catch Potential

We developed an empirical relationship to predict maximum catch potential of a species based on NPP and the biogeography and ecology of marine water-breathers.

First, based on theories linking trophic energetics and allometric scaling of metabolism, a theoretical model was developed that relates the maximum catch potential of a species to its trophic level, geographic range, and mean NPP within the species' exploited range (Cheung et al. 2008a). Therein, the relationship between metabolic rate and body size of marine organisms, as quantified by an allometric equation and the energy available for a specific population of animals at trophic level (λ) in an ecosystem, was calculated based on a trophic transfer efficiency (TE) set at 10% (Pauly and Christensen 1995; Ware 2000). Finally, maximum sustainable yield (MSY) of the population was obtained from $rB_{\infty}/4$, where B_{∞} is the biomass at carrying capacity and r is the intrinsic rate of population increase, as

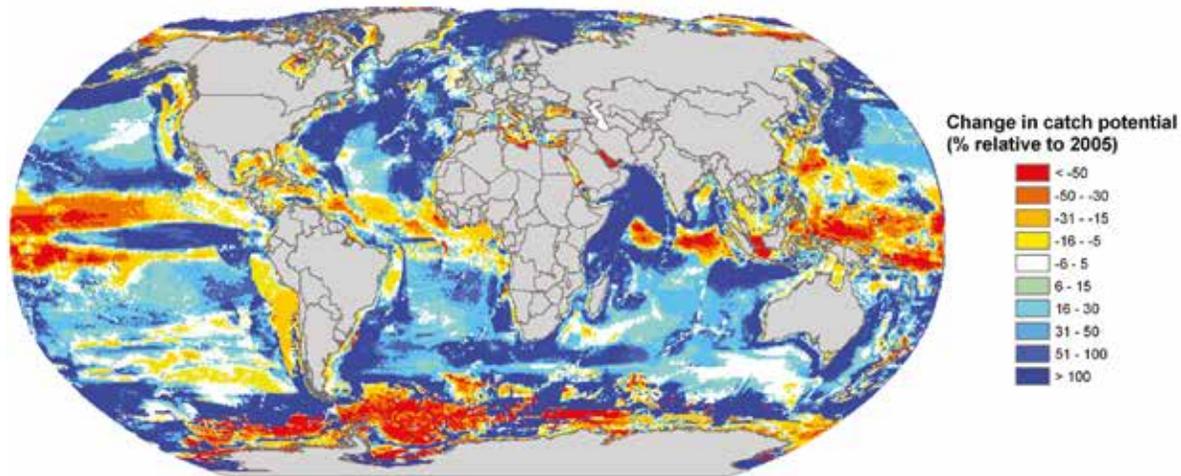


Figure 8.4. Projected change in maximum catch potential by 2050 relative to 2005 (10-year average) under the SRES A1B scenario. (Adapted from Cheung et al. 2010.)

implied in Schaefer (1954) and stated explicitly in Ricker (1975, p. 315) and Pauly (1984a, p. 140). This led to a theoretical relationship in which MSY was expressed as a function of NPP, λ , and TE.

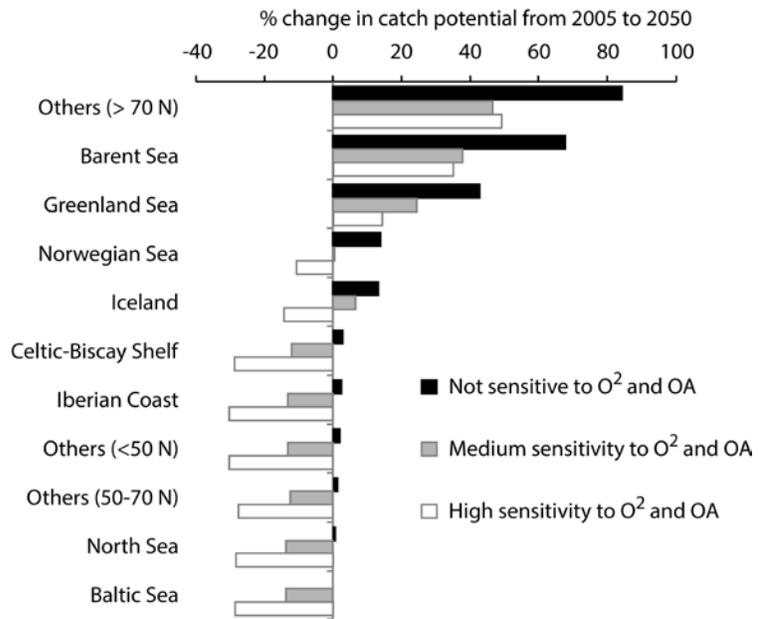
This model was fitted to catch, ecological, and biogeographical data from 1,000 species of exploited marine fish and invertebrate species. This led to an empirical relationship (i.e., a multiple regression) between these species' approximated maximum catch potential and their ecology and biogeography. Therein, maximum catch potentials were assumed to be approximated by the average of their five highest annual catches (from 1950 and 2006), nearly the same assumption as made by Srinivasan et al. (2010). Additional variables were included in the empirical model to correct for biases resulting from the uncertainty inherent in the original catch data. The empirical model had a high explanatory power ($R^2 = 0.703$), and the signs and magnitudes of the partial slopes agreed with theoretical expectations. Friedland et al. (2012) suggest that chlorophyll A concentration is a better predictor of catch potential, but reanalysis of Cheung et al. (2008a) using chlorophyll A concentration instead of NPP does not result in a significantly better model. Thus, the empirical model can be combined with the DBEM to project the impacts of

climate change on global marine fisheries, our next topic.

Projecting Future Catch Potential

By applying the empirical model described in the last section to projected future distributions derived from the DBEM, we could then estimate changes in global maximum catch potential for 1,066 species of exploited marine fish and invertebrates from 2005 to 2055 (Cheung et al. 2010). Species distribution projections were obtained from Sarmiento et al. (2004), working with the IPCC Special Report on Emission Scenarios (SRES) A1B and B2, along with projected changes in NPP. Once this information was incorporated into the empirical equation, it appeared that climate change would lead to a large-scale redistribution of global catch potential, with an average of 30%–70% increase in high-latitude regions and a drop of up to 40% in the tropics (figure 8.4). Moreover, predicted maximum catch potential declined in the lower-latitude margins of semienclosed seas, while it increased near the poleward tips of continental shelf margins, particularly in the Pacific Ocean. Among the twenty Exclusive Economic Zones (EEZs) with the highest landings according to the FAO, those with the highest increase in catch potential by 2055 belonged to Norway, Greenland, the United States (Alaska), and

Figure 8.5. Projected change in maximum catch potential in Large Marine Ecosystems in the northeast Atlantic by 2050 relative to 2005 (10-year average) under the SRES A2 scenario. OA, ocean acidification. (Adapted from Cheung et al. 2011.)



the Russian Far East. In contrast, the catch potential of Indonesia, the contiguous United States, Chile, and China have EEZs whose catch potential was predicted to decline most strongly. These results highlight the need to develop adaptation and mitigations policies for climate change impacts on fisheries, particularly in the tropics.

Because the above studies did not account for the effects of changes in ocean biogeochemistry and phytoplankton community structure, a version of the DBEM was developed that incorporated these factors and was used to project the distributions and maximum catch potentials of 120 species of exploited demersal fish and invertebrates in the northeast Atlantic (Cheung et al. 2011). Using projections from the U.S. National Oceanic and Atmospheric Administration’s Geophysical Fluid Dynamics Laboratory Earth System Model (ESM2.1) under the SRES A1B, we predicted ocean acidification and reduction in oxygen content to 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 that did not consider these factors (figure 8.5). Consideration of changes in 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.

Projecting Maximum Body Size of Fish and Invertebrates

Both theory and empirical observations support the hypothesis that warming and reduced oxygen will reduce body size of marine fishes (Pauly 1998a) and invertebrates (Pauly 1998b). Changes in temperature, oxygen content, and other ocean biogeochemical properties directly affect the ecophysiology of marine water-breathing organisms. Particularly, their physiological performance, including their growth rate and size at first reproduction, are strongly dependent on temperature and oxygen (Pauly 1981, 1984a, 1984b, 1998b, 2010; Pörtner and Farrell 2008). An organism’s low oxygen tolerance threshold varies across species, body size, and life stage and is highest for large organisms. The oxygen tolerance threshold is set by the capacity of an organism’s respiratory and circulatory systems to supply O₂ and cover demand. A corollary of the above is that distribution, growth, size at first reproduction, maximum body size, and survival of fishes are controlled

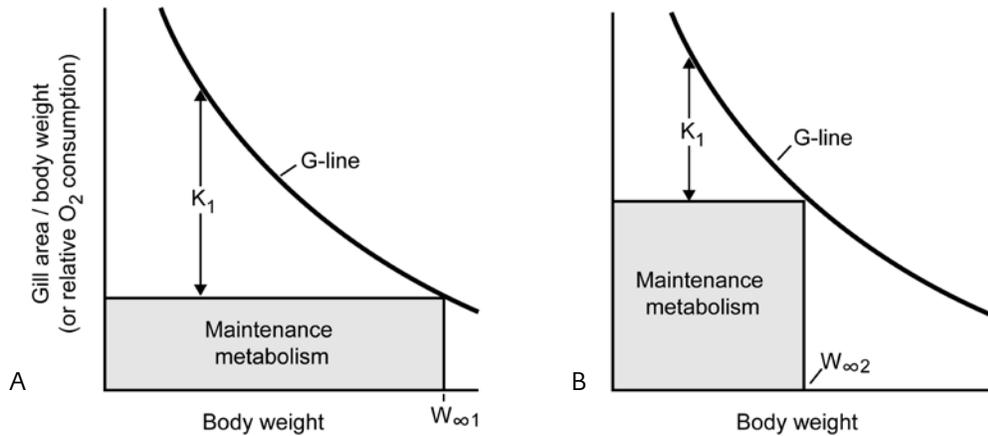


Figure 8.6. Diagram illustrating how maintenance metabolism determines asymptotic weight (W_{∞}), given a “G-line” defined by the growth of the gills relative to body weight, because at W_{∞} , relative gill area (and hence oxygen supply) is just enough for maintenance metabolism (shaded areas). (A) Fish exposed to a low level of stress (e.g., low temperature, abundant oxygen, abundant food). (B) Fish exposed to a higher level of stress (low oxygen concentration, high temperature, causing rapid denaturation of body protein, or low food density, requiring O_2 to be diverted to foraging rather than protein synthesis). Note that food conversion efficiency and hence also the scope for growth are directly related to the distance, in these graphs, between the G-line and the level of maintenance metabolism (see Pauly, 1981, 1984b, 2010). (Adapted from Pauly 2010.)

by the balance between oxygen supply and demand under different temperatures (Pütter 1920; Pauly 1981, 2010; Kolding et al. 2008). As fishes increase in size (weight), mass-specific oxygen demand increases more rapidly than oxygen supply (Pauly 1997). Thus, fish reach maximum body size when oxygen supply is balanced by oxygen demand (figure 8.6A). Moreover, the scope for aerobic respiration and growth decreases when size increases, that is, oxygen supply per unit body weight decreases (figure 8.6B). The decrease in food

conversion efficiency that this implies decreases the biomass production of fish and invertebrate populations.

However, although the interrelationships of temperature, oxygen, and growth in water-breathers are well established in the laboratory (Pauly 2010), the extent to which maximum body size of fishes would be affected by projected changes in temperature and oxygen level in the oceans remained unexplored. The DBEM was thus used to examine the integrated biological responses of more

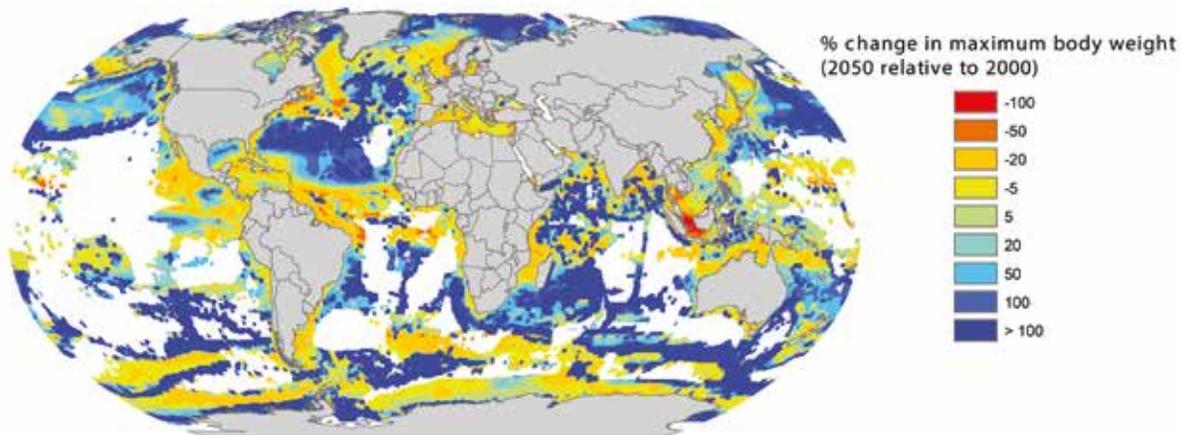


Figure 8.7. Projected change in maximum body weight of exploited fishes by 2050 relative to the 2000 period (20-year average) under the SRES A2 scenario. (Adapted from Cheung et al. 2013b.)

than 600 species of marine fishes to changes in distribution, abundance, and body size (Cheung et al. 2013a, 2013b), based on explicit representations of ecophysiology, dispersal, distribution, and population dynamics. The result was that assemblage-averaged maximum body weight is expected to decline by 14%–24% globally from 2000 to 2050 under a high-emission scenario (figure 8.7). The projected magnitude of decrease in body size is consistent with experimental (Forster et al. 2012; Cheung et al. 2013b) and field observations (Baudron et al. 2014). About half of this shrinkage is caused by changes in distribution and abundance, the remainder by changes in physiological performance. The tropical and intermediate latitudinal areas will be heavily affected, with an average reduction of more than 20%. Decreases in growth and body size should reduce the biomass production of fish populations, and hence fishery catches, and potentially alter trophic interactions.

CONCLUSION

In their series of studies, the authors and their collaborators detected a signature of ocean warming on global fisheries in the last four decades, and they also projected that such changes would continue over the next 40 years, leading to strong species turnover, redistribution of fisheries catch potential, and decreases in the maximum body sizes of exploited species of fishes and invertebrates. Results from these global-scale analyses highlighted the inequity of climate change impacts to different regions of the world. Specifically, the tropics will be affected by a high rate of local species extinction, a decrease in catch potential, and a larger decrease in body size of fishes. Many tropical communities are highly dependent on local fisheries for food and livelihood (e.g., Zeller et al. 2015), but their economic and societal capacity to adapt to climate change impacts

on fisheries is often low. Thus, tropical fisheries are highly vulnerable to climate change, although tropical countries contribute little to the greenhouse gas emissions that cause climate change.

Future studies should address additional challenges to detecting, attributing, and projecting climate change and ocean acidification impacts on marine fisheries. First, the adaptive scope of exploited marine species and their fishers to impacts from climate change and ocean acidification should be evaluated. Second, different modeling approaches in projecting future seafood production under climate change and ocean acidification should be tested, to assess the utility of these approaches and quantify the level of uncertainty associated with the model projections. Third, the effects of multiple stressors (i.e., climate and nonclimate) and their interactions must be explored. In addition, more regional studies to downscale the global analyses must be conducted, through which the weaknesses associated with the coarse projections of ocean properties from global circulation models can be better addressed. Such regional-scale analyses are more useful for informing national fisheries and coastal management agencies, which will both be challenged by global warming in coming years.

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NOTE

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