Projecting future changes in distributions of pelagic fish species of Northeast Pacific shelf seas

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A R T I C L E   I N F O

A B S T R A C T

Marine life is being affected by changes in ocean conditions resulting from changes in climate and chemistry triggered by combustion of fossil fuels. Shifting spatial distributions of fish species is a major observed and predicted impact of these oceanographic changes, and such shifts may modify fish community structure considerably in particular locations and regions. We projected future range shifts of pelagic marine fishes of the Northeast Pacific shelf seas by 2050 relative to the present. We combined published data, expert knowledge, and pelagic fish survey data to predict current species distribution ranges of 28 fish species of the Northeast Pacific shelf seas that occur in the epipelagic zone and are well-represented in pelagic fish surveys. These represent a wide spectrum of sub-tropical to sub-polar species, with a wide range of life history characteristics. Using projected ocean condition changes from three different Earth System Models, we simulated changes in the spatial distribution of each species. We show that Northeast Pacific shelf seas may undergo considerable changes in the structure of its pelagic marine communities by mid-21st century. Ensembles of model projections suggest that the distribution centroids of the studied species are expected to shift poleward at an average rate of 30.1 ± 2.34 (S.E.) km decade^{-1} under the SRES A2 scenario from 2000 to 2050. The projected species range shifts result in a high rate of range expansion of this group of species into the Gulf of Alaska and the Bering Sea. Rate of range contraction of these species is highest at the Aleutian Islands, and in the California Current Large Marine Ecosystem. We also predict increasing dominance of warmer water species in all regions. The projected changes in species assemblages may have large ecological and socio-economic implications through mismatches of co-evolved species, unexpected trophic effects, and shifts of fishing grounds. These results provide hypotheses of climate change impacts that can be tested using data collected by monitoring programmes in the region.

Introduction

Anthropogenic climate change is causing changes in ocean conditions that are much more rapid than previously known natural change (Brierley and Kingsford, 2009; Hoegh-Guldberg and Bruno, 2010). These include physical (e.g., temperature, ocean current patterns) and chemical (e.g., acidity, oxygen content) changes (Doney et al., 2012), which have in turn led to biological changes including effects on physiologies, spatial distributions, phenologies (timing), and species assemblages (e.g., Dulvy et al., 2008; Edwards and Richardson, 2004; Hiddink and Ter Hofstede, 2008; Nye et al., 2009; Perry et al., 2005; Pörtner, 2010). Poleward shifts in distributions are one of the most commonly observed changes in marine fishes and invertebrates, given that the physiology, reproduction, and dispersal of marine species are strongly responsive to temperature and ocean current patterns (Poloczanska et al., 2013).

Community-wide distribution shifts were recently observed on the Bering Sea continental shelf where the centres of distribution of 40 taxa of fishes and invertebrates shifted northward by an average of 34 km from 1982 to 2006 (Mueter and Litzow, 2008). A meta-analysis of survey data from around North America shows that temperature change is a significant factor explaining the magnitude and direction of shifts in latitude and depth of more than 300 species or species groups (Pinsky et al., 2013). Such changes

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are suggested to have led to shifts in commercial fisheries catch compositions worldwide (Cheung et al., 2013a).

In the Northeast Pacific (including the Eastern Bering Sea, Gulf of Alaska and California Current large marine ecosystems), sea surface temperature changed by an average of 0.27 °C, 0.37 °C and −0.07 °C, respectively from 1982 to 2006 (Belkin, 2009); region-wide, it is projected to increase by 1.0–1.5 °C by 2050 relative to 2000 (Overland and Wang, 2007). Such changes are likely to have large, yet poorly understood, implications for species distributions and the overall biological community of this region (King et al., 2011). The decline of eulachon (*Thaleichthys pacificus*) in the southern part of its range (Moody and Pitcher, 2010), the recent invasion of the Humboldt squid (*Dosidicus gigas*) along the west coast of North America from Central and South America (Brodeur et al., 2006; Zeidberg and Robison, 2007), poleward shifts of oceanic fish larvae (Hsieh et al., 2009), and faunal shifts to more southern species along the California coast (Miller and McGowan, 2013) are all potentially linked to changes in climate and regional ocean conditions. Changes in temperature, primary production, and phytoplankton size structure (IPCC, 2014) are also projected to affect fish abundance (Cheung et al., 2012), including in the North Pacific (Woodworth-Jefcoats et al., 2013). Shifts in pelagic fish and invertebrate communities in the Northeast Pacific are expected to continue during the coming decades, and probably at an increasing rate, given observed and projected changes in oceanographic conditions there. A wide variety of biological changes have been observed and are expected in Canada's Pacific marine ecosystems in response to a variety of regional manifestations of global environmental change (Okey et al., 2014), notwithstanding the recent predominance of a cool regime that has likely temporarily slowed the pace of biological change. These biological changes will modify the functioning of marine ecosystems and the goods and services they provide, in ways and at rates that are challenging to estimate.

The West Coast of North America from the Mexican Pacific to the Bering and Chukchi Seas is a highly dynamic and productive region that consists of several biological domains (Ware and McFarlane, 1989). The coastal Gulf of Alaska is generally considered to be primarily a downwelling domain with high freshwater input that feeds into an energetic North and West flowing boundary current. From off the West Coast of Vancouver Island to Mexico, the California Current is dominated by southerly flow and high levels of episodic upwelling in summer, leading to highly seasonal productivity that peaks latitudinally off Vancouver Island (Checkley and Barth, 2009; Ware and Thomson, 2005). The area off the northern and central coasts of Canada's Pacific region is transitional between these two currents of opposite direction (Ware and McFarlane, 1989). These form a set of contrasting ecosystems that is useful for understanding the ecological effects of climate change in the region. The development of scenarios of ecological changes associated with projected oceanographic changes, in conjunction with the monitoring of ecological indicators in these Northeast Pacific domains, will allow appropriate fisheries management and conservation policies to be developed.

The goal of this study was to develop scenarios of potential effects of climate change on fishes of the Northeast Pacific shelf seas that spend considerable amount of time in the epipelagic zone at least during portions of their life cycles. Oceanographic conditions of the epipelagic zone are expected to be particularly sensitive to climate change and variability, leading to relatively rapid changes in associated biological communities (Cheung et al., 2009a). With the projected increase in temperature in this region, it is hypothesized that many fishes in the epipelagic zone will shift their distribution northward, resulting in an increased dominance of warmer-water species. Using our understanding of the distribution, life history, and ecology of pelagic fishes in the region, we

employed a dynamic bioclimatic envelope model that integrates ocean physical and biogeochemical changes (Cheung et al., 2011) to quantitatively project potential changes in their distributions and assemblage by 2050 relative to 2000. We focus specifically on 28 species that are well represented in the pelagic fish surveys of the Northeast Pacific shelf seas conducted by the U.S. National Oceanographic and Atmospheric Administration (NOAA) and the Department of Fisheries and Oceans (DFO) of Canada (Orsi et al., 2007). These are quasi-synoptic surveys that were originally aimed at examining the distributions of juvenile salmon throughout much of the coastal Northeast Pacific Ocean during the period since the late 1990s (Fisher et al., 2007). However, the surveys also quantified the abundance and distribution patterns of other major non-salmonid fish and elasmobranch species. We used the catch data from these surveys (Orsi et al., 2007) to evaluate the results of our model. We examine the robustness of the projections by using outputs from different Earth System Models. We discuss how results of our projections will provide a quantitative hypothesis of potential climate change impacts of this fish assemblage that could be evaluated and refined by these surveys in the future. Our specific focus on the NE Pacific coast and the linkages to existing survey programs, should provide results that could contribute to monitoring and assessment of impacts, vulnerability, and adaptive capacity of marine ecosystems and fisheries in the region, thereby complementing and helping to advance such assessments (e.g., DFO, 2013; Hunter et al., 2014; Okey et al., 2014).

Methods

Sample of species and their current distributions

This study included a sample of 28 fishes ranging from warm- to cool-water species (Table 1) that are well-represented in ongoing coastal pelagic fish surveys in this region (Brodeur et al., 2005, 2003; Harding et al., 2011; Orsi et al., 2007). These consist mainly of pelagic species, but they also include some demersal species that are common in the coastal epipelagic zone as juveniles. These species were selected because of their high numerical abundance in pelagic fish survey samples and that these species had a spectrum of temperature preferences. The coastal pelagic fish surveys consisted of surface and midwater net tows for adults and large juveniles (see Orsi et al. (2007) for details about these surveys).

The current spatial distributions of these species, representing the average pattern of relative abundance across life stages of the species in recent decades (i.e., 1980–2000), were produced using an algorithm developed by the *Sea Around Us* (see Cheung et al., 2008; Close et al., 2006; www.seaaroundus.org). The algorithm predicts the probability of occurrence of a species on a 30′ latitude × 30′ longitude grid based on the species' depth range, latitudinal range, and polygons encompassing their known occurrence regions. A bi-modal latitudinal distribution was assumed for subtropical/temperate species that occur in both the Northern and Southern hemisphere, reflecting the low suitability of tropical habitats for these species e.g., Pacific sardine. The distributions were further refined by assigning habitat preferences to each species, such as affinity to shelf (inner, outer), estuaries and rocky reef habitats, and accounting for equatorial submergence. The required input data and habitat information was obtained from FishBase (www.fishbase.org), which contains key information on the distribution of the species in question.

Comparing predictions with data

Predicted current spatial distributions were compared against observations of distributions from the coastal pelagic fish surveys,

Table 1
List of species sampled by the pelagic fish surveys (Orsi et al., 2007) that are included in this study. Taxonomy and distributional information are based on FishBase (www.fishbase.org).

Family	Scientific name	Common name	Latitudinal range
Alopiidae	*Alopias vulpinus*	Thresher shark	67°N–58°S
Ammodytidae	*Ammodytes hexapterus*	Pacific sand lance	63°N–32°N
Anoplopomatidae	*Anoplopoma fimbria*	Sablefish	64°N–23°N
Carangidae	*Trachurus symmetricus*	Pacific jack mackerel	65°N–13°N
Carcharhinidae	*Prionace glauca*	Blue shark	66°N–55°S
Centrolophidae	*Icichthys lockingtoni*	Medusafish	60°N–30°N
Clupeidae	*Alosa sapidissima*	American shad	60°N–22°N
	Sardinops sagax	Pacific sardine	61°N–47°S
Engraulidae	*Engraulis mordax*	California anchovy	51°N–21°N
Gadidae	*Theragra chalcogramma*	Pacific pollock	68°N–34°N
Gasterosteidae	*Gasterosteus aculeatus*	Three-spined stickleback	71°N–26°N
Hexagrammidae	*Pleurogrammus monopterygius*	Atka mackerel	66°N–32°N
Lamnidae	*Lamna ditropis*	Salmon shark	66°N–22°N
Osmeridae	*Allosmerus elongatus*	Whitebait smelt	60°N–30°N
	Hypomesus pretiosus	Surf smelt	57°N–34°N
	Mallotus villosus	Capelin	79°N–40°N
	Thaleichthys pacificus	Eulachon	61°N–36°N
Salmonidae	*Oncorhynchus gorbuscha*	Pink salmon	79°N–29°N
	Oncorhynchus keta	Chum salmon	67°N–24°N
	Oncorhynchus kisutch	Coho salmon	72°N–22°N
	Oncorhynchus mykiss	Steelhead	67°N–32°N
	Oncorhynchus nerka	Sockeye salmon	72°N–42°N
	Oncorhynchus tshawytscha	Chinook salmon	72°N–27°N
Scomberesocidae	*Cololabis saira*	Pacific saury	67°N–18°N
Scombridae	*Scomber japonicus*	Chub mackerel	60°N–55°S
Squalidae	*Squalus suckleyi*	Spiny dogfish	73°N–56°S
Trichodontidae	*Trichodon trichodon*	Pacific sandfish	66°N–38°N
Zaproridae	*Zaprora silenus*	Prowfish	66°N–34°N

as expressed using the Area Under Curve (AUC) of the Receiver Operating Characteristics (ROC) test statistics (using the pROC package in the statistical software R). Observed ROC curves were generated for each species, expressed as the plotted difference between true positive rate (number of true occurrences/total number of predicted occurrences) and the false positive rate (number of false predicted occurrences/total number of absence). An AUC of the ROC curve of 0.5 indicates that predictions are no better than random; higher AUC values indicate increasing prediction performance. Geo-referenced observed occurrence data were obtained from the Northeast Pacific shelf seas pelagic fish surveys and Ocean Biogeographic Information System (OBIS, www.iobis.org). Occurrence data from OBIS from the NE Pacific region were selected, and were quality-screened to identify obvious errors, including occurrence on land. All the occurrence data were aggregated into $30' \times 30'$ grid to make them comparable to the predicted distribution data. Species-specific thresholds of 0 percentile, 1 percentile and 10 percentile of predicted relative abundance value of the modelled distributions were applied, meaning that any cells with predicted relative abundance over the specific threshold were considered to be occupied by the species in question. Confidence intervals of the AUC values were generated using a method described in DeLong et al. (1988) (implemented in the pROC package).

We examined whether predicted species distributions resulted in patterns of species richness that would be comparable to observed patterns calculated from survey data. From the pelagic fish surveys we extracted the occurrence records in each sampling station (Fig. 1). We then aggregated these records into a set of sample subareas in this region (Table 2) and calculated species richness (number of species occurring) of the 28 pelagic fish species in each of those subareas. We calculated the predicted species richness in each subarea by tallying the number of examined species with positive predicted probability of occurrence per unit area. We then evaluated the correlation between the observed and predicted species richness using the Pearson correlation test.

Projecting change in species distributions

Using the dynamic bioclimate envelope model (DBEM) described in Cheung et al. (2011), we projected changes in distributions of the 28 species under different climate change scenarios. The model identified species' preferences to environmental conditions that are defined by sea water temperature (surface), salinity, distance from sea-ice, and habitat types (e.g., estuaries, seamounts, shelf). Because the survey locations do not systematically stratify the possible environmental gradients of the species, we calculated the temperature preference profile of each species by overlaying the predicted species distribution with observed annual sea surface temperature (30-year climatology) representing the 1971–2000 period (from Hadley Centre gridded SST data), rather than overlaying observed data from the survey with temperature.

The DBEM furthermore simulates how changes in temperature and oxygen content (represented by O_2 concentration) would affect growth of marine fishes and invertebrates using a sub-model derived from a generalized von Bertalanffy growth function (VBGF; Cheung et al., 2013a, 2013b):

$$\frac{dW}{dt} = H \cdot W^a - kW \tag{1a}$$

$$W_t = W_\infty \cdot \left[1 - e^{-K(t-t_0)}\right]^{\frac{1}{1-a}} \tag{1b}$$

where H and k are the coefficients for anabolism and catabolism, W_∞ is the asymptotic weight, (i.e., the mean weight the fish of a given population would reach if they were to grow forever); K is the rate (time^{-1}) at which W_∞ is approached; t_0 relates absolute age (t) to the origin of the curve; a is a scaling parameter; and W_t is the predicted weight at age t. Here we assume for simplicity that $a = 0.7$, although empirical studies show that a generally varies from 0.50 to 0.95 among fish species (Pauly, 1981, 2010), with 2/3 corresponding to the special or standard VBGF.

Metabolism is temperature dependent while aerobic scope is dependent on oxygen availability in water. Maintenance metabolism is affected by physiological stress. Thus:
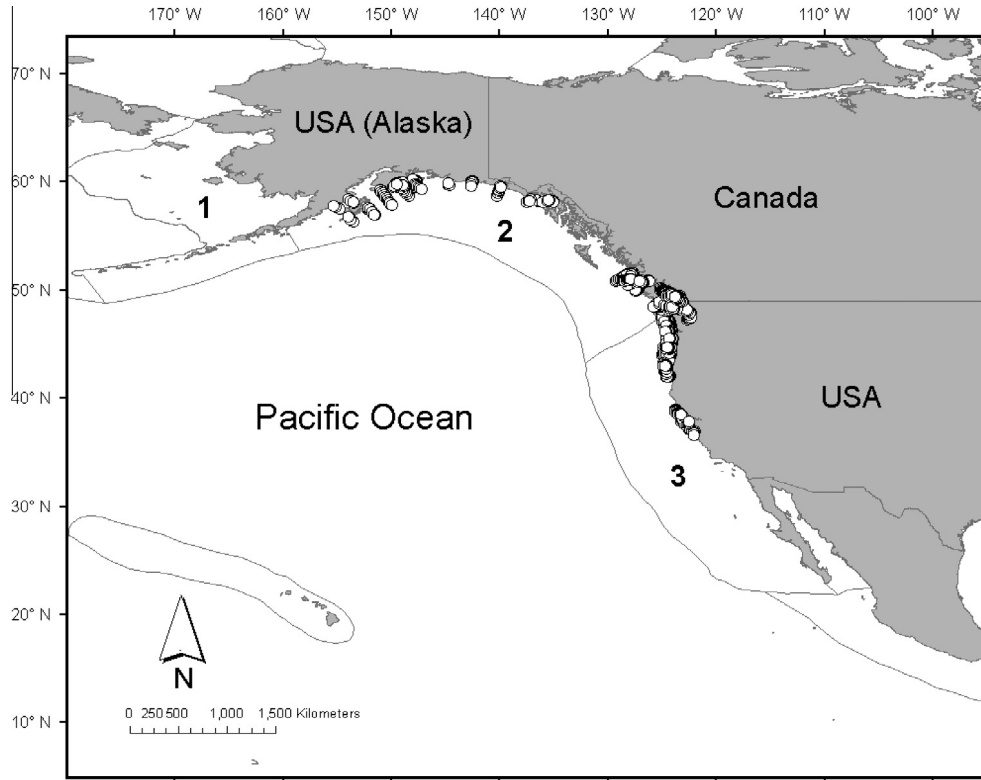
Fig. 1. Locations of sample stations of the pelagic nekton surveys described in Orsi et al. (2007) (open circles) and boundary of the Large Marine Ecosystems: (1) Eastern Bering Sea, (2) Gulf of Alaska and (3) California Current.

Table 2
Sample subareas and their corresponding geographical boundaries.

Sample area in model	Latitudinal range (°N)	Longitudinal range (°W)
1	60.0–60.5	147.5–148.5
2	58.0–60.5	136.0–145.0
3	56.0–60.0	144.5–155.5
4	58.0–58.5	134.5–136.5
5	50.5–51.0	126.0–128.0
6	49.5–51.5	127.0–129.5
7	48.0–50.5	123.0–125.5
8	47.5–49.0	124.5–126.0
9	46.0–48.0	124.0–125.0
10	41.5–46.0	124.0–125.0
11	48.0–49.0	123.0–125.0
12	47.0–48.5	122.0–123.0
13	37.0–39.0	121.5–124.0
14	37.5–38.0	122.0–122.5

$$H = g \cdot [O_2] \cdot e^{-j_1/T} \quad (2)$$

$$k = h \cdot e^{-j_2/T} \quad (3)$$

where $j = E_a/R$ with E_a and R are the activation energy and Boltzmann constant, respectively, while T is temperature in Kelvin. In addition, the aerobic scope of marine fishes and invertebrates decreases as temperature approaches their upper and lower temperature limits (Pörtner, 2010). The coefficients g and h were derived from the average W_∞, K, and environmental temperature (T_o) of the species reported in the literature. Thus, based on Eqs. (1)–(3), we obtain:

$$g = \frac{W_\infty^{1-a} \cdot K}{[O_2] \cdot e^{-j_1/T_o}} \quad (4a)$$

$$h = \frac{K/(1-a)}{[H^+] \cdot e^{-j_2/T_o}} \quad (4b)$$

The model predicts changes in VBGF parameters according to changes in temperature and oxygen in each ocean spatial cell where the species occur relative to the initial conditions, as:

$$W_\infty = \left(\frac{H}{k}\right)^{\frac{1}{(1-a)}} \quad (5a)$$

$$K = k \cdot (1-a) \quad (5b)$$

Species' environmental preferences were linked to the expected carrying capacity in a population dynamic model in which growth, mortality, and spatial dynamics of adult movement and larval dispersal along ocean currents were explicitly represented (Cheung et al., 2008, 2009b). The model simulated changes in relative abundance of a species by:

$$\frac{dA_i}{dt} = \sum_{j=1}^{N} G_i + L_{ji} + I_{ji} \quad (6)$$

where A_i is the relative abundance of a $30' \times 30'$ cell i, G is the intrinsic population growth and L_{ji} and I_{ji} are settled larvae and net migrated adults from surrounding cells j, respectively. The distance and direction of larval dispersal are a function of the predicted pelagic larval duration estimated based on an empirical equation (O'Connor et al., 2007). The model explicitly represents larval dispersal through ocean current with an advection–diffusion-reaction model (see (Cheung et al., 2008) for details).

$$\frac{\partial Lav}{\partial t} = \frac{\partial}{\partial x}\left(D\frac{\partial Lav}{\partial x}\right) + \frac{\partial}{\partial y}\left(D\frac{\partial Lav}{\partial y}\right) - \frac{\partial}{\partial x}(u \cdot Lav)$$
$$- \frac{\partial}{\partial y}(v \cdot Lav) - \lambda \cdot Lav \quad (7)$$

where change in relative larvae abundance over time ($\partial Lav/\partial t$) is determined by diffusion and current-driven movements. λ is the mortality rate of the larvae. Diffusion is characterized by a diffusion parameter D, while advection is characterized by the two current velocity parameters (u, v) which describe the east–west and north–south current movement. In addition, animals are assumed to migrate along the calculated gradient of habitat suitability. Thus, changes in habitat suitability in each cell, determined by ocean conditions, lead to changes in the species' carrying capacity, population growth, net migration, and thus relative abundance in each cell.

We use outputs from the GFDL ESM2M (hereafter referred to as 'GFDL'), IPSL-CM4-LOOP ('IPSL') and NCAR Community Climate System Model 3 ('CCSM') Earth System Model to examine the sensitivities of key results to different environmental forcings. Further details about these three models and the experimental setup is given in Steinacher et al. (2010). The models are forced with the IPCC's Special Report on Emission Scenario (SRES) A2, which assumes atmospheric CO_2 concentration of around 860 ppm by 2100. We interpolated the original resolution of the model outputs onto a 30′ × 30′ grid by using the nearest neighbour method. The outputs from the Earth System Models considered by the DBEM included sea surface temperature, oxygen concentration, surface current advection (horizontal), salinity and sea ice concentration. In addition, to compare the SRES A2 scenario (from the IPCC's 4th Assessment Report) with Representative Concentration Pathway (RCP, from the IPCC's 5th Assessment Report), we also projected species range shifts using RCP 2.6 and RCP 8.5 representing lower and high emission scenarios, respectively. Ocean properties under the RCPs were projected from GFDL ESM2M.

We applied a 'Delta Method' to correct for bias associated with projected SST from the Earth System Models (Stock et al., 2010):

$$SST' = \left(PSST_t - \frac{\sum_{yr=1971}^{2000} PSST_{yr}}{30} \right) + OSST_o \tag{8}$$

where SST' is the bias-corrected SST projections, $PSST_t$ is the SST in year t projected from Earth System Models, and $OSST_o$ is the observed 30-year climatology of SST from the Hadley Centre gridded SST data.

Using the projected changes in species distributions, we estimated the rate of species' distribution expansion and contraction. Here, rates of species' distribution expansion (invasion) and contraction (local extinction) were measured for each cell by the number of species newly occurring in, or disappearing from, the cells relative to its original distribution, respectively. Additionally, we calculated the rate of shift in distribution, measured by the latitudinal and longitudinal movement of the centroid of the species distribution within the Northeast Pacific. For each species, the latitudinal centroid (LC) was calculated by:

$$LC = \frac{\sum_{i=1}^{n} L_i \cdot Abd_i}{\sum_{i=1}^{n} \cdot Abd_i} \tag{9}$$

where L_i and Abd_i are the latitudinal coordinates and species' relative abundance at the centre of cell i, respectively. Relative abundance is weighted by the area of sea in each 30′ × 30′ cell. n is the total number of cells within the study region. The difference between latitudinal centroids in projected and reference years (DC) was then calculated in kilometres (km) by:

$$DC = (LC_{y1} - LC_{y2}) \cdot \frac{\pi}{180} \cdot 6378.2 \tag{10}$$

where $y1$ and $y2$ are the projected and reference years. We then calculated the rate of range shift from the slope of changes in DC from 1991 to 2060, standardized across species.

We examined shifts in species assemblages by calculating the Mean Temperature of Relative Abundance (MTRA), a metric that is similar in concept to the Mean Temperature of Catch (Cheung et al., 2013a). The MTRA was computed from the average inferred temperature preference as documented in Cheung et al. (2013a, 2013b) weighted by their predicted relative abundance. i.e.,

$$MTRA_{yr} = \sum_{i=1}^{n} T_i \cdot Abd_{i,yr} \left/ \sum_{i=1}^{n} Abd_{i,yr} \right. \tag{11}$$

where T_i is the median temperature preference of species i, and n is the total number of species.

Sensitivity analysis

We conducted a sensitivity analysis by projecting future distributions of the species with alternative sets of initial parameter values. We randomly generated 3 different sets of initial parameter values for the simulations. The parameters included intrinsic population growth rate, VBGF parameters, diffusion coefficient, larval survival and settlement rates, and the metabolic scaling coefficients (j_1 and j_2 in Eqs. (4a) and (4b)). Parameter values were varied by a maximum of ±50% of the initial values. We calculated ensemble estimates of projected rates of range shifts.

Results

Current species distributions

The median preferred temperatures of the 28 studied species range from 4 to 26 °C (Fig. 2a), with species such as thresher shark (*Alopias vulpinus*), chub mackerel (*Scomber japonicus*) and Pacific sardine (*Sardinops sagax*) being classified as warm-water species. Species such as pink salmon (*Oncorhynchus gorbuscha*), chum salmon (*O. keta*), coho salmon (*O. kisutch*) and capelin (*Mallotus villosus*) were grouped as cold-water species. Species with medium preferred temperature such as medusafish (*Icichthys lockingtoni*), steelhead (*O. mykiss*) and sablefish (*Anoplopoma fimbria*) were classified as cool-water species. Generally, the median preferred temperature of the species varied positively and in curvilinear fashion with the range of the preferred temperature (calculated from the difference between the 5% and 95% percentiles of the cumulative predicted relative abundance of each species across the temperature range) (Fig. 2b) (p-value = 0.0018, R^2 = 0.40). This suggests that cold-water species tend to have a narrower range of preferred temperature than species with medium and warm preferred temperatures.

The species included in this study were predicted to occur mostly in coastal and shelf areas in the Northeast Pacific region (Fig. 3). All the species were predicted to occur in the Gulf of Alaska and off the coasts of British Columbia, Oregon, and northern California, while more than half of the species occur in the southern Bering Sea or off southern California (Fig. 3a). Moreover, the predicted species number per unit area in the model sample area was significantly correlated with the number of species occurring in the corresponding sampling stations of the pelagic fish surveys (Orsi et al., 2007) ($p < 0.01$, Pearson correlation test) (Fig. 3b). Moreover, the AUC values for all the species are significantly higher than 0.6 across all thresholds (median = 0.82). The uses of different thresholds of minimum relative abundance do not significantly affect the AUC value. Thus, for the rest of the manuscript, we applied a 1 percentile value as threshold. Overall, these results provide support for the representativeness of the predicted species distributions.
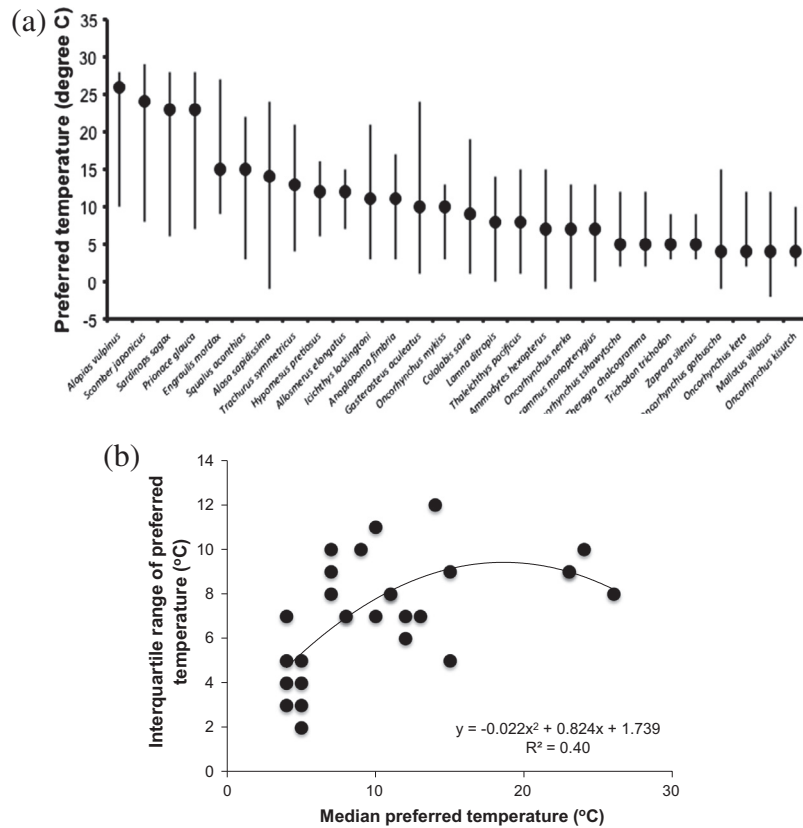
Fig. 2. Inferred temperature preference profiles of the studied fish species: (a) with the median (black circles) and the lines delineating the 5 and 95 percentiles of the cumulative predicted relative abundance of each species across a range of sea surface temperature; (b) with the 5 and 95 percentiles range of preferred temperature plotted against the median preferred temperature. A quadratic curve was fitted to the data points.

Projected future species distributions

The latitudinal centroids of the studied species were projected to shift northward when atmospheric CO_2 concentration increases in the future. Under the SRES A2 scenario, SST is projected by the three Earth System Models to increase by an average rate of 0.152 °C decade^{-1}, 0.148 °C decade^{-1} and 0.185 °C decade^{-1} in the Eastern Bering Sea, Gulf of Alaska and California Current large marine ecosystems, respectively, from 2000 to 2060 (Fig. 4). Regional-wide average annual change in SST during this period projected is 0.181 °C decade^{-1} under the SRES A2 scenario. In comparison, under the RCP 2.6 and 8.5 scenarios, average SST in the NE Pacific is projected to increase by 0.12 and 0.25 °C decade^{-1}, respectively, during the same period. As a result, the latitudinal centroids of the species were projected to shift poleward at an average rate of at 16.1 ± 0.36 (S.E.) km decade^{-1}, 20.5 ± 0.53 km decade^{-1} and 53.5 ± 1.15 km decade^{-1} with forcing from Earth System Models GFDL, IPSL and CCSM, respectively, under the SRES A2 scenario (Fig. 5). The ensemble rate of poleward range shift was estimated to be 30.1 ± 2.35 km decade^{-1}. Under the RCP 2.6 and 8.5 scenarios, average range shifts were projected to be 18.9 ± 0.5 km decade^{-1} and 30.1 ± 0.63 km decade^{-1}, respectively. The average rate of range shift under the RCP 2.6 scenario is significantly lower than the rate projected under RCP 8.5 ($p < 0.001$ ANCOVA) and SRES A2 scenario ($p < 0.001$ ANCOVA) (for consistency of the comparison, only outputs from GFDL were examined).

The poleward distribution shifts resulted in changes in species assemblages in the Northeast Pacific shelf regions (Fig. 6). Under the SRES A2 scenario, the ensemble (from the three Earth System Models) projected northward shift in species distributions of these selected west coast fish species led to higher rates of species invasion in the northern region (Fig. 6a). Particularly, high rates of species invasion were projected to occur in the northern Bering Sea and the northern Gulf of Alaska. Local extinction rates were highest in the California Current region (Fig. 6b). Areas of agreement, indicated by results from two or more earth system models showing species invasion or local extinction, are also concentrated in these regions (Fig. 6). The northern Bering Sea stood out as having the highest agreement on species invasion, while the coasts of Oregon and California exhibited the highest agreement on local extinction.

Changes in the Mean Temperature of Relative Abundance (MTRA), calculated from the projected changes in relative abundance of the species, suggest that increased greenhouse gas emissions will lead to increased warmer-water species in the Northeast Pacific region (Fig. 7). Specifically, the ensemble average rates of increase in MTRA were 0.12 °C decade^{-1}, 0.17 °C decade^{-1} and 0.32 °C decade^{-1} in the Bering Sea, Gulf of Alaska and California Current regions, respectively, under the SRES A2 scenario. Variation in projected change in MTRA between ESMs is highest in the Bering Sea, followed by Gulf of Alaska and California Current.

The ensemble mean rate of range shifts from the three alternative sets of model parameterizations was projected to be 45.4 ± 6.33 km decade^{-1} (Fig. 8). Although the rate of range shifts is higher than the projection from the main set of parameterizations, the overall trend remains consistent.

Discussion

Projections from this study provide quantitatively explicit hypotheses of potential effects of climate change on the
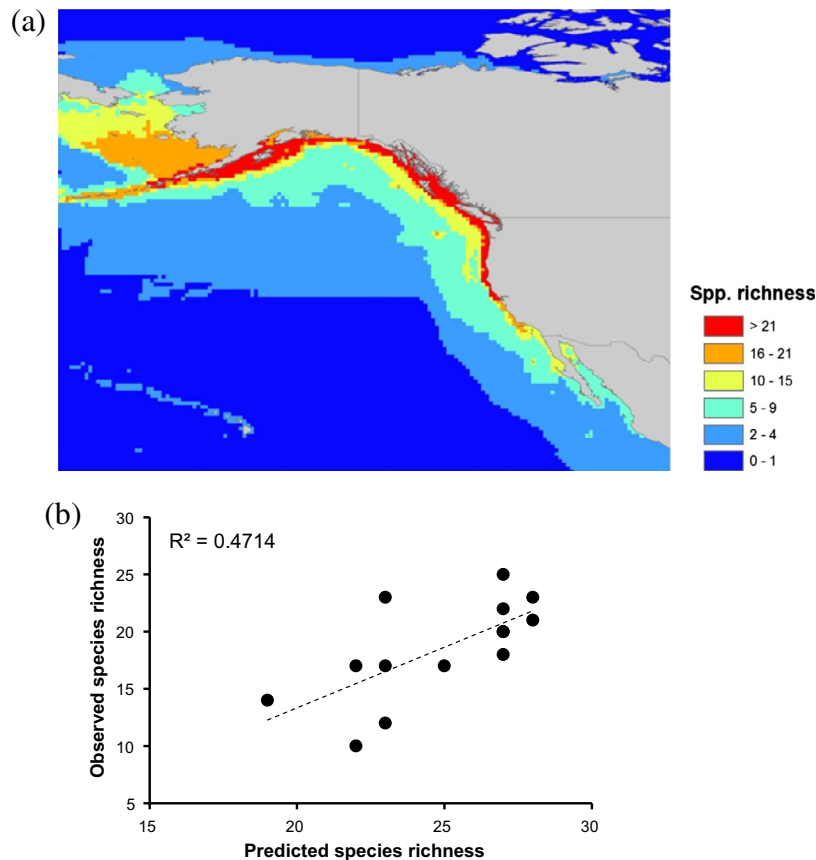
Fig. 3. Predicted species richness of 28 pelagic fish species calculated by counting the number of species with positive predicted relative abundance (a) plotted on a 30′ × 30′ grid map, and (b) compared against observed species richness in each sampling grid (Fig. 1). Dotted line is the best-fitted line from linear regression (ANOVA $p < 0.01$): observed species richness = 1.061 × predicted species richness – 7.864 .

distributions and assembly of 28 fish species that are well-represented in the pelagic fish surveys in the Northeast Pacific region. These hypotheses are: (1) the median of the latitudinal centroids of the species will shift northward with a rate that is dependent on the greenhouse gas emission trajectory; (2) occurrence of the study species will increase in the northern part of the region covered here, such as the Gulf of Alaska and the Bering Sea; (3) the epipelagic fish community will shift toward warm water species (indicated by the MTRA), particularly in the Gulf of Alaska and along the coast of British Columba.

Comparison with observed occurrence data and published data on thermal tolerance of the studied species suggests that the predicted present distributions are a reasonable representation of their observed ranges. Thermal tolerance limits of some of our studied species have been identified previously from laboratory studies—the upper thermal tolerance of *Sardinops sagax, Engraulis mordax* and *Gasterosteus aculeatus* were estimated to be 31.3 °C (Martínez-Porchas et al., 2009), 27.0 °C (Brewer, 1976) and 25.2 °C (Jordan and Garside, 1972), respectively, while the lower thermal tolerance of *S. sagax* and *E. mordax* were 6.3 °C and 11.5 °C, respectively. These upper and lower thermal tolerance estimates are close to those (5 and 95 percentile of the full preference scope) predicted from our model. The model predictions from occurrence records are within the range of those estimated from experiments. This is expected because wild fish avoid living in habitats at the edges of their temperature tolerance where mortality rates are higher. Our predictions are also consistent with observed temperature ranges of spawning habitat for *S. sagax* and *E. mordax*,

which are 13–25 °C and 11.5–16.5 °C, respectively (Lluch-Belda et al., 1991). Temperature ranges where pelagic eggs or larvae of these species are generally found are 13–20 °C and 15–28 °C, respectively for the two species (Takasuka et al., 2008). The temperature of spawning habitat is thus within the thermal tolerance ranges estimated from experiments (Brewer, 1976; Martínez-Porchas et al., 2009) and the preference ranges predicted here. This is expected as the latter estimates represent thermal ranges of all juvenile and adult stages, instead of just for spawning. Moreover, the ocean distribution of sockeye salmon (*O. nerka*) was estimated from survey data to have an upper thermal tolerance limit ranging between 7–15 °C (Welch et al., 1998), which is similar to the prediction from our model (12 °C). The agreement between these independent estimates of thermal tolerance and our predictions provides support to the validity of the predicted distributions.

The projected range shifts generally agree with empirical observations and other model projections. For example, our projected rate of shift in distribution centroid falls within the observed range [72.0 ± 13.5 km per decade at leading (poleward) range edges and 15.8 ± 8.7 km per decade at trailing (equatorial) edges] from a meta-analysis that included 857 marine species and assemblages (Poloczanska et al., 2013). Our projected range shift rates were slightly higher than the observed rates in the Bering Sea (Mueter and Litzow, 2008), the North Sea (Perry et al., 2005) and the Northeast U.S. continental shelf (Nye et al., 2009) over the last three decades. These studies included largely demersal species, which are suggested to have a slower response to climate change
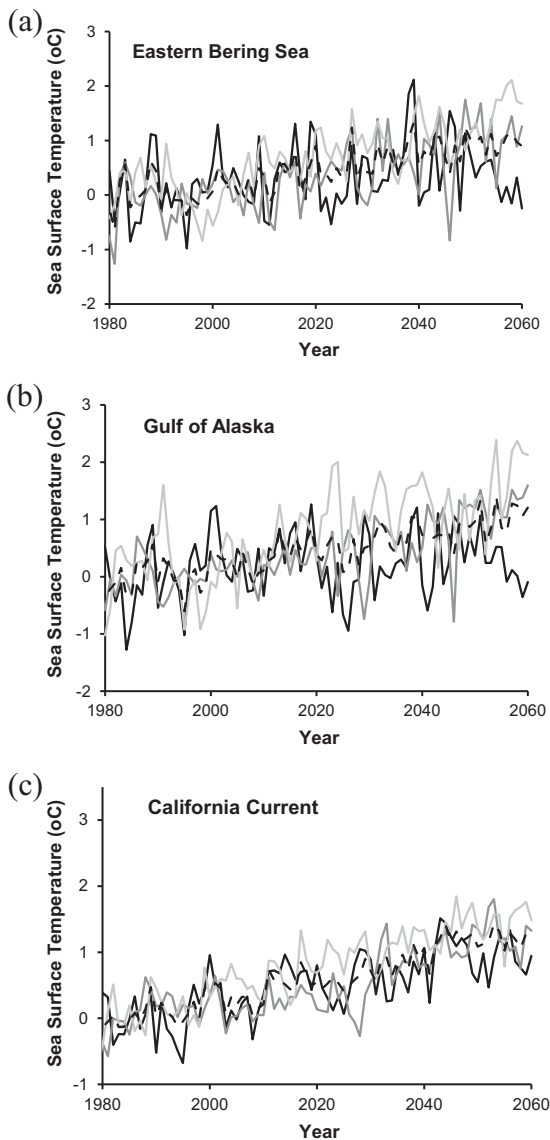
Fig. 4. Projected SST anomalies (relative to the average of 1971–2000 period) from 1971 to 2060 by (black) NOAA's GFDL ESM2M, (dark grey) IPSL-LOOP, (light grey) CCSM3 and (dotted line) ensemble average under the SRES A2 scenario: (a) East Bering Sea, (b) Gulf of Alaska and (c) California Current Large Marine Ecosystems.

2009b), our study included largely temperate species. Also, the projected rapid change in Arctic sea-ice extent in the next few decades, which is incorporated as an environmental factor in our model, increased the magnitude of changes in habitat conditions in these high latitude regions relative to lower latitude area. The projected sea ice trends from CMIP5 Earth System Models (include the three models used in this study) are generally consistent with observations (Stroeve et al., 2012). Simultaneously, the shift of warmer-water species into the high latitude regions would lead to considerable changes in community structure.

The shape of the coastline may also affect the extent of shifts in distributions and the resulting changes in community structure and function. Northward shifts of species ranges in the Northeast Pacific are limited by the landmass of Alaska. Further northward distribution shifts from the Gulf of Alaska can thus occur only through the Bering Sea and Bering Strait into the Arctic Ocean. Direction of shift may be following longitudinal temperature gradient instead of latitudinal gradient, as shown by an analysis of historical survey data (Pinsky et al., 2013).

Our estimates of changes in species richness are limited to the selected 28 fish species that represent a subsample of the species occurring in the West Coast of North America. These species are caught in large numbers in these pelagic fish surveys, which under-represent tropical species, particularly in the southern part of the study region. Furthermore, species diversity increases with decreasing latitude in the Northern Hemisphere, so there is a strong likelihood that many southern species whose centre of distributions lie to the south of our present study area may move into our region as observed off the West Coast of the US during El Niño or other warm anomaly years (Brodeur et al., 2006; Pearcy and Schoener, 1987). Differential spatiotemporal responses of species will reassemble biological communities and may lead to non-linear changes in ecosystem function through mis-matches of co-evolved species and novel and exotic interactions. The appearance of southern apex predators are also likely to alter the abundances and distributions of the examined species causing more community reorganization (Hazen et al., 2012). Analyses that consider the full assemblages of species and their interactions may result in larger projected changes in species compositions and richness, especially for the southern subareas. Future studies should include tropical species from areas south of the present study area to identify the broader set of potentially invading species.

The hypotheses of possible changes in major pelagic fish distributions and assemblage under climate change could also be examined by using observations from future pelagic fish surveys in the region. For example, average latitudinal centroids of the species over a time period included here could be calculated from catch-per-unit-effort (CPUE) data obtained from the surveys. Similar analyses examining the shift in species distributions were conducted elsewhere (e.g., North Sea; Perry et al., 2005). A simple index of species richness could be used to track species turnover and the community index presented in this paper could be calculated from observed changes in CPUE of the sampled species obtained from the surveys. Changes in these indices over time and between different regions could be compared against our model projections. Our analysis focused on species and geographic areas that are well-represented in the pelagic fish surveys (Orsi et al., 2007), thus making the projections more relevant to these surveys.

The effect of fishing is a major confounding factor in comparing future survey data with our projections to evaluate potential climate change signals in fish assemblages. The model used in our study does not account for fishing effects, but fishing is a major factor in shaping fish community structure, rendering it difficult to attribute observed community changes to climate and fishing effects. Populations with more vulnerable life histories e.g., large
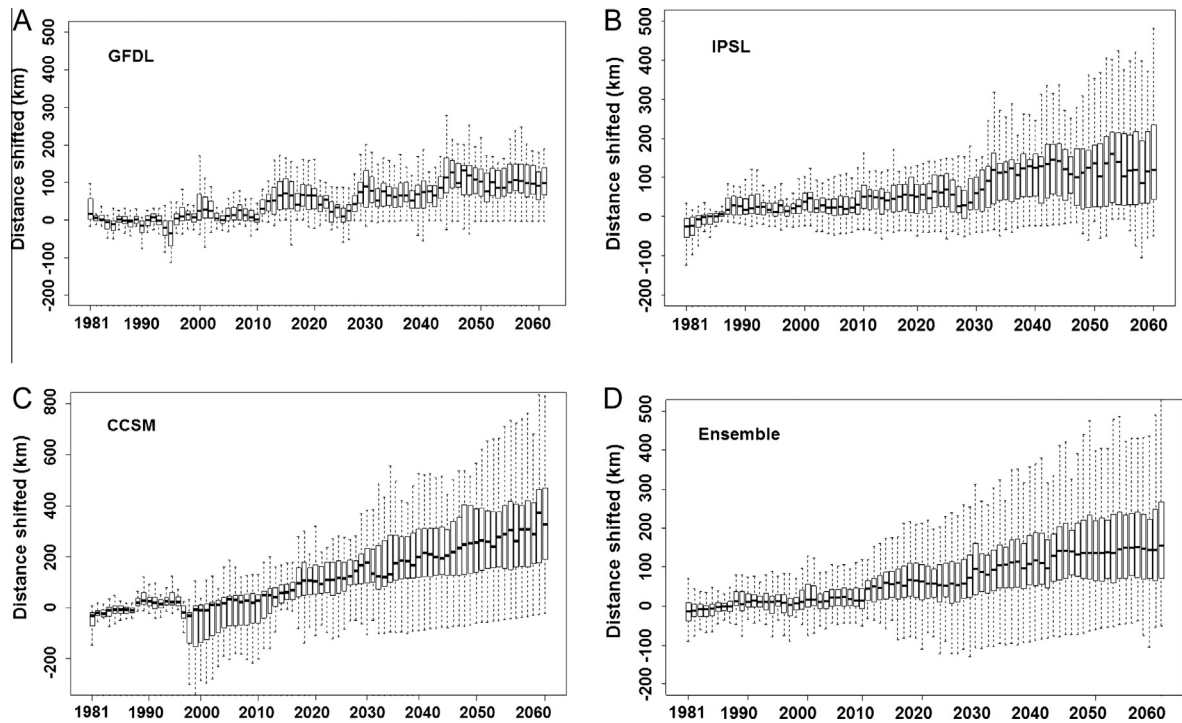
than pelagic species (Cheung et al., 2009b; Perry et al., 2005). For example, our predictions are similar to the shift rates of the pelagic species reported in Nye et al. (2009). The comparisons amongst warming scenarios in this study suggests that the rate of range shift is correlated with the rate of temperature change, with faster shift under higher emission scenario (SRES A2 and RCP 8.5) relative to the lower one (RCP 2.6). Thus, it is expected that the future rates of range shifts will be faster than those observed during the last few decades. Our projections are also comparable to the projected rate of range shift of pelagic fishes off Australia (Hobday, 2010).

The high latitude regions such as the Gulf of Alaska and Bering Sea may become 'hotspots' of changes. Cold-water associated species appear to have a narrower temperature preference range relative to warm water species, rendering them more sensitive to ocean warming (see Welch et al. (1998), on salmon in the Gulf of Alaska). Although tropical species have been shown to have a narrow temperature preference range as well (Cheung et al., 2013a,

Fig. 5. Predicted latitudinal centroids of the 28 pelagic fish species from 2005 to 2055 under the SRES A2 scenario that were driven by outputs from Earth System Models (a) GFDL (b) IPSL, (c) CCSM and (d) ensemble of projections driven by the three Earth System Models. The thick black line represents median, the box represents 25 and 75 percentiles while the dotted line represents upper and lower limits. Positive values represent poleward range shifts.

body size, late maturing, may be more sensitive to fishing (Cheung et al., 2007). Thus, insights about the relative influences of climate and fishing effects on observed population changes may be gained from comparison of changes in relative abundance and distribution of species with contrasting life history characteristics in terms of their vulnerability to fishing (Planque et al., 2010).

There are considerable uncertainties associated with the present projections, but the general trends revealed from the analysis should be robust. The first source of uncertainty is the projections of oceanographic conditions. These oceanographic projections were generated from a global atmospheric-oceanographic coupled model with a resolution of around 100 km (Stock et al., 2010). Such models generally have poor representation on the finer scale coastal and shelf sea processes, such as coastal upwelling. Indeed, warming may actually intensify coastal upwelling (Bakun et al., 2010), which would lead to cooler sea surface temperatures, but this is poorly-represented in global climate models. Some empirical evidence to support this comes from the observation that out of 63 Large Marine Ecosystems (LMEs) examined, only two showed decreases in temperature over the period 1982–2006, and both of these (California Current and Humboldt Current LMEs) were eastern boundary current upwelling ecosystems (Belkin, 2009). Bakun's hypotheis is also supported by a recent meta-analysis of published literature (Sydeman et al., 2014). Increases in offshore upwelling due to wind stress curl have occurred over the last few decades in the Southern California Current (Rykaczewski and Checkley, 2008), and this may also slow down coastal warming in the California Current region. There are also other inherent model and parameter uncertainties associated with the climate model. Regional oceanographic models (ROMs) may provide finer-scale projections that are more representative of the regions. However, at the time of this study, we did not have access to outputs from ROMs. The analysis presented here could be repeated

when outputs from ROMs become available and sensitivity to different model outputs could be evaluated.

There are uncertainties associated with the dynamic bioclimatic envelope model, and these have been discussed in detail in Cheung et al. (2011). These uncertainties include the equilibrium assumption of present species distributions, potential effects of factors not included in the model such as ocean acidification, trophic interactions, and species' evolutionary responses. However, coarse comparisons of projected rates of range shifts (in terms of latitudinal and bathymetric centroid shifts) from the dynamic bioclimatic envelope model with observations suggest that the projected trends are robust (Cheung et al., 2013b).

Sudden and dramatic shifts in oceanographic conditions ('regime shifts'), may lead to a major community and ecosystem reorganization in the Northeast Pacific (Anderson and Piatt, 1999; Chavez et al., 2003; Litzow and Ciannelli, 2007). The associated ecological changes such as prey availability or predation mortalities are not captured in our model. On the other hand, comparing data to be gathered in future surveys with these projections would help enable a subsequent version of the model to address these uncertainties. Also, the results from our study could be used as inputs to ecosystem or trophodynamic models to investigate the combined effects of range shifts and trophic interactions on biological communities and fisheries (Ainsworth et al., 2011). However, comparison of model outputs between dynamic bioclimate envelope models with and without consideration of trophic interactions in the North Atlantic and with stock assessment data suggest that consideration of trophic interactions increases the goodness-of-fit of the model outputs with data only slightly (Fernandes et al., 2013). This agrees with a meta-analysis of survey data around North America suggesting that temperature is more important than species characteristics in explaining observed species distribution shifts (Pinsky et al., 2013). Moreover, multi-model comparison of projected shifts
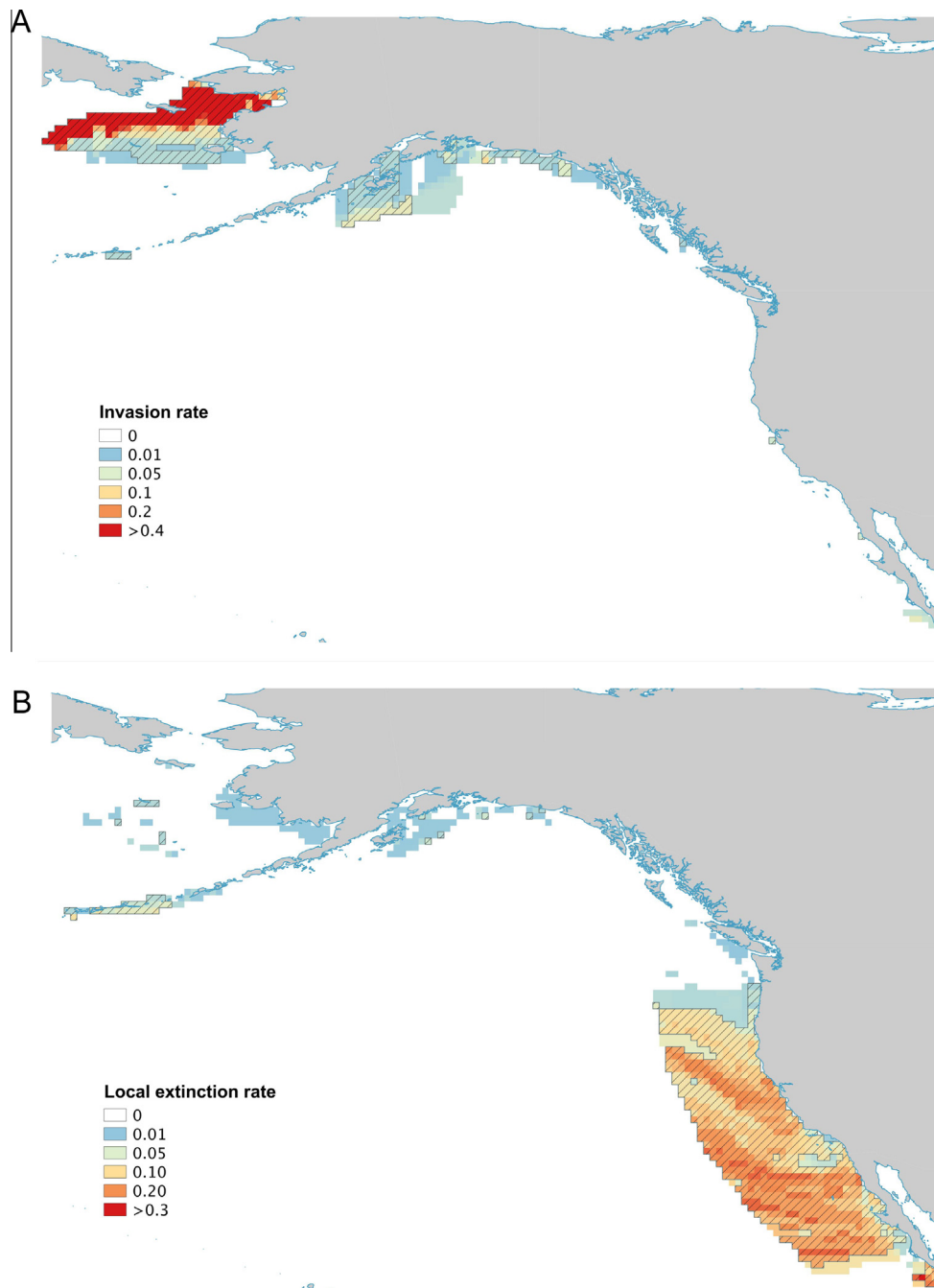
Fig. 6. Predicted changes in species assemblages in each 30′ × 30′ cell by 2050 relative to 2005 represented by (a) rate of species invasion and (b) rate of local extinction under the SRES A2 scenario. The results are ensemble outputs driven by the three Earth System Models. Cross-hatching represents areas where outputs from two or more models agree in the direction of changes.

in distribution that were driven by different climate models using three different species distribution models, including the dynamic bioclimate envelope model used in this study, did not find significant differences in the rates of range shifts amongst models (Jones et al., 2013). These studies suggest that, although the quantitative projections would vary between climate model outputs and structural and parameter uncertainty of the species distribution model, the general pattern should be more robust to these uncertainties.

Climate change may substantially affect ecosystem functions in the Northeast Pacific and especially in northern regions such as the

Bering Sea and the Gulf of Alaska due to large indicated assemblage shifts and likely major changes in community structure. Although the full effects of such community and ecosystem changes are difficult to predict, some insights may be gained by examining historical changes caused by climate variability. For example, in the Central Baltic Sea, reduced salinities and increased temperatures led to changes in dominance between the copepods *Pseudocalanus acuspes* and *Acartia* spp., while changes in hydrography and fishing effects led to changes in the dominance of fishes from cod (*Gadus morhua*) to sprat (*Sprattus sprattus*) (Möllmann et al., 2008). In the Bering Sea, changes in climate, sea ice extent and hydrographic
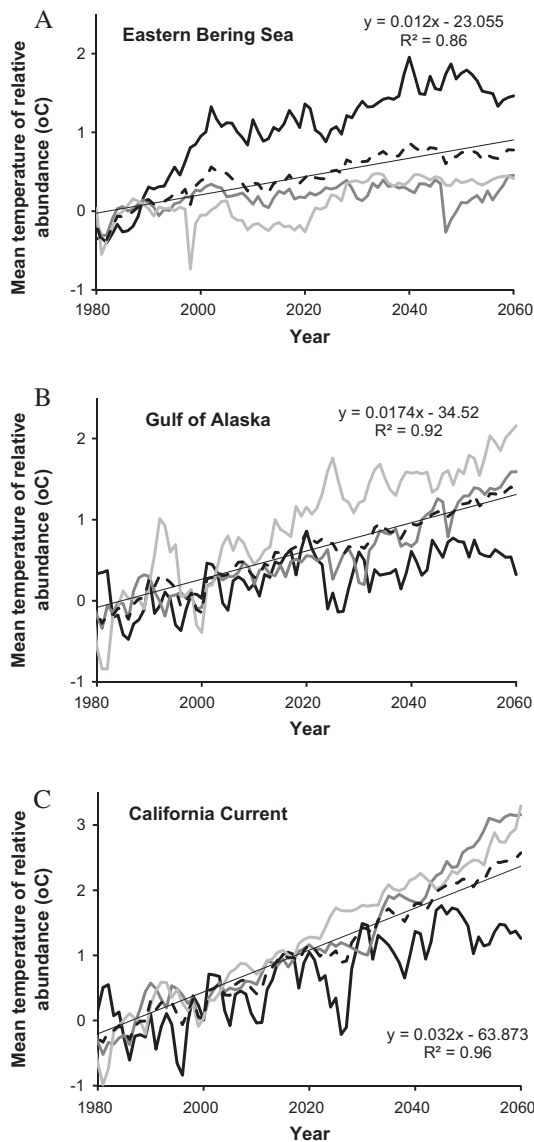
Fig. 7. Calculated Mean Temperature of Relative Abundance from 2000 to 2050 under the SRES A2 scenario based on outputs driven by GFDL (black line), IPSL (grey line), CCSM (dotted line) and the multi-model ensemble (red line) in (a) the Eastern Bering Sea, (b) the Gulf of Alaska; and (c) the California Current. Positive index values indicate increased warmer-water species in the community while negative index values indicate increased cold-water species.

Fig. 8. Sensitivity analysis showing the variation in projected range shifts from three alternative sets of model parameters. Ensemble of rate of latitudinal distribution centroid shifts simulated using three different sets of initial model parameter settings. The thick black line represents median, the box represents 25 and 75 percentiles, and the dotted line represents upper and lower limits. Positive values represent poleward range shifts.

Conclusions

Using results from a dynamic bioclimatic envelope model, we developed quantitatively explicit hypotheses of possible changes in the distributions and assembly of fishes in the coastal epipelagic zone commonly captured over Northeast Pacific Ocean continental shelves. These hypotheses include poleward migration of species, increased species invasions, and shifts to more warm-water dominant communities by 2050 if the current trajectory of greenhouse gas emissions continues. Our projections indicate that impacts will be most intensive in the northern subareas, such as the Gulf of Alaska and the Bering Sea, but changes in the southern part of our study area may have been underestimated due to the limited set of species examined. Our projections focus on species and subareas that are well-represented the pelagic fish surveys that have been conducted in the over North-eastern Pacific continental shelves since the 1990s. We propose that the hypotheses generated from this study should be tested with data collected from future surveys. Although there are high uncertainties associated with our projections, the overall trends should be robust with the exception of the possible southern underestimation bias discussed above. Data collected from the surveys and the availability of projections from Regional Oceanographic Models would be useful to improve the analysis and projections of climate change effects on pelagic communities in the region.

Acknowledgements

conditions in the past decade lead to changes in biological communities, including shifts in marine mammal distributions, reductions of benthic prey populations, and increases in pelagic fishes (Grebmeier et al., 2006). These changes may have large implications for ecosystem services, particularly fisheries (Benson and Trites, 2002). Recent projections suggest that shifts in distributions and changes in primary productivity under likely greenhouse gas emission scenarios may result in large changes in potential catches, with potential gains in higher latitudinal regions such as Alaska whereas tropical regions such as the Pacific coast of Mexico may experience decreases in potential catch (Cheung et al., 2010). Since, according to Pinsky and Fogarty (2012), commercial fisheries may not keep pace with the poleward shift in target species distributions, studies developing scenarios of potential climate change impacts from biophysical to socio-economic changes will be useful for developing climate mitigation and adaptation policies in the regions (Melnychuk et al., 2014).
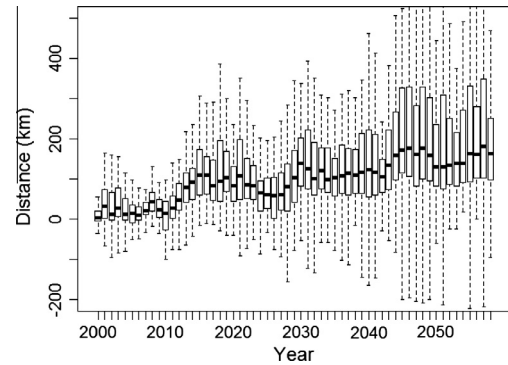
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