

Potential impacts of climate change on Northeast Pacific marine foodwebs and fisheries

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Although there has been considerable research on the impacts of individual changes in water temperature, carbonate chemistry, and other variables on species, cumulative impacts of these effects have rarely been studied. Here, we simulate changes in (i) primary productivity, (ii) species range shifts, (iii) zooplankton community size structure, (iv) ocean acidification, and (v) ocean deoxygenation both individually and together using five Ecopath with Ecosim models of the northeast Pacific Ocean. We used a standardized method to represent climate effects that relied on time-series forcing functions: annual multipliers of species productivity. We focused on changes in fisheries landings, biomass, and ecosystem characteristics (diversity and trophic indices). Fisheries landings generally declined in response to cumulative effects and often to a greater degree than would have been predicted based on individual climate effects, indicating possible synergies. Total biomass of fished and unfished functional groups displayed a decline, though unfished groups were affected less negatively. Some functional groups (e.g. pelagic and demersal invertebrates) were predicted to respond favourably under cumulative effects in some regions. The challenge of predicting climate change impacts must be met if we are to adapt and manage rapidly changing marine ecosystems in the 21st century.

Keywords: Alaska, British Columbia, California, climate change, dissolved oxygen, Ecopath, Ecosim, ocean acidification, primary production, range shift, sea surface temperature.

Introduction

Human activities since the industrial revolution have changed the Earth's physical environment in a variety of ways. Over this period, air and ocean temperature have increased and ocean pH and dissolved oxygen levels have decreased (Sabine *et al.*, 2004; Byrne *et al.*, 2010). There is strong evidence that anthropogenic emissions of greenhouse gases have contributed to these changes and the rate of emissions is projected to increase (IPCC, 2007). Therefore, global climate change could be accelerated with adverse and prolonged consequences for the Earth's biota (Cox *et al.*, 2000). Such climatological changes have implications for the conservation of biodiversity and for the ecosystem services on which humans rely (Rappport *et al.*, 1998). Although uncertainty is high in both the extent of climate change and the nature of its impacts on species, we are obliged to try to understand better the potential impacts on populations and ecosystems, so that we can adapt to changing conditions and mitigate impacts (Lawler *et al.*, 2010).

Impacts of climate change on marine communities will be determined by the direct response of species to changing physical,

biological, and chemical conditions and by indirect responses because of species interactions at both micro- and macroecological scales (Araújo and Luoto, 2007; Gilman *et al.*, 2010; Walther, 2010). Understanding how these impacts at the species level will scale up to the community level requires modelling tools that can simulate important species interactions, such as foodweb effects. Differential response of species in a foodweb to an altered environment might change the balance of predators to prey or producers to consumers in a way that drives some species towards extinction or results in a previously rare species becoming more dominant in the community. Such changes clearly have the potential of affecting fisheries and other human interests.

In this article, we take a cursory look at some of the potential implications of climate change on the marine foodweb structure in North Pacific shelf ecosystems. Using simulations from five Ecopath with Ecosim (EwE) foodweb models, offering continuous geographic coverage from Cape Mendocino, CA, to Yakutat Bay, AK (latitude 40°26'N to 59°45'N), we analyse the marine foodweb responses to changing climate with respect to five

major aspects of climate change. They are changes in the annual mean level of primary production, temperature-induced latitudinal range shifts of fish and invertebrates, and changes in the size structure of zooplankton communities, ocean acidification, and ocean deoxygenation. We impose the five climate change effects singly to explore the response of the ecosystem and in combination to determine whether imposing the effects simultaneously produces cumulative or synergistic impacts. We opt to focus on results that are most relevant to resource managers: fisheries yields, biomass of important fished and unfished functional groups, and ecosystem diversity and trophic indices. Although our results are quantitative, they are best interpreted in a qualitative way (e.g. the types of community response that occur, not their magnitude), given the substantial process and model uncertainty inherent in our projections.

Material and methods

Study area

We focused our analyses on five shelf ecosystems of the northeast Pacific Ocean: Prince William Sound (PWS: Okey and Pauly, 1999), southeast Alaska (SEA: Guénette, 2005), northern British Columbia (NBC: Ainsworth et al., 2008), west coast of Vancouver Island (WCVI: Martell, 2002), and the northern California Current (NCC: Field, 2004; Table 1). A useful review of these and other EwE models of the Northeast Pacific is available in Guénette et al. (2007). Together, the models offer almost continuous spatial coverage of the North Pacific eastern boundary current system (Figure 1). These ecosystems are characterized by broadly similar species assemblages, and they share a subset of dominant environmental drivers (e.g. oceanic currents, wind-driven upwelling) because of their geographic proximity. Commonalities in their reactions will help generalize ecosystem impacts of climate change, whereas discrepancies could highlight the role of biogeography in determining outcomes (see Supplementary Table S1 for a description of each model and information on functional group structures).

Ecopath with Ecosim

EwE is a trophodynamic ecosystem model that summarizes living and non-living components of the ecosystem into functional groups: groups of species aggregated according to life-history and niche characteristics (Christensen and Pauly, 1992; Christensen et al., 2005). The model acts as a thermodynamic accounting system, tracking the flow of energy between groups (biomass pools) according to a diet matrix, while accounting for energy lost in respiration, emigration, and decomposition. Ecopath

represents a static “snapshot” of the ecosystem rooted in two basic assumptions: (i) mass balance within functional groups and (ii) conservation of energy between groups (see Christensen and Pauly, 1992, for equations). Ecopath provides the initialization state for Ecosim, a time-dynamic simulator that follows changes in functional group biomass according to Equation (1) (for primary producers) and Equation (2) (for consumers).

$$\frac{dB_i}{dt} = cB_i \left(\frac{P}{B} \right)_i EE_i - \sum_{j=1}^n f(B_i, B_j) - M_i B_i \text{ and} \quad (1)$$

$$\frac{dB_j}{dt} = cg_j \sum_{i=1}^n f(B_j, B_i) - \sum_{j=1}^n f(B_i, B_j) + I_j - B_j(M_j + F_j + E_j). \quad (2)$$

In these equations, B_i and B_j are the biomasses of prey (i) and predator (j), respectively; P the production rate; EE the ecotrophic efficiency; $f()$ a functional relationship used to predict consumption rates; I the immigration rate out of the ecosystem; M and F the natural mortality and fishing mortality, respectively; E the emigration; g the growth efficiency; and n the number of functional groups. For more information, refer to Christensen and Pauly (1992) and Walters et al. (1997). The scalar c is used in this article to introduce forcing functions (see below).

Standardized simulation of climate change impacts

Different climate change effects are predicted to influence marine species in different ways. For instance, changing physical conditions (sea surface temperature, currents, and salinity) will alter the biomass abundance of species in our study areas (Cheung et al., 2009), whereas ocean acidification is likely to act through different physiological pathways, such as calcification, reproduction, photosynthesis, and nitrogen fixation, depending on the organism (Doney et al., 2009). Because of the idiosyncratic nature of alternative climate change impacts and because Ecosim (version 5.1) offers a limited set of options for introducing climate change impacts to foodwebs, we decided to standardize the application of climate effects in the model foodwebs. Though we explain the details of how the five climate change impacts were applied in the following sections, our approach generally was to modify the scalar c in Equations (1) and (2) to achieve a change in the production rates of functional groups matching the assumed climate effects. To do so, we manipulated forcing functions affecting the predator search rates. This approach makes consumers into super predators (or inferior predators) allowing them to consume more (or less) prey per unit energy spent searching,

Table 1. Five EwE models of the northeast Pacific used in this study.

Model	Number of living groups	Number of age-structured groups	Number of fishing gears	Fitted to time-series data	Approximate area	Reference
Northern British Columbia	53	11	17	Y	70 000 km ²	Ainsworth et al. (2008)
Northern California Current	65	4	7	Y	70 000 km ²	Field (2004)
Prince William Sound	48	4	3	N	9 000 km ²	Okey and Pauly (1999)
Southeast Alaska	40	2	6	Y	120 000 km ²	Guénette (2005)
West Coast Vancouver Island	15	3	3	N	17 000 km ²	Martell (2002)

Further information on model design is available in the Supplementary material.

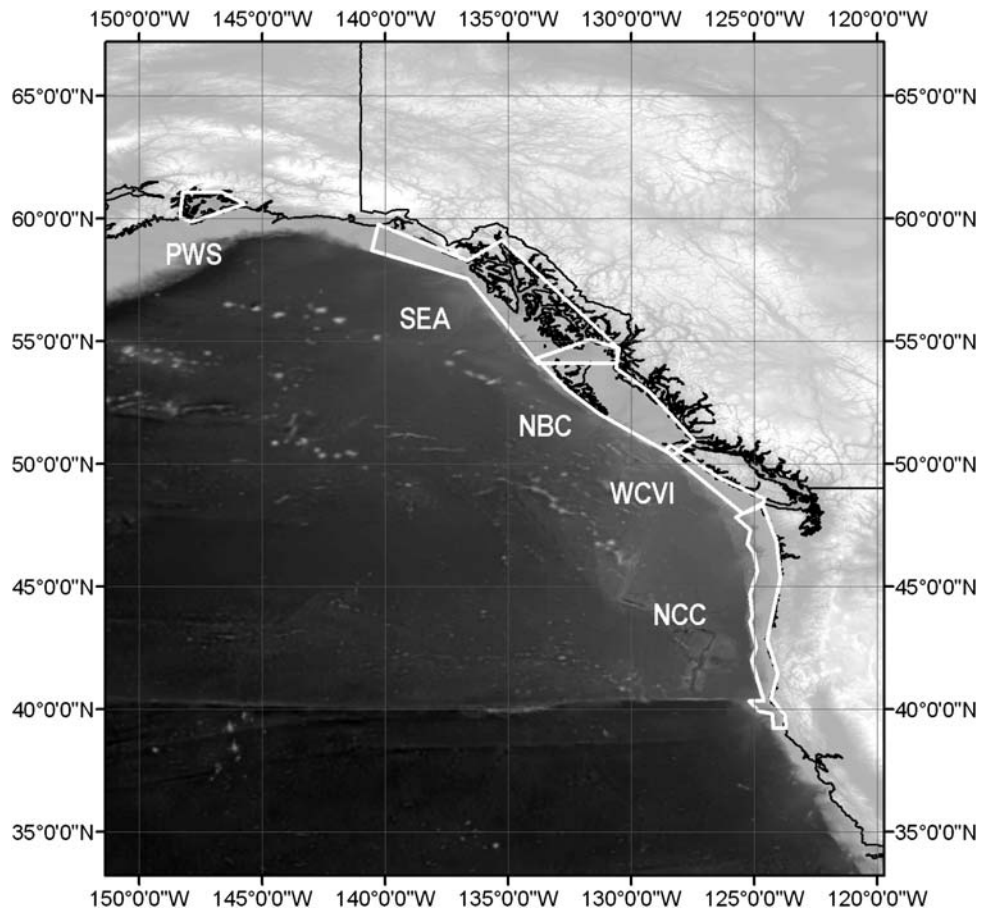


Figure 1. Coverage of five EwE models of the Northeast Pacific. Prince William Sound (PWS); southeast Alaska (SEA), northern British Columbia (NBC), west coast Vancouver Island (WCVI), northern California Current (NCC).

consequently increasing (or decreasing) their biological productivity. Applied to primary producers, the term directly modifies biological production. Forcing production in this way is a convenient, but basic, method to simulate complex climate effects; the implications of this simplification will be discussed below. The forcing functions for all simulations are presented in Supplementary Figure S1.

Simulation overview

Simulation procedures for each of the five climate effects are described below. The model simulation length used was 50 years, from 2010 to 2060. We assumed that each of the models’ base states was representative of 2010. As published, the models represented a range of periods from 1997 (PWS) to 2004 (NCC), though they each consist of data that span several years. To address uncertainty inherent in predictions about climate change and to evaluate the sensitivity of the EwE models to different magnitudes of impacts, we divided the simulations into three scenarios representing conservative, moderate, and substantial climate effect strengths. The moderate scenario represented the best available estimate of changes in functional group productivity, whereas the conservative and substantial scenarios assumed productivities 50% less than and greater than the moderate scenario, respectively. Table 2 summarizes which functional groups were affected by each of the five climate change effects in our models

Table 2. Functional groups affected by climate change effects and direction of impact on group productivity used in forcing functions.

Climate change effect	Functional groups affected	Impact on group productivity
Primary productivity	Phytoplankton	Increase or decrease
Zooplankton community structure	Zooplankton	Increase or decrease
Range shifts	Fished functional groups	Increase or decrease
Ocean acidification	Crustaceans (esp. shrimp), echinoderms, molluscs, euphausiids	Decrease
Ocean deoxygenation	All species, except birds, mammals, primary producers	Decrease

The direction and magnitude of these effects are provided in Supplementary Figure S1.

(chosen based on a literature review). We acknowledge that we did not attempt to simulate all the potential effects of climate change on all affected species, but chose effects and species for which there existed ample evidence to infer productivity changes. We present simulation results for fisheries landings, biomass of targeted and non-targeted functional groups, and

ecosystem characteristics (diversity and trophic indices), collating relevant functional groups in the various EwE models into common categories (Supplementary Tables S2 and S3).

Impacts of primary productivity changes

We implemented changes in primary productivity based on outputs from the Geophysical Fluid Dynamics Laboratory (GFDL) Earth System Model (ESM2.1; Supplementary Figure S2), which includes the Tracers of Ocean Phytoplankton with Allometric Zooplankton (TOPAZ) model of ocean ecosystems and biogeochemical cycles, in addition to atmospheric and terrestrial components (see Supplementary material for details). Simulations were based on the IPCC AR4 protocols (Special Report on Emission Scenarios, A1B scenario).

Changes in mean annual primary production for the model regions from year 2010 to 2060 were extracted from the ESM2.1. The predicted change in phytoplankton biomass was re-created in EwE by adding a long-term forcing function on phytoplankton groups that was proportional in each year to the predicted primary production trend from the ESM2.1 model. The magnitude of the forcing function was iteratively adjusted to achieve the predicted amplitude of change in phytoplankton biomass predicted by the ESM2.1 model. The forcing functions were applied to phytoplankton groups in all models (Table 2, Supplementary Table S1). Note that the EwE primary production simulations conducted in this study are similar in principle and methodology to those conducted for Australian ecosystems by [Brown et al. \(2010\)](#).

Impacts of biogeographic range shifts

One of the major expected effects of climate change is a shift in the ranges occupied by species ([Perry et al., 2005](#)). We simulated these effects for fished fish and invertebrates in our study areas using output from a dynamic bioclimatic envelope model ([Cheung et al., 2009](#)). Our focus was limited to exploited species, because these are better studied than non-exploited species and have sufficient distributional and biological data to support the envelope model. Because exploited species tend to have high biomass, we capture a large portion of the marine metazoan biomass ([Cheung et al., 2009](#)). Changes in total relative abundance of the species found in three of the study areas (SEA, NBC, and NCC) from 2010 to 2060 relative to the 10-year average from 2001 to 2010 were extracted from the projections of [Cheung et al. \(2009\)](#), expressed as relative abundance on a $0.5^\circ \times 0.5^\circ$ grid of the world's oceans. Data for the other systems were unavailable. This model simulates changes in the spatial distribution of relative abundance of marine fish and invertebrates based on species' preferences to environmental conditions (temperature, salinity, bathymetry, association with habitats, etc.). Changes in these ocean conditions, as projected by the NOAA/GFDL coupled model 2.1, then affect the carrying capacity for the species according to the inferred environmental preferences. The model also explicitly accounts for movement of adults and dispersal of larvae via ocean currents to suitable habitats (see [Cheung et al., 2009](#), for details).

We calculated the average change in relative abundance of species belonging to fish and benthic macroinvertebrate functional groups of each model (NBC model, 20 groups; NCC model, 31 groups; SEA model, 19 groups). Forcing functions [input as values for c in Equations (1) and (2)] were developed iteratively until the biomass change projected by the bioclimatic envelope model was achieved in EwE. During this process, all other

functional groups (except for the group undergoing range shift) were assumed to remain at constant biomass levels.

Impacts of zooplankton community size structure changes

Rising ocean temperatures are expected to affect the species composition of phytoplankton, increasing the relative abundance of small-bodied phytoplankton relative to large-bodied ones ([Morán et al., 2009](#)). The shift in size structure could have a critical impact on foodweb structure, if specialized or gape-limited predators are affected by changing availability of their preferred prey. We therefore assumed that shifts in phytoplankton size classes correspond to equivalent shifts in zooplankton, which the northeast Pacific EwE models disaggregate into size classes. For body size calculations, we assumed that euphausiids and copepods were representative of the body size for large and small zooplankton groups, respectively, because these are the dominant taxa in the region ([Mackas and Tsuda, 1999](#)). Implicitly, the models include other zooplankton species, but we have assumed that these will vary in abundance like other similarly sized organisms.

We used an empirical relationship described by [Bouman et al. \(2003\)](#) to predict the change in the relative abundance of large and small zooplankton in our study areas between 2010 and 2060 because of changing ocean temperature (driven by GFDL coupled model 2.1 A1B scenario; Supplementary Figure S3, Supplementary Table S4). We assumed that the relative abundance of large zooplankton changes by a factor X_L [Equation (3)], whereas that of small zooplankton will change by a factor X_S [Equation (4)].

$$X_L = \frac{(L + S)(\theta - C)}{L(E - C)} \text{ and} \quad (3)$$

$$X_S = \frac{(L + S) - X_L}{S}. \quad (4)$$

In these equations, L and S are the biomasses of large and small zooplankton pools, respectively, θ the mean equivalent spherical diameter in 2060 (Supplementary Table S4), E the euphausiid body size (assumed 0.002 m), and C the copepod body size (0.0002 m). The purpose of Equations (3) and (4) is to ensure that the total biomass pool of zooplankton remains constant as mean cell diameter changes (i.e. as the relative proportion of small and large zooplankton pool changes). We are therefore using a reductionist approach to study the effects of changing community size composition independently of changes in total zooplankton biomass (a more realistic scenario is achieved under combined impacts). Calculations imply that individual zooplankton cell diameters will decrease from ~ 1 to 12% by 2060, depending on the study area (Supplementary Table S4), with NCC experiencing the greatest decrease in mean size because of its wide temperature shift and PWS experiencing the smallest. Using this method, the biomass pool of large zooplankton in NCC is predicted to decrease by 15% by 2060. For comparison, the change observed in this region since the 1950s constitutes an 8% decrease ([Mullin et al., 2003](#)). The slopes of monotonic, linear production forcing functions were adjusted iteratively until we achieved the change in small and large zooplankton biomasses specified in Supplementary Table S4.

Impacts of ocean acidification

Ocean carbon chemistry is changing in response to increasing concentrations of atmospheric carbon dioxide (Caldeira and Wickett, 2003; Feely *et al.*, 2004). Higher atmospheric carbon dioxide levels cause dissolved carbon dioxide and bicarbonate ions to increase and seawater pH and bicarbonate ions to decrease, a phenomenon collectively called ocean acidification (Raven *et al.*, 2005). Changes in seawater carbon chemistry can affect the marine biota through a variety of physiological and physical processes. For example, acidification alters the saturation state for calcium carbonate compounds, affecting calcification rates (Feely *et al.*, 2004, 2008). Since the industrial revolution, mean ocean pH has decreased to the lowest level in 20 million years and the trend is expected to continue (Caldeira and Wickett, 2003; Feely *et al.*, 2004; Sabine *et al.*, 2004; Orr *et al.*, 2005). Within this century, surface waters corrosive to aragonite are expected to occur first at high latitudes because of an inverse relationship with temperature (Orr *et al.*, 2005; Byrne *et al.*, 2010), making the northeast Pacific vulnerable. In addition, because of its position at the end of the ocean's global conveyor belt, northeast Pacific waters at depth have not recently interacted with the atmosphere, so contain some of the world's lowest pH levels, resulting from accumulated carbon dioxide from biotic respiration (Feely *et al.*, 2008).

There is little information on the impacts of ocean acidification for many taxa. As such, predictions here are limited to groups on which there is published research. Moreover, data produced in the laboratory are not easily transferred to the EwE framework. In addition, the response to ocean acidification is variable among species, including those that are closely related, requiring caution when generalizing data from one species to predict the response of another (Miller *et al.*, 2009). Finally, models of the progression of ocean acidification into the future do not capture accurately the carbon chemistry of coastal waters, because of uncertainties regarding the land–sea interface (Feely *et al.*, 2010). For these three reasons, we chose the standardized approach described earlier to implement changes in productivity.

The response of each functional group to climate change was decided using information on the species composition of functional groups and, when available, their relative biomass, and a review of the literature of the biological impacts of ocean acidification (D. S. Busch, unpublished manuscript, NWFSC-NOAA, 2725 Montlake Blvd E., Seattle, WA 98112, USA, e-mail: shallin.busch@noaa.gov). We categorized whether each functional group's productivity was likely to respond to ocean acidification or not, and if so, we assigned an expected effect size (small, medium, or large) based on the literature review (D. S. Busch, unpublished manuscript). We acknowledge that the magnitudes of these effects are guesses. Taxa predicted to be affected included crustaceans (especially shrimp), echinoderms, molluscs, and euphausiids (Supplementary Table S5). Effect strengths for conservative, moderate, and substantial scenarios are designated in Table 3; the values were chosen arbitrarily to capture a broad range of potential species responses. Similar to Brown *et al.* (2010), we implemented linear changes in the production rates.

Impacts of ocean deoxygenation

Increasing ocean temperature and upper water column stratification is expected to decrease the dissolved oxygen in the global ocean by between 1 and 7% this century and such declines

Table 3. Change in productivity of functional groups after 50 years for dissolved oxygen and ocean acidification scenarios.

Organism susceptibility	Effect size		
	Conservative (%)	Moderate (%)	Substantial (%)
Deoxygenation effect			
Small	−4	−7	−11
Medium	−11	−22	−33
Large	−18	−37	−55
Ocean acidification effect			
Small	−5	−10	−15
Medium	−15	−30	−45
Large	−25	−50	−75

These values were used as relative endpoints of linear functions forcing affecting productivity. Small, medium, and large effects sizes (vertical axis) were assigned to functional groups depending on the expected level of impact from climate change (see Supplementary Tables S5 and S6 for assignments). Conservative, moderate, and substantial effect strengths (horizontal axis) were used to parenthesis uncertainty. Values for ocean deoxygenation were based on a 22% benchmark from Whitney *et al.* (2007; see text); values for acidification were based on a previous literature review (D. S. Busch, unpublished manuscript, contact: shallin.busch@noaa.gov).

could continue for millennia (Sarmiento *et al.*, 1998; Keeling *et al.*, 2010). These changes will not manifest evenly, and the North Pacific Ocean stands out as an area that has already experienced rapid deoxygenation during the past 50 years (i.e. 22% decrease; Whitney *et al.*, 2007; Keeling *et al.*, 2010). Expansion of oxygen minimum zones (OMZs) is predicted wherever they occur throughout the world's oceans (Whitney *et al.*, 2007), and shoaling of OMZs up and onto the continental shelf is becoming a conspicuous new phenomenon along the west coast of North America (Grantham *et al.*, 2004; Whitney *et al.*, 2007). Only ~2% of the world's continental margins are exposed to hypoxia from OMZs, and the eastern subtropical North Pacific is among them (Helly and Levin, 2004).

The sensitivity and susceptibility of biota to deoxygenation varies considerably among taxa (Vaquer-Sunyer and Duarte, 2008) and sublethal impacts, such as avoidance or increases in predation vulnerability, can happen at oxygen concentrations only slightly lower than existing concentrations. That said, most marine taxa appear to be insensitive to variations in dissolved oxygen above particular thresholds of sublethal and lethal impacts (Vaquer-Sunyer and Duarte, 2008; Keeling *et al.*, 2010). Therefore, as with ocean acidification, the biological and ecological impacts of deoxygenation can be extremely complex and difficult to estimate (Portner and Knust, 2007).

In our model simulations, we assumed a 1:1 relationship between predicted changes in dissolved oxygen concentration (e.g. from Whitney *et al.*, 2007) and changes in productivity [c in Equations (1) and (2)] of consumer functional groups that do not breathe air. We designated effect strength for each functional group as small, medium, or large based on the reviewed literature (Supplementary Table S6). Though the effect strengths were based on empirical observations by Whitney *et al.* (2007) in the Northeast Pacific, we acknowledge that the magnitudes of these effects are guesses. Similar to Brown *et al.* (2010), changes in the production rates of affected functional groups over 50-year simulations were assumed to be linear. Effect strengths used for conservative, moderate, and substantial scenarios are designated in Table 3.

Combined climate change impacts

In addition to simulating the five climate change effects individually, we evaluated the combined impacts of all climate effects operating simultaneously. Determining how these different impacts interact to influence marine species is not a trivial task. Indeed, both additive and non-additive effects are likely to be common (Darling and Cote, 2008). We assumed that the five climate change effects would act additively (except where group productivity would fall below 0%). Note that the assumption of additive effects on individual species does not pre-empt the possibility of non-additive effects on aggregate properties of the foodwebs (e.g. fisheries landings, diversity). For instance, if simulated shifts in biogeographic ranges act on a subset of species distinct from those influenced by ocean acidification and the two subsets of species interact trophically, the combined impacts on fisheries landings, functional groups, and ecosystem metrics like diversity could be synergistic or antagonistic. Spatial domains of two of these models (WCVI and PWS) are too small relative to the resolution of the range shift projection, rendering the range shift projection unrepresentative of the two modelled systems. We therefore present results from the combined impacts of all five climate effect for three models (NCC, NBC, and SEA) and from the combined impacts of four climate effects (PP, PCS, OA, and OD) for all five models.

Responses of fisheries and foodwebs

We assessed impacts of the five climate change effects on fisheries landings, the biomass of fished and unfished functional groups, and ecosystem characteristics. In particular, we analysed the difference in ecosystem state in the 50th year of the EwE simulations among the different scenarios (usually, this represented an equilibrium condition). Fishing effort was held constant at current levels (model baseline) for all simulations. We present these results in two ways. First, we describe the regional response to climate change, calculated as the average response across the five models and provide a comparison of the relative effects of each impact. Second, we describe the responses within each model domain to examine geographic variation. Note that fishing effort was held constant at current levels (model baseline) for all simulations. Kite diagrams are used to compare results across the study areas; these provide a summary of important changes in ecosystem structure (Garcia and Staples, 2000; Shin et al., 2010). Each axis corresponds to a particular ecosystem component, and axes are scaled such that a value of 1 indicates no difference from the baseline simulation, a value of <1 indicates a reduction in the ecosystem component relative to the baseline simulation, and a value of >1 indicates an increase in the ecosystem component relative to the baseline simulation. The predicted range of outcomes (because of uncertainty in effect strength) is denoted by the shaded area.

Response variables include landings and biomass for composite species groups (i.e. groups of functional groups, combined to facilitate comparison between models), ecosystem-scale biodiversity [Shannon's entropy function: Shannon and Weaver (1949) and Kempton's Q index adapted for ecosystem models: Ainsworth and Pitcher (2006)], and trophic indices (mean trophic level of landings and mean trophic level of the ecosystem). These indices are defined in the Supplementary Table S7.

Note that because the number of species (functional groups) in the EwE models is fixed, the Shannon diversity index primarily reflects changes in evenness, whereas Kempton's Q index tracks

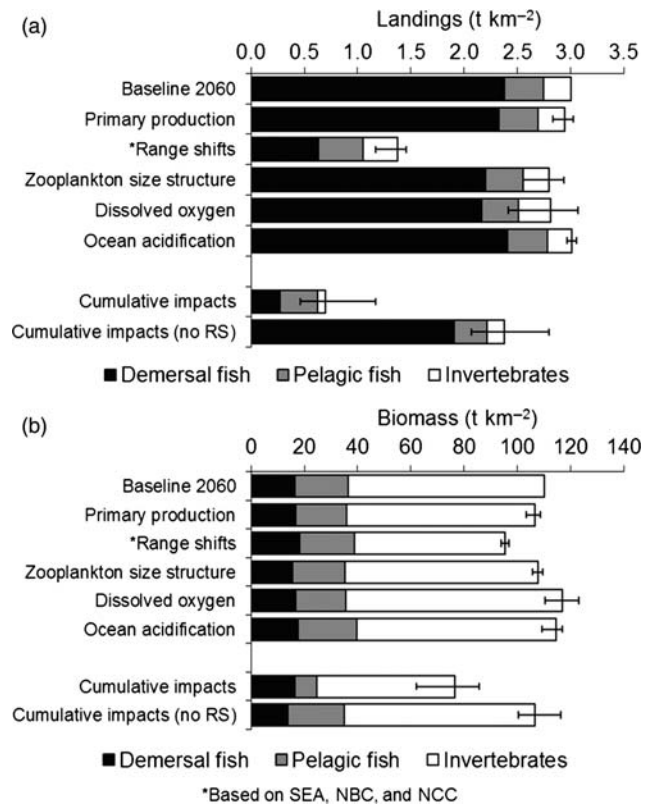


Figure 2. Projected fisheries landings and biomass in 2060 under climate change scenarios. Values are averaged across all EwE models, except for range shift (RS), which is averaged over SEA, NBC, and NCC. Baseline indicates projected landings or biomass in 2060 without climate change. Error bars indicate the range of outputs predicted using three effect sizes (conservative, moderate, and substantial); bar indicates median. (a) Fisheries landings; present-day total catch (ca. 2010) is $3.51\ t\ km^{-2}$. Constant harvest rate is assumed. (b) Biomass; present-day total biomass (ca. 2010) is $111.5\ t\ km^{-2}$.

changes in both evenness and richness (the latter measured as the amount of biomass in the foodweb; Ainsworth and Pitcher, 2006). Kempton's Q index, adapted for ecosystem models, is based on the slope of the cumulative species log-abundance curve. It is reasonably invariant to model structure, because each functional group has the potential of affecting only one point on the log-abundance curve; therefore, changing the overall slope only slightly (Ainsworth and Pitcher, 2006). The Shannon index is more sensitive to the aggregation style used by the model. However, we interpret the Shannon index only by considering changes relative to a base state (i.e. without climate effects). Functional group aggregation style can also influence the behaviour of models (Fulton et al., 2003). Because the models used here were developed for a variety of purposes and employ different aggregation styles (Supplementary Table S1), agreement among them lends credibility to findings.

Results

Regional responses to climate change impacts: fisheries landings

When we treat all the regional study areas as a single North Pacific unit (averaging results across models), individual climate effects affect fisheries landings minimally (Figure 2a). Primary

production, zooplankton size structure, dissolved oxygen, and ocean acidification effects, acting independently, reduce catch by no more than 7% relative to the control scenario without climate effects (baseline 2060), affecting pelagic fisheries, demersal fisheries, and invertebrate fisheries to similar degrees. However, the cumulative impacts of these effects reduced landings 20% relative to the expected landings in 2060. When we factored in the effects of range shifts, the impacts of climate change on fisheries landings increased considerably. Considered in isolation, range shifts account for a 54% reduction in fisheries landings. The cumulative impacts of all climate effects together (including range shifts) reduce landings by 77% under the moderate climate effect strength scenario and by as much as 85% under the severe climate effect strength scenario. Range shifts negatively affected the pelagic fisheries the most, such as for salmon and herring (see Supplementary Table S2 for groups). Because range shifts feature heavily in the cumulative impacts, we can expect a redistribution of fisheries catch in addition to any changes in the total amount. This could result in local economic impacts where stocks migrate across political boundaries.

Regional responses to climate change impacts: species biomass

Ecosystem biomass did not respond strongly to changes in primary production, zooplankton community size structure, dissolved oxygen, or ocean acidification when these effects were applied individually (see Supplementary Table S3 for groups). At this aggregate scale, none of these effects perturbed the ecosystem far from the condition expected without climate change; in fact, small relative increases in biomass might be possible in some cases (Figure 2b). In contrast, cumulative impacts caused a substantial (30%) reduction in total ecosystem biomass. Using this simple metric, cumulative impacts, including range shifts, accounted for a reduction in ecosystem biomass greater than the sum of all the reductions caused by constituent effects. This suggests that synergies can occur through foodweb dynamics. As with changes in fisheries landings, only range shifts had a clear impact on ecosystem biomass, reducing demersal invertebrate biomass by 23%, but increasing demersal fish biomass by 12%.

Fished species were affected by climate change more severely than unfished species (compare Figure 2a and b). The baseline simulation without climate change impacts predicted that fished species would constitute 2.7% of total ecosystem biomass in 2060. Factoring in range shifts, the biomass of exploited species was expected to constitute only half that amount (~1.4%) and still less under the cumulative impacts scenario that included range shifts (0.9%).

Regional responses to climate change impacts: ecosystem attributes

Of the individual climate effects, only range shifts produced a noticeable change in ecosystem biodiversity (Figure 3a). Shannon's diversity index, measuring species evenness, increased slightly with climate change impacts. However, increases in species evenness can reflect a decline in fished functional groups, which tend to have high biomass. Kempton's *Q* index also increased in response to climate change impacts and it is less sensitive to relative changes in biomass than Shannon's diversity index. The increase in Kempton's *Q* index we observed in this study under range shifts can be traced back to marked increases in squid and non-fished species (see Supplementary Table S7).

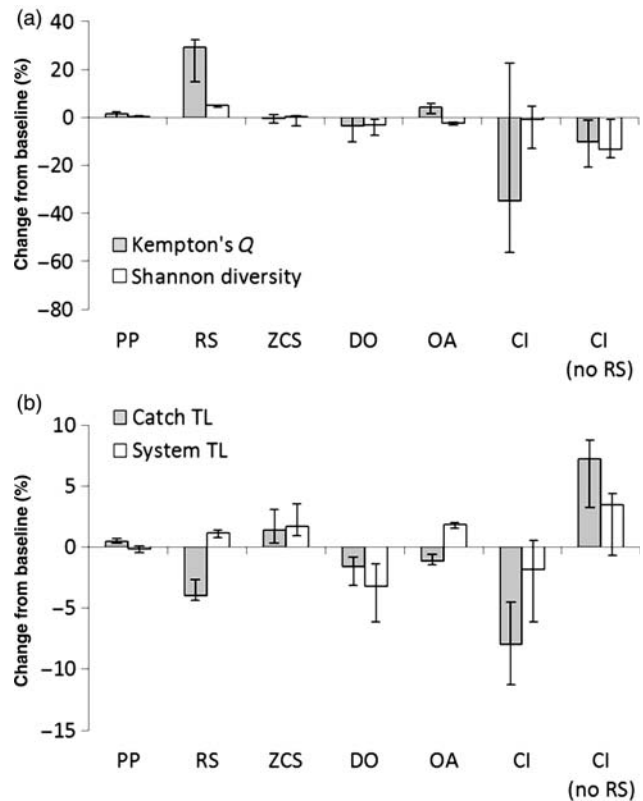


Figure 3. Ecosystem response to climate change effects. Primary production (PP), range shifts (RS), zooplankton community size structure (ZCS), dissolved oxygen (DO), ocean acidification (OA), and combined impacts (CI). Values are averaged across all EwE models (except RS, which is averaged over SEA, NBC, and NCC). (a) Biodiversity: Shannon index (Shannon and Weaver, 1949), Kempton's *Q* adapted for ecosystem models (Ainsworth and Pitcher, 2006). (b) Mean trophic level of catch, mean trophic level of ecosystem. Error bars indicate range of outputs observed by varying the strength of climate effects (i.e. including conservative, moderate, and substantial scenarios); bar indicates median.

The cumulative impact scenarios (with or without range shifts) consistently resulted in biodiversity loss as measured by either metric. The loss is greater when range shifts are included, an unanticipated response, because range shifts in isolation increased the biodiversity. However, this general result is highly dependent on the effect strength employed.

Changes in the mean trophic level of the ecosystem and of fisheries catch were minor when each climate effect was considered separately (Figure 3b), with range shifts producing the most pronounced impacts (e.g. compare cumulative impacts with and without range shifts). When range shifts are examined in isolation, we see an overall increase in the biomass of fished species (three of three ecosystems increased in Supplementary Table S7). However, large piscivores tend to fare poorly. In addition to the decrease in the mean trophic level of the catch (Figure 3b), we see an overall decline in pelagic fish biomass (e.g. in three of three ecosystems, Supplementary Table S7). The impact on other groups and on fisheries landings (e.g. total landings, demersal landings, and pelagic fish landings) is variable between ecosystems and depends on species proportions present.

Cumulative climate impacts have an ambiguous effect on ecosystem biodiversity (Figure 4a), but there could be a decline in some systems [also see Supplementary Table S7: Shannon: four of five systems decreased for cumulative impacts (CI) and three of three decreased for cumulative impacts with range shifts (CIRS); Kempton: four of five decrease for CI and three of three decrease for CIRS)]. The large error bars on the WCVI model in Figure 4a suggest that this outcome is highly dependent on the strength of the climate effect; this might be the result of model structure. Because the WCVI model uses so few functional groups, it is very sensitive to species evenness measurements. Kempton's *Q* index displays a greater decline than the Shannon biodiversity index in most models, signalling decreases in species biomass. Factoring in range shifts in the models for which these data were available exacerbates the loss of biodiversity in every model. Note that the strong signal from WCVI does not strongly reflect in Figure 3—recall that the WCVI data are present in “CI (no RS)” but not in “CI”, because no range-shift calculations were performed on WCVI.

The regional models predicted negligible changes in the mean ecosystem trophic level and trophic level of catch under the cumulative impacts scenario without range shifts and displayed little agreement on the direction of change (Figure 4b). WCVI gave an appreciable result in the positive direction, but the magnitude of response could be influenced by the model's simple structure.

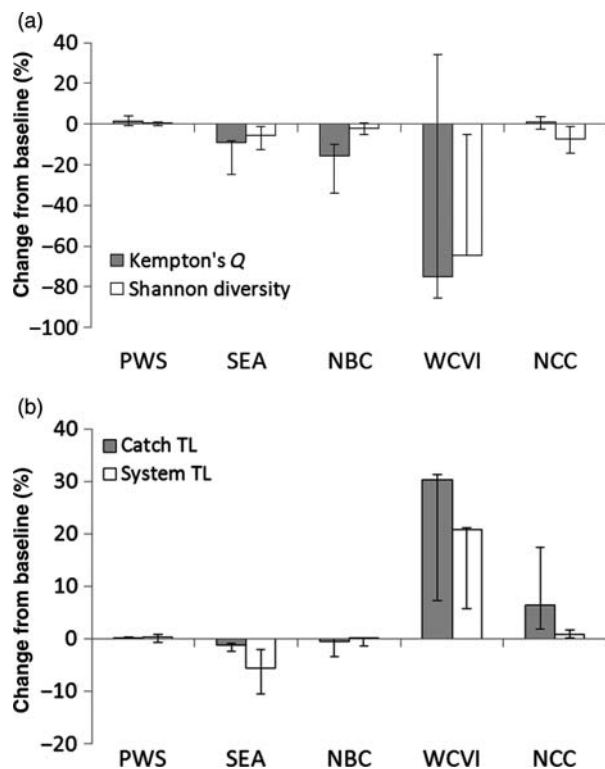


Figure 4. Ecosystem response by study area under cumulative climate effects (except range shift). (a) Biodiversity: Shannon index (Shannon and Weaver, 1949), Kempton's *Q* adapted for ecosystem models (Ainsworth and Pitcher, 2006). (b) Mean trophic level (TL) of catch, mean trophic level of ecosystem. Error bars indicate the range of outputs observed by varying the strength of climate effects (i.e. including conservative, moderate, and substantial scenarios); bar indicates median.

When we included range shifts, the mean ecosystem trophic level and trophic level of catch decreased more [mean ecosystem trophic level decreasing by as much as 16% relative to baseline (SEA and NBC models) and trophic level of catch decreasing by 10%].

Geographic variation in climate change: fisheries

When all climate effects were combined, the models from different regions produced a wide range of possible outcomes. However, there is tacit agreement on a couple of points: forage fish fisheries consistently declined and almost all other fisheries were vulnerable to declines depending on the assumed strength of climate effects (Figure 5). Although in PWS most species appeared to respond positively to the cumulative impacts scenario, the results for this model do not factor in range shifts, which tend to affect fisheries negatively. Almost all fisheries in the SEA, NCC, and WCVI models were predicted to decline under the cumulative impacts scenario. However, NBC fisheries for shellfish and rockfish do better under some scenarios. This response is a direct consequence of range shifts: southern rockfish populations are predicted to establish themselves in British Columbia and supplement existing fisheries. However, note that this outcome is highly dependent on climate change effect strength (the possible range of outcomes also includes a total collapse of rockfish fisheries). The predicted increase in shellfish landings results from trophic impacts and hinges on the increased availability of zooplankton under the cumulative impacts scenario. This increase in zooplankton cannot be attributed to any particular climate effect; it occurs only in the cumulative impacts scenario and appears to be the product of synergisms that reduce planktivory.

Geographic variation in climate change: species biomass

We observed a mixed response from the study areas regarding species biomass composition under the cumulative impacts scenario (Figure 6). Pelagic invertebrates (mainly squid) could double in density with respect to the baseline scenario, which includes no climate effects. Demersal fish populations (including fished and unfished groups) also remained strong regardless of the study area or strength of the climate effects (an outcome revealed also in the previous figure by consistent yields in flatfish fisheries). The impacts of climate change on small pelagic fish appears highly dependent on the assumed strength of effect; all study areas, except PWS (which does not factor in range shifts), agree that the abundance of small pelagic fish could range from near zero to near the current levels, but will not increase. Species of conservation concern, sharks, birds, and mammals display greater consistency under a range of effect strengths, decreasing more under extreme climate scenarios, but generally remaining between 50 and 100% of biomass levels with respect to the baseline scenario. Of these, birds tended to benefit from climate shifts regardless of whether range shifts were considered or not (see Supplementary Table S7: four of four systems increase for CI and two of three increase for CIRS), mammals lost at most 20% of their biomass under even the substantial climate effect strength scenario (with or without range shifts present), and sharks displayed a more significant decrease, losing 50–60% of their biomass under the substantial climate effect strength scenario (and decreasing in five of five systems for CI and two of three for CIRS for the moderate climate effect strength scenario; Supplementary Table S7).

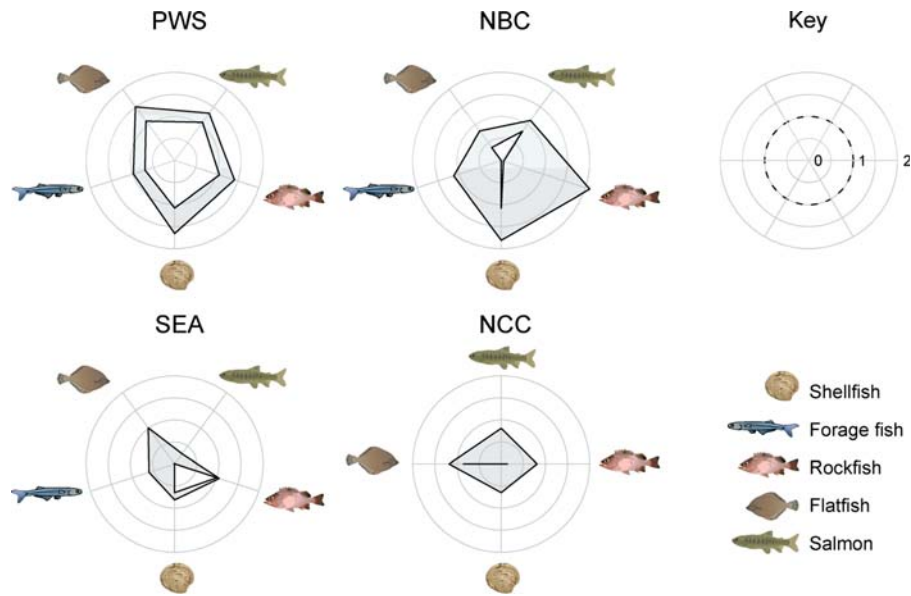


Figure 5. Fisheries landings in 2060 under the combined-effects climate change scenario (SEA, NBC, and NCC include range-shift effects). Dashed line (key) indicates landings in 2060 without climate change (baseline, defined as 1); axial scale is linear. Shaded grey area indicates range of outputs observed by varying the strength of climate effects (i.e. including conservative, moderate, and substantial scenarios). WCVI is not presented, because fisheries are aggregated into only two fleets (both of which achieve less than 25% of the baseline landings). In these figures, the shaded area is the error range because of effect strength and the distance from zero indicates the quantity of landings such that values <1 represent fewer landings than baseline, and values >1 represent greater landings than baseline.

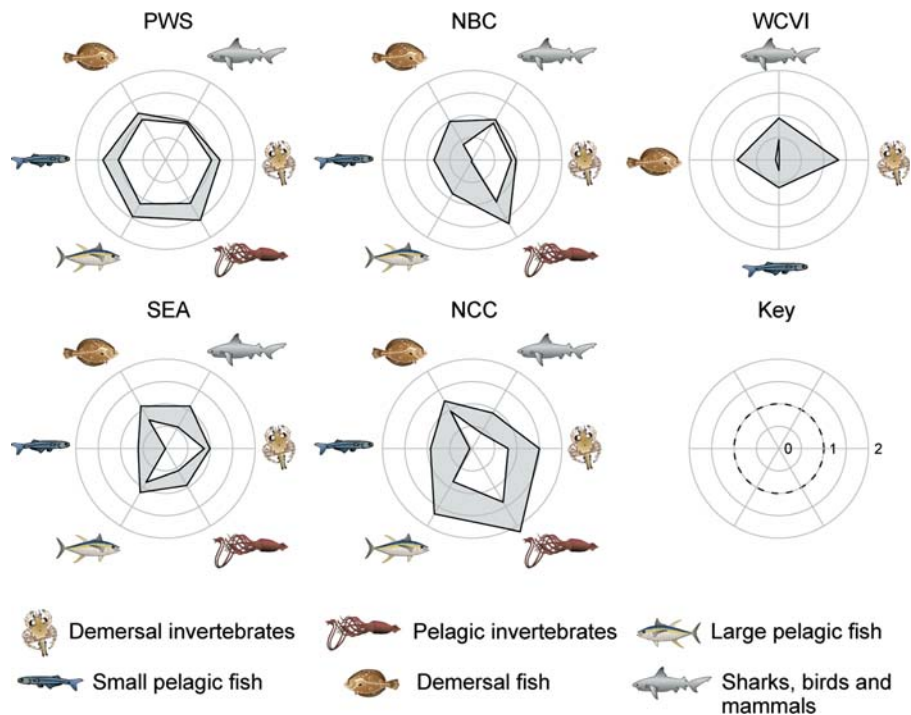


Figure 6. Biomass in 2060 under the combined-effects climate change scenario (SEA, NBC, and NCC include range-shift effects). Dashed line (key) indicates biomass in 2060 without climate change (baseline, defined as 1); axial scale is linear. Shaded grey area indicates the range of outputs observed by varying the strength of climate effects (i.e. including conservative, moderate, and substantial scenarios). In these figures, the shaded area is the error range because of effect strength and the distance from zero indicates the quantity of biomass, such that values <1 represent less biomass than baseline, and values >1 represent more biomass than baseline.

Discussion

Ecological forecasts are laden with uncertainty, yet can offer guidance to decision-makers by providing insight into possible futures (Clark *et al.*, 2001). Even our coarse representation of potential climate change impacts on North Pacific fisheries and foodwebs can offer three windows into these possible futures. First, some fisheries and some species will increase, whereas others will decline, because of both direct and indirect effects of climate change (Harley *et al.*, 2006). Second, fisheries and species will not necessarily respond the same way in all regions. Third, interactions between different climate change effects might result in different changes in fisheries and species than would be predicted from studying each climate change effect in isolation. Though there are many caveats regarding the quantitative and qualitative nature of the responses predicted by our model simulations, these three points are likely robust to our assumptions on climate effect strengths, on the additivity of climate effects, and on model structure and parametrization, and hence offer a prospectus for future empirical and modelling research.

Our model simulations predicted that the performance of fisheries and the relative abundance of species in the northeast Pacific are expected to change, but not uniformly. Despite the implementation of mainly negative forcing functions (that reduce productivity, see Supplementary Figure S1), many fisheries, and species, benefit because of indirect feeding relationships. Overall, fisheries do worse under climate change. Fished species tended to decline more severely than unfished species, which suggests that these exploited animals could face double jeopardy. Fishing acts as an additional stressor and it could exacerbate the impacts of climate change (Kirby *et al.*, 2009). For example, fishing reduces the age and size of fish and the biodiversity of stocks, potentially reducing the resilience of populations to perturbation, whereas physiological and behavioural impairments might affect stock growth and reproduction (Brander, 2007). Moreover, coastal ecosystems are stressed by a broad suite of human activities not addressed in this exploration. These too might interact and compound (Crain *et al.*, 2008; Halpern *et al.*, 2008).

There is substantial variation between the models in the predicted impacts of climate change. For example, rockfish fisheries increase in NBC and PWS, but they decrease in SEA and NCC. This variation is certainly related to differences in the way that species are aggregated, but it also reflects regional differences in species composition and the pattern of trophic flows implemented in the models (i.e. the relative importance of top-down vs. bottom-up mortality control). These are likely to be important factors determining an ecosystem's response to climate change and ones that can be studied using the EwE approach.

Just as recognition of community interactions can improve understanding for single-species fisheries management (Mangel and Levin, 2005), anticipating that climate change will affect multiple factors with potentially interactive impacts on marine species might improve management and conservation responses. The relatively minor impacts of various effects as studied in isolation might, when combined, produce changes in species composition, system biomass, and biodiversity greater than we would expect by simply summing the effects of each factor individually. Synergies might also exist at the biochemical level; for example, decreased carbonate saturation could affect calcifying organisms in a way that depends on ocean temperature, light levels, and nutrient availability (Kleypas *et al.*, 2006).

Beyond these three general messages, so little is known about the effects of climate change on marine ecosystems that the future scenarios presented in this paper should be interpreted only with a suite of caveats in mind. The major sources of uncertainty include:

- (i) the nature and extent of physiological effects occurring at the organismal level in all species in the marine community, including sublethal effects and particularly involving ocean acidification, deoxygenation, and changes in ocean temperature;
- (ii) the presence of feedbacks and ecological thresholds beyond which climate effects might act to produce non-linear changes in ecosystem structure and function (Fagre *et al.*, 2009; Bulling *et al.*, 2010; Walther, 2010);
- (iii) important factors we did not attempt to represent, such as increased variability of climate, the adaptive capabilities of species, and the presence of pathways other than trophic interactions by which climate effects might propagate throughout the ecosystem (e.g. by affecting refuge and breeding space, altering animal behaviour, affecting hydrodynamic transports, etc.);
- (iv) the relative importance of simulated climate effects.

Some of these uncertainties can be addressed by laboratory experiments and *in situ* monitoring of ecosystem conditions, but simulation studies also have a role to play. A priority for narrowing the range of error in studies like this one should be to develop realistic population forcing functions from theoretical or empirical models that can control the response of species to climate influences. This would free us from our simple approach of using standardized stock–production forcing functions and allow us to represent additional impacts, such as the effects of temperature on animal metabolism and reproductive success (W. L. Cheung, unpublished manuscript, School of Environmental Sciences, University of East Anglia, Norwich NR4 7TJ, UK, e-mail: william.cheung@uea.ac.uk). In addition, with more credible models driving the organism-level effects, it would be possible to expand the analysis using the current modelling software, EwE, to consider the influence of habitat changes and animal behaviour through mediation functions and apply more sophisticated forcing functions that affect recruitment, vulnerability to predators, and changes in the habitable area. A new modelling approach would be required to investigate other potentially important factors: for example, the influence of changing oceanographic regimes in nutrient/waste cycling and larval transport and the influence of seasonal cycles on phenology.

Range shifts emerged as the dominant aspect of climate change in our analysis. Of all the factors considered in this paper, this one and primary production have the firmest foundation regarding the supporting science, whereas the simulated effects of ocean acidification, ocean deoxygenation, and phytoplankton community structure rely on simple assumptions with limited theoretical or empirical backing. The dominance of range shifts in the results could be partly an artefact of the modelling approach. The Northeast Pacific models used here (and EwE models generally) focus on higher trophic levels and fish species in particular; so did the underlying range shift calculations. Hence, the results tend to emphasize the portion of the foodweb most sensitive to

the impact of range shifts. In contrast, ocean acidification, for example, might act mainly on invertebrates and basal species; this would be less evident, because of species aggregation in EwE. Moreover, the projected range shifts employed here do not account for all relevant factors (e.g. ocean biogeochemistry; Cheung *et al.*, 2009), nor have we attempted to represent non-exploited species. Finally, the decreases in catch associated with range shifts are probably overestimated, because it is likely that fishers would capitalize on new species as northern populations establish. This human opportunism is not captured by our approach. Similarly, biomass declines projected here assume that fishing mortality remains constant. In reality, fisheries management would adapt to new conditions to reduce or avoid depletions.

Two new articles are in preparation by the authors that will build on the current effort. Busch *et al.* will challenge our assumption that climate factors combine additively, testing potential consequences of multiplying or averaging climate impacts on functional group productivity. Samhoury *et al.* will explore further how higher-order trophic interactions influence forecasts made by single-species bioclimatic prediction models like the one by Cheung *et al.* (2009). These contributions have evolved from presentations made at the PICES 2010 Annual Meeting.

As new information becomes available on the organismal and community-level effects of climate change, ecosystem models should become increasingly valuable for understanding cumulative impacts and the impacts on the human societies and economies that rely on living resources. This exercise, although not intended to provide tactical guidance regarding the appropriate management responses to climate change, helps build better knowledge of climate change impacts and might help in identifying future avenues of research. In particular, the finding that not all fisheries and species will respond negatively to climate change implies that the development of ecosystem-based adaptation strategies could provide flexibility for resource managers in a changing climate. Though some responses to climate change are likely to be generalizable to the entire North Pacific region, the geographic variation in responses seen here suggests that local management strategies might be worthwhile; a one-size-fits-all climate change adaptation strategy might be inefficient or ineffective. Although much more progress is needed, simulation models can play a critical role in helping us to adapt to coming changes in marine ecosystems and help us discover what we can do to protect critical features of ecosystem functioning. The challenge of predicting cumulative impacts of climate change is enormous, but must be met if we are to adapt and manage rapidly changing marine ecosystems in the 21st century.

Supplementary material

The following supplementary material is available at the online ICES/JMS version of this paper: a description of the EwE models used here, a key to the functional groups included in landings and biomass metrics, output of the ESM2.1 model (primary production) and the GFDL CM2.2 model (temperature), with additional information on both models, input data for Equations (3) and (4), and group/effect size assignments for ocean acidification and deoxygenation simulations.

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