

Original Articles

Predicting the habitat suitability for populations of Pacific cod under different climate change scenarios considering intraspecific genetic variation

Linjie Li^a, Linlin Zhao^b, Jinbo Fu^a, Bin Sun^a, Changdong Liu^{a,*}

^a Department of Fisheries, Ocean University of China, Qingdao, Shandong, China

^b First Institute of Oceanography, Ministry of Natural Resources, Qingdao, Shandong, China



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ABSTRACT

Several studies have demonstrated the importance of integrating intraspecific genetic variation in forecasting the habitat suitability of species under climate change scenarios. The Pacific cod (*Gadus macrocephalus*) is an economically important fish species in the North Pacific that can be classified into western and eastern populations based on molecular phylogeographic data. Herein, we first quantified the realized niche of the two Pacific cod populations using n -dimensional hypervolumes and estimated the niche differentiation between the populations. We then projected the habitat suitability based on the georeferenced occurrence records and environmental predictors using species distribution models (SDMs) at the population and species levels. The low niche overlap demonstrated the marked niche differentiation between the two populations. The distinct responses of the populations to climate predictors implied that the population-level SDM produced more reliable projections than the corresponding species-level SDM. The model indicated that the eastern population expanded its suitable area northward, while maintaining most of its current habitat and exhibited resilience to climate impacts. However, the western population lost much of its current suitable area, while colonizing a new habitat in a small section of the offshore waters of the Japanese Sea, implying the vulnerability of this population to climate change. This study highlights the necessity of incorporating intraspecific genetic variation into SDMs to predict the habitat suitability of Pacific cod on the global scale. The spatiotemporal predictive maps of habitat suitability provide crucial information for designing climate-adaptive conservation and management strategies based on more precise taxonomic units for the sustainability of Pacific cod.

1. Introduction

Global climate change and anthropogenic activities have dramatic impacts on the population dynamics of species worldwide, resulting in significant changes in geographic range, phenology and species interactions (Walther et al., 2009). Oceans serve as a major carbon reservoir for the global ecosystem and absorb large amounts of heat in the climate system (Reid et al., 2009). This has caused significant changes in the marine environment, such as a decline in net primary productivity, a rise in water temperature, hypoxia, acidification (IPCC, 2019), which are probably beyond the ecophysiological limits and result in habitat loss, even extinction of many species (Penn and Deutsch, 2022). Marine communities are more likely to be affected by environmental alteration induced by climate change than terrestrial

communities (Sorte et al., 2010). Previous studies have indicated that many marine species will migrate to higher latitudes or deeper waters to search for suitable niches in the face of changing climate (Dulvy et al., 2008; Fossheim et al., 2015; Kleisner et al., 2016, 2017; Sorte et al., 2010; Spies et al., 2020). Fishes are important members of marine communities. Thus, exploring the potential distribution of the critical economic and ecological species under future climate change scenarios will help guide the conservation and management of these species (Ciannelli et al., 2020). The studies on climate impacts have generally focused on the conservation of endangered species (e.g., Fu et al., 2021; Tulloch et al., 2018; Zhang et al., 2020b). More recently, several studies realized the importance of estimating climate impact on the habitat distributions of some key fish species for designing adaptive conservation and management strategies (Chang et al., 2021; Chen et al., 2021;

* Corresponding author at: Department of Fisheries, Ocean University of China, No. 5, Yushan Road, Qingdao, Shandong, China.
E-mail address: changdong@ouc.edu.cn (C. Liu).

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Zhang et al., 2019).

Pacific cod is a typical cold-water demersal fish species that is widely distributed around the rim of the North Pacific (Alderdice and Forrester, 1971). As prey, Pacific cod is a staple food for many marine mammals, including the endangered Steller sea lion (Calkins, 1998). Historically, Pacific cod has supported both large- and small-scale commercial fisheries because of its abundance and high nutritional value (Cunningham et al., 2009). Due to overfishing and environmental degradation, the Pacific cod population has undergone a substantial overall decline, with a trend toward recovery in recent decades (FAO, 2020). Given the economic significance of Pacific cod, it is vital to estimate the impacts of climate change on the habitat of this species.

Over the past two decades, species distribution models (SDMs) have been extensively used to study the habitat suitability of species (e.g., Elith and Leathwick, 2009; Guisan and Thuiller, 2005; Guisan et al., 2017). They establish species-environment relationships based on geographical species occurrence data and related environmental variables (e.g., climatic and topographic variables). The SDMs generated with observed data can be used to predict the future potential distribution of species when the future predictor variables can be projected based on different assumptions regarding greenhouse gas concentration. The SDMs applied in marine systems in recent decades have primarily been constructed at the species level following the traditional theory of “niche conservatism” (Marshall et al., 2014; Robinson et al., 2011). This theory assumes that the entire species responds consistently to climatic features and maintains an identical niche space over time and space (Guisan et al., 2017; Peterson et al., 1999; Smith et al., 2019). However, the insurance hypothesis proposed by Yachi and Loreau (1999) suggests that intraspecific genetic variation contributes to the ability of a species to use resources (Joshi et al., 2001; Kreyling et al., 2011) and thus adapt to climate change (Davis and Shaw, 2001; Seiler-Marie et al., 2004; Skelly et al., 2007). Studies have shown that it is relatively common for spatially segregated populations of the same species to evolve to exhibit a locally optimal phenotype when experiencing spatially varying environments; this phenomenon is known as “local adaptation” (Davis and Shaw, 2001; Hereford, 2009; Kawecki and Ebert, 2004). Therefore, establishing SDMs at the population level, as opposed to the species level, may lead to more reliable results (Smith et al., 2019).

Approximately 3 to 3.5 million years ago, soon after the Bering Strait opened, Pacific cod dispersed into the Pacific Ocean (Grant and Ståhl, 1988). The western Pacific Ocean is characterized by complex hydrographic conditions with dramatically variable water depths, water temperatures and complex coastlines compared with the eastern Pacific Ocean (Ma et al., 2021). Over a long evolutionary history, the populations of Pacific cod living in the distinct environmental conditions of the western and eastern Pacific Ocean will gradually adapt to their respective environmental conditions. Meanwhile, the high fidelity of Pacific cod (Spies, 2012) combined with the presence of barriers in the form of currents (Gaylord and Gaines, 2000), deep ocean trenches (Schüller, 2011) and temperature gradients (Stevenson and Lauth, 2019) likely decreased the genetic exchange and contributed to the population divergence of Pacific cod. Previous molecular phylogeographic studies revealed that since the Pleistocene ice-ages, Pacific cod has differentiated into two distinct genomic groups: the western population (WP) and the eastern population (EP) of the North Pacific (Grant et al., 1987; Canino et al., 2010).

Global warming has been shown to have a greater negative impact on cold-water species than on warm-water species because of the decreased range of suitable habitats (Ma et al., 2021, 2019; Tian et al., 2008). In this study, we quantified the realized niches of the cold-water species of Pacific cod and constructed SDMs at the species and population levels to test the following hypotheses: (1) the niche spaces of WP and EP are highly divergent because of local adaptation; (2) the two populations respond differently to climate change, and the SDMs at the population level produce more reliable results than those at the species level; and (3) the potential distribution of Pacific cod under future climate

conditions will shift to higher latitudes or deeper waters. The results of our study are expected to provide important information for designing adaptive conservation and management strategies for the Pacific cod under climate change scenarios.

2. Materials and methods

2.1. Study area and species occurrence records

The North Pacific and part of the Arctic Ocean are known to be the main distribution areas of Pacific cod and were selected as our study locations (i.e., 115°E–120°W, 25°N–75°N; Fig. 1). Occurrence data of Pacific cod were obtained from the published literature (Li et al., 2021; Napazakov, 2008; Sakuma et al., 2019; Smirnova et al., 2015; Suda et al., 2017) and two online databases: Ocean Biogeographic Information System (OBIS, <https://obis.org>) and Global Biodiversity Information Facility (GBIF, <https://www.gbif.org>). To minimize sampling bias, we spatially thinned the occurrence data by setting a radius of 9.2 km consistent with the environmental layer resolution using the R package *spThin* (Aiello-Lammens et al., 2015). After this data cleaning procedure, a total of 2585 occurrence records were retained. According to the genetic differentiation studies of Grant (1987) and Canino (2010), Pacific cod has differentiated into two populations: the WP, with 371 occurrence records, and the EP, with 2214 occurrence records (Fig. 1).

2.2. Predictor variables

Due to data availability and considering species-environment associations, we initially selected ten environment variables which potentially affected the distribution of Pacific cod (Table 1). Water temperature, current velocity, salinity and ocean depth have been proven to be the critical factors limiting the distribution of marine fish species (Bosch et al., 2018; Goldsmit et al., 2018). Pacific cod is omnivorous, feeding on algae, crustaceans, cephalopods and fish species (Lang and Livingston, 1996). Chlorophyll concentration, usually used as a proxy for primary productivity, affects the prey distribution of Pacific cod (Gregor and Maršálek, 2004; Huot et al., 2007). Therefore, chlorophyll concentration was selected as a predictor. Since it is a benthic species, bottom topography is likely to affect the distribution of Pacific cod. Because of the lack of topography data, we included distance to shore as a predictor considering its general correlation with topography. All the predictor variables were downloaded from the online datasets of Bio-ORACLE v2.1 (Assis et al., 2018) and MARSPEC v1.0 (Sbrocco and Barber, 2013) with a spatial resolution of 5 × 5 arc-minutes (i.e., 9.2*9.2 km at the equator; Table 1).

To reduce the impact of collinearity on the estimation of the importance of predictors, the pairwise Pearson’s correlation coefficients among the 10 predictors were calculated. One of the two variables with a Pearson’s correlation coefficient greater than |0.7| was removed (details in Supporting Information Fig. S1) (Dormann et al., 2013). Finally, seven predictor variables, including mean water temperature (Tmean), mean current velocity (CV), mean salinity (Sal), mean chlorophyll concentration (Chlmean), minimum chlorophyll concentration (Chlmin), ocean depth (Dep) and distance to shore (DTS), were retained for modeling analysis (Table 1).

Bio-ORACLE provides future predictive values for current velocity, salinity, water temperature and chlorophyll concentration using 3 atmospheric-ocean general circulation models (AOGCMs: CCSM4, HadGEM2-ES and MIROC5) under four Representative Concentration Pathways (RCPs): RCP 2.6, RCP 4.5, RCP 6.0 and RCP8.5. We used the average predictive values of three AOGCMs to represent future climate conditions to reduce uncertainty (Assis et al., 2018). RCP2.6-RCP8.5 represent greenhouse gas concentrations from low (optimistic emission levels) to high (pessimistic emission levels) (Moss et al., 2010). Here, we used two RCPs (RCP 2.6 and RCP 8.5) for future distribution prediction in the periods of the 2050s (2040–2050) and 2100s

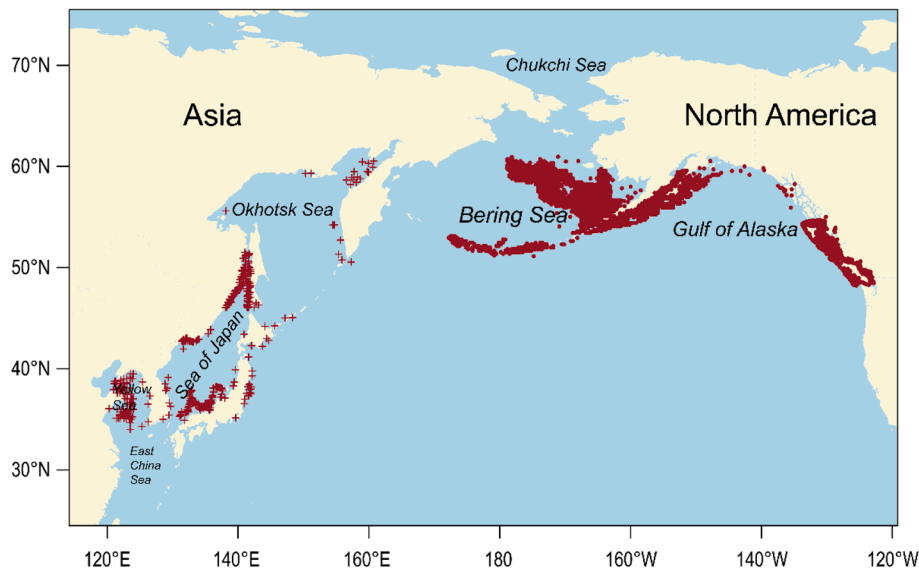


Fig. 1. Map of the study area. Red crosses and red points correspond to the available occurrence records of WP and EP of Pacific cod, respectively. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 1

Ten environment variables were initially selected for the model analysis. Chlorophyll concentration was measured at surface and the other variables except for water depth and distance to shore were measured at bottom. ‘√’ indicated the variable was retained after the collinear estimation and ‘×’ indicated the variable was removed because of its high correlation with other variables.

Environment variable	Unit	Source	Used (√) or not (×)
Mean current velocity	m/s	https://www.bio-oracle.org	√
Mean salinity	PSS	https://www.bio-oracle.org	√
Maximum water temperature	°C	https://www.bio-oracle.org	×
Minimum water temperature	°C	https://www.bio-oracle.org	×
Mean water temperature	°C	https://www.bio-oracle.org	√
Maximum chlorophyll concentration	mg/m ³	https://www.bio-oracle.org	×
Minimum chlorophyll concentration	mg/m ³	https://www.bio-oracle.org	√
Mean chlorophyll concentration	mg/m ³	https://www.bio-oracle.org	√
Water depth	m	https://marspec.weebly.com/modern-data.html	√
Distance to shore	km	https://marspec.weebly.com/modern-data.html	√

(2090–2100). Water depth and distance to shore were assumed to be unchanged in the future (Zhang et al., 2020a).

2.3. Niche comparison between the WP and EP

The seven environmental predictors were used to describe the environmental conditions where the Pacific cod occurred. To reduce the dimension of niche space, we first conducted a principal component analysis (PCA) on these predictors and the first four principal components were retained since they cumulatively explained 83.6 % of the total variance (Fig. S2). We then calculated the four-dimensional hypervolumes for the WP and EP respectively based on the values of retained principal components corresponding with the occurrence records of each population using the R package *hypervolume* (Blonder, 2019). The size of the realized niche space can be quantified by the volume of hypervolume (a unitless metric). We overlapped the hypervolumes of the WP and EP populations to estimate the niche

differentiation between these two populations using the R package *BAT* (Cardoso et al., 2021). The total niche differentiation (β_{Total}) can be decomposed into two components: niche shift, corresponding to the replacement of space between the hypervolumes occupied by two species, and niche contraction/expansion, indicating the net differences between the amount of space encompassed by each hypervolume (Carvalho and Cardoso, 2020; Mammola et al., 2020). β_{Total} ranges from 0 to 1, representing complete overlap to complete separation of two hypervolumes (Carvalho and Cardoso, 2020).

2.4. Modeling procedures

We conducted SDM analysis based on the *biomod2* package in the R platform (Thuiller et al., 2020). Ten modeling algorithms are included in this package: multiple adaptive regression splines (MARS), maximum entropy (Maxent), random forest (RF), surface range envelope (SRE), artificial neural network (ANN), flexible discriminant analysis (FDA), classification tree analysis (CTA), generalized boosting model (GBM), generalized linear model (GLM), and generalized additive model (GAM). Since true absence data were lacking, we simulated 20,000 random pseudo-absence records based on the environmental conditions contrasting with those of species presence (Barbet-Massin et al., 2012; Guisan et al., 2017). The predictive performance of each model was tested using a fivefold cross-validation method (Guisan et al., 2017). This method splits the data randomly in a 4:1 ratio; 80 % of the data are used to train the model, and the remaining 20 % are used to validate the model (Guisan et al., 2017). True skill statistics (TSS) and the area under the receiver operating characteristic curve (AUC) were calculated for each model to assess the predictive performance (Allouche et al., 2006; Swets, 1988).

To reduce the uncertainty of individual models, we constructed an ensemble model using a weighted averaging algorithm that included models with relatively high predictive performance (Guisan et al., 2017; Thuiller et al., 2019). Individual models with mean TSS > 0.8 and AUC > 0.9 were retained to build the ensemble model (Araujo et al., 2005). In addition to TSS and AUC, we also used the continuous Boyce index (CBI), a threshold-independent metric, to assess the predictive ability of the model due to its superiority for presence-only data (Allouche et al., 2006; Hirzel et al., 2006). This index ranges from -1 to 1, where positive values indicate that model predictions are consistent with the distribution of the test dataset, values close to zero indicate predictions made by chance and negative values indicate poor predictive quality. The

modeling analysis was conducted at the species level (species model) and population level (WP model and EP model).

The relative importance of each predictor variable for modeling the distribution of Pacific cod was assessed by a randomization method (Guisan et al., 2017). This method calculated the Pearson correlation (r) between the predictions based on all predictor variables and the predictions where the predictor variable being evaluated was randomly permuted; high correlations between the two predictions indicated that the evaluated variable was not important. The relative importance of each environmental factor was calculated by $1 - |r|$. Continuous habitat suitability maps for the present time and in the 2050s and 2100s assuming RCP 2.6 and RCP 8.5 were built based on the outcomes of the ensemble models at the species and population levels. For ease of interpretation, continuous habitat suitability projections were converted into binary maps by maximizing the probability threshold of TSS (Liu et al., 2013).

3. Results

3.1. Realized niche comparison between the two populations

The four-dimensional hypervolume of the WP (155.41) was slightly larger than that of the EP (122.00). The niche differentiation between the two populations was large ($\beta_{Total} = 0.827$), mainly due to contraction/expansion (0.142), accounting for 17.17%, and niche shift (0.685), accounting for 82.83% (Fig. 2). Comparison of the position of the niche centroid of the two populations revealed that the second principal component (PC2), mainly explained by salinity and ocean depth, did not cause niche differentiation between the two populations (Figs. 2, 3). Niche differentiation was primarily caused by Tmean, Chlmean and Chlmin (Figs. 2, 3, S2).

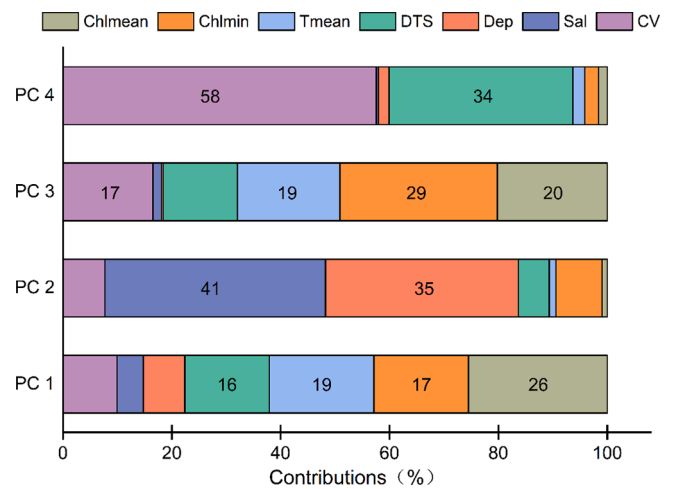


Fig. 3. Contribution of environmental predictors to each principal component (PC). The number in the bar indicates the contribution rate (%) of each predictor to PC axes, and only values >15% are shown. Chlmean - mean chlorophyll concentration; Chlmin - minimum chlorophyll concentration; Tmean - mean temperature; DTS - distance to shore; Dep - ocean depth; Sal - salinity; CV - current velocity.

3.2. SDM projections

The predictive performance varied among the 10 modeling algorithms indicated by different TSS and AUC values. The modeling algorithms with the highest predictive performance retained for building the ensemble models at the population and species levels were the same: ANN, CTA, FDA, GAM, GBM, GLM, MARS, MAXENT and RF (Fig. 4). The

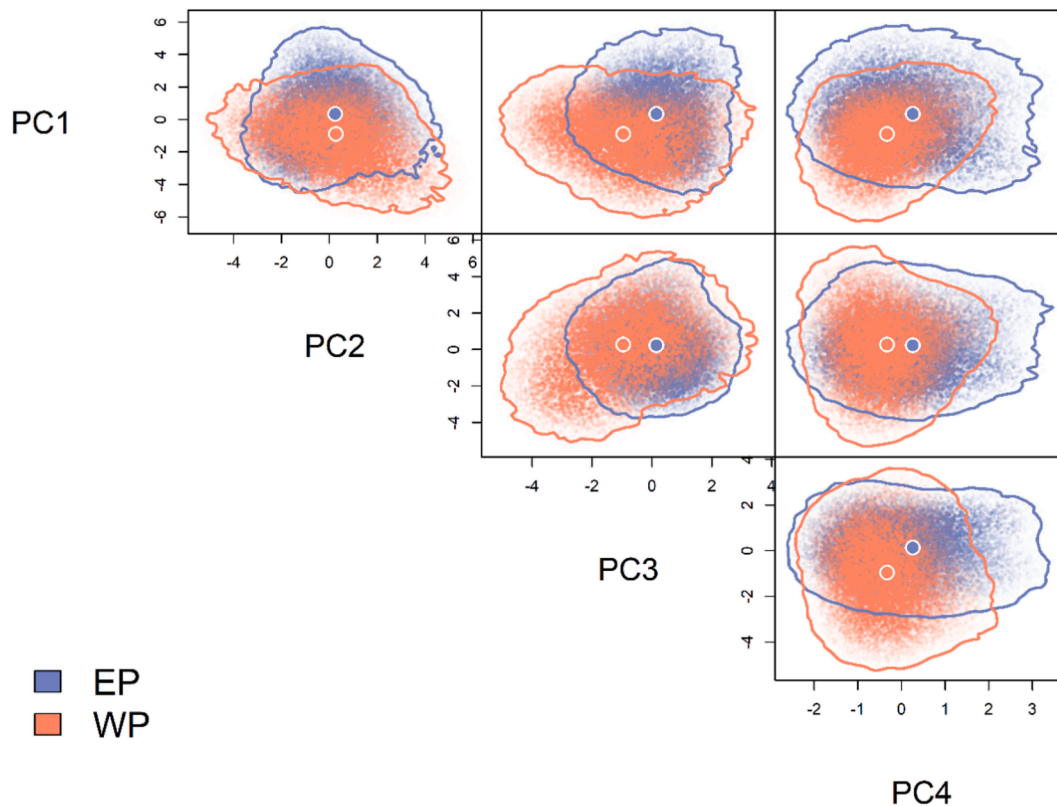


Fig. 2. The realized niches of the two populations of Pacific cod quantified via four-dimensional hypervolumes. To visualize the shape and boundary of the hypervolumes in two dimensions, a random selection of 20,000 stochastic points for each hypervolume was used. The large blue and orange points indicate the mean niche position (niche centroid) of EP and WP, respectively. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

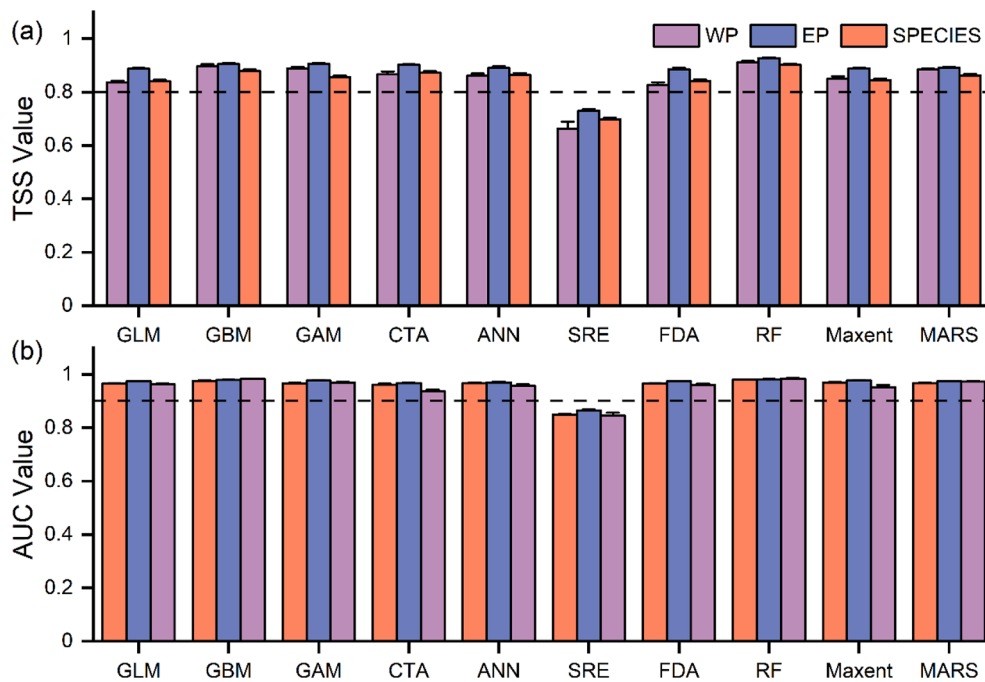


Fig. 4. Predictive abilities of the ten modeling algorithms in projecting the distribution of Pacific cod at the population and species levels. (a) the True Skill Statistics (TSS) value; (b) the Area Under the receiver operating characteristic Curve (AUC) value. Data are expressed as mean \pm standard error. The dashed line indicates the cut-off value used to build the ensemble model.

high TSS (WP: 0.939, EP: 0.925, Species: 0.905) and CBI (WP: 0.997, EP: 0.978, Species: 0.994) values of the three ensemble models indicated high predictive accuracy.

The relative importance of each environmental predictor varied among the three ensemble models (Fig. 5). The population-level model showed that Sal and DTS contributed most to the distribution of the WP, whereas Tmean and Chlmean were the most important predictors of the distribution of EP. The species-level model showed that Sal and Tmean were the most important predictors affecting the distribution of Pacific cod.

3.3. Habitat suitability under current and future climate scenarios

The predicted distributions of Pacific cod from the EP and WP were mainly located in the eastern and western areas of the North Pacific, respectively, implying the niche differentiation of western and eastern populations (Fig. 6). The predicted suitable habitat for the EP (3,471,000 km²) was larger than that of the WP (2,879,100 km²), and a substantial part of the suitable area for the EP was located close to the Bering Sea. The predicted results from the species model are presented in Fig. 7 a, c. Both the continuous and binary predictive plots showed that the predicted suitable area from the species model is similar to that from the EP model in the east of the North Pacific and is smaller than

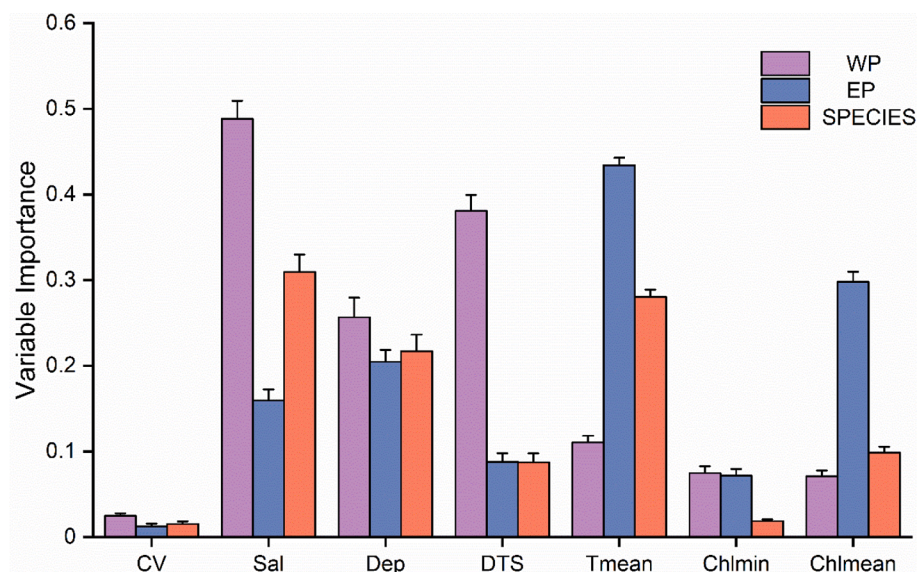


Fig. 5. Relative importance of the seven predictor variables in the three ensemble models built at population and species levels. Data are expressed as mean \pm standard error. CV - current velocity; Sal - salinity; Dep - ocean depth; DTS - distance to shore; Tmean - mean temperature; Chlmin - minimum chlorophyll concentration; Chlmean - mean chlorophyll concentration.

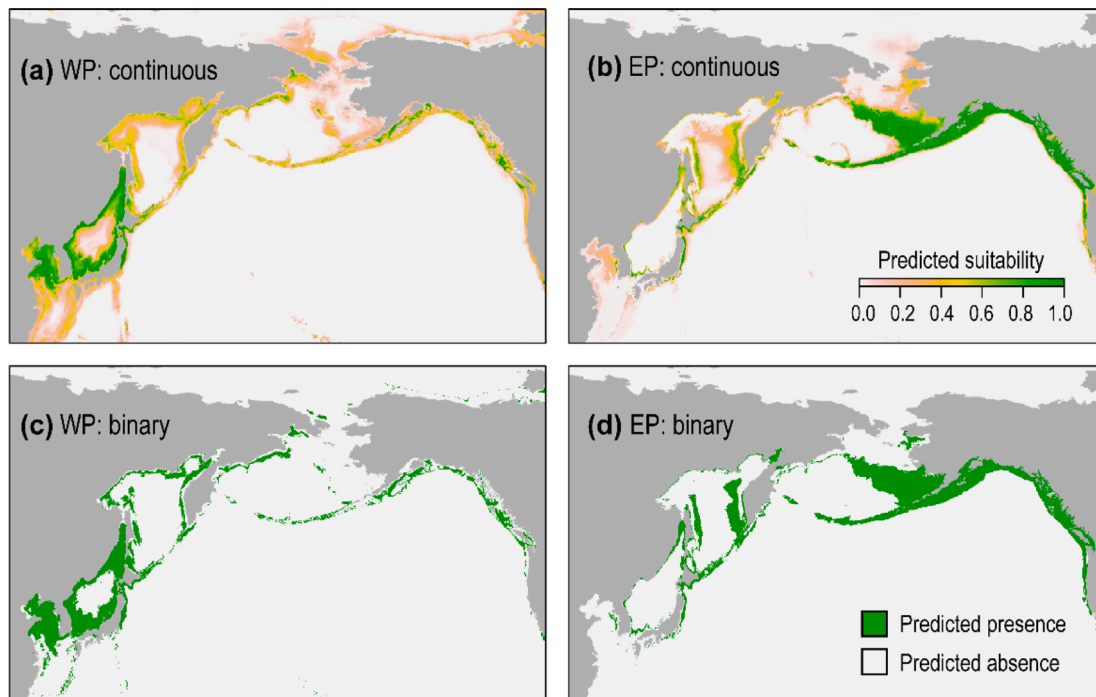


Fig. 6. Habitat suitability map of Pacific cod projected by ensemble models built at the population level under current climate scenario. (a, c) are the respective continuous and binary plots of the WP; (b, d) are the corresponding plots of the EP.

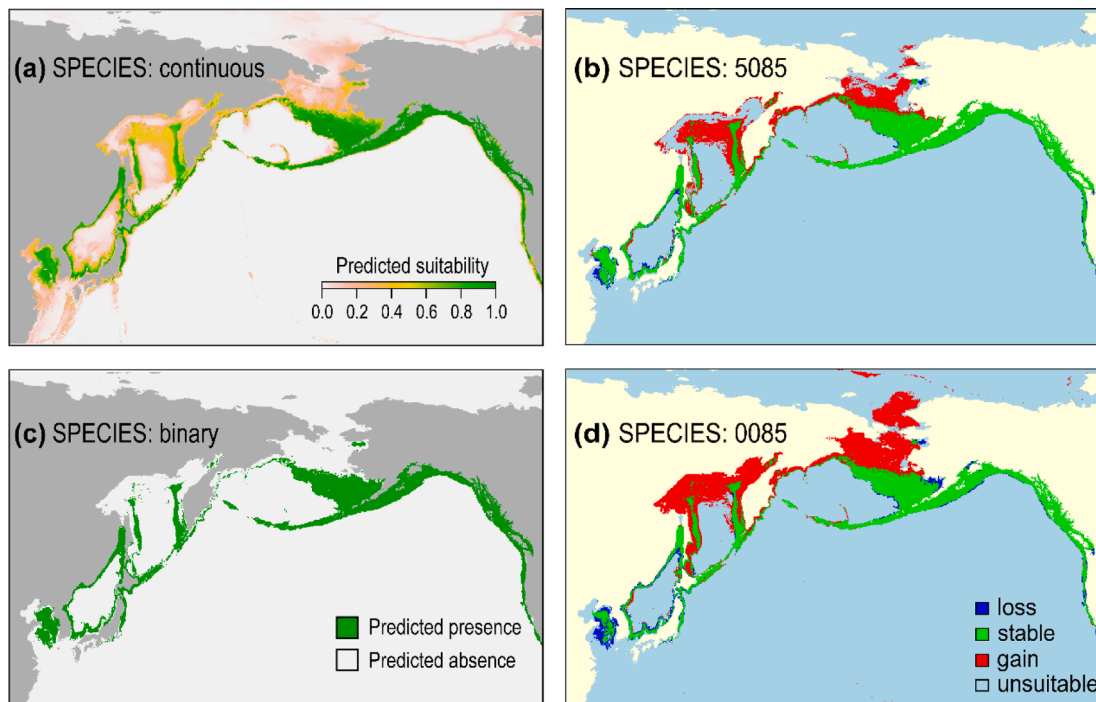


Fig. 7. Habitat suitability map of Pacific cod projected by the ensemble models built at the species level under current and future climate scenarios. (a, c) are the respective continuous and binary plots of the species; (b, d) are the predicted change of the suitable habitat in 2050 s under RCP 8.5 (5085) and in 2100 s under RCP 8.5 (0085).

that from the WP model in the west of the North Pacific.

The predicted change in suitable habitat implied the differentiated responses of the two populations to climate change (Table S1, Fig. 8). For the WP, the suitable area was mainly stable in the Sea of Japan, with a small increase (3.66 %) for RCP 2.6 in the 2050 s and a decreasing trend in all other climate change scenarios. The results of the EP model

predicted that most of the suitable area would be retained in the future, additional suitable area would be found in the Northwest Pacific, close to the north Bering Sea and the Sea of Okhotsk, and a small part of the current suitable area in the southeastern part of the Northeast Pacific would be lost (Table S1). The predicted results of the species model were similar to those of the EP model (Fig. 8 b, d).

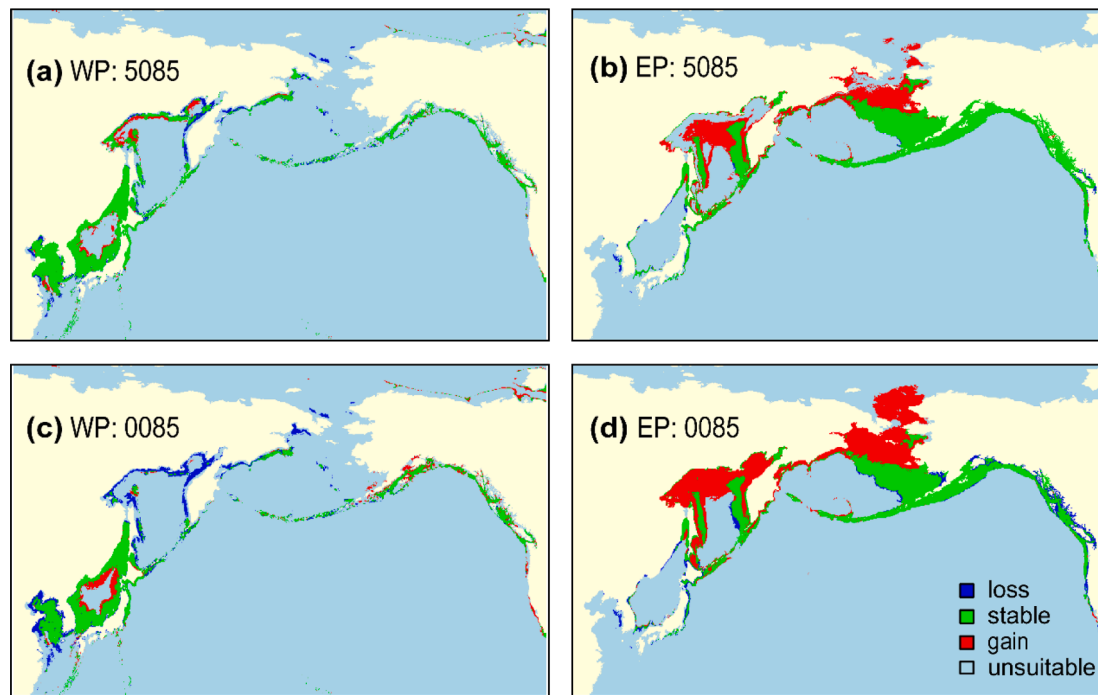


Fig. 8. The predicted change of the suitable habitat based on the ensemble models built at the population level in 2050 s under RCP 8.5 (5085) and in 2100 s under RCP 8.5 (0085) for WP (a, c) and EP (b, d).

4. Discussion

In this study, we quantified the realized niches of two Pacific cod populations and found significant niche differentiation between the two populations; this was driven mainly by niche shift. The results indicated that the spatially separated populations of Pacific cod occupy different niche spaces, and niche conservatism does not apply to this species. We then developed SDMs for the WP and EP separately considering the local adaptation of these populations to environmental conditions when estimating the impacts of climate change on their potential distribution. The WP and EP exhibited different responses to predictor variables, implying the distinct environment conditions where they lived probably led to the genetic divergence of these populations. This highlights the importance of considering intraspecific genetic variation in projecting the potential distribution of species when local adaptation exists.

4.1. Intraspecific variation in SDMs

Previous SDMs were commonly constructed at the species level based on the “niche conservatism” theory assuming intraspecific phylogenetic homogeneity (e.g., Chefaoui et al., 2018; Hällfors et al., 2016; Jayathilake and Costello, 2018; Peterson et al., 1999; Zhao et al., 2020). Recently, however, more studies have demonstrated intraspecific differential response to climatic predictors and highlighted the importance of focusing on the population level when implementing SDMs (e.g., Collart et al., 2021; Hu et al., 2021; Ikeda et al., 2017; Zhang et al., 2021). The genetic differentiation evidenced by the previous molecular analyses coupled with the niche differentiation verified by this study for the WP and EP implied the significance of building SDMs at the population level to account for local adaptation (Grant et al., 1987; Canino et al., 2010). Our population-level SDMs demonstrated the variable responses of populations to environmental gradients, implying that pooling population data to construct a global SDM at the species level may mask local differences in response to environmental conditions. Liu et al. (2017) explored the relationships between walleye (*Sander vitreus*) distribution and habitat variables in Lake Erie and found significant spatially variable responses of this species to habitat variables. They

postulated that the variable responses to environmental predictors were due to intraspecific genetic differences. However, as Collart et al. (2021) suggested, in the absence of evidence of niche divergence, SDMs should be constructed at the species level to reduce the uncertainty of model predictions, especially for small datasets.

The WP model projected the potential distribution of the WP in the western North Pacific, encompassing all the occurrence records; the EP model led to a contrasting result (Fig. 6). This implies that the niche differences between the two populations required separate models. The species model that treats Pacific cod as a homogeneous unit, masks the local differences in population response to climate predictors and reduces the accuracy of the projected results. Several studies have highlighted that species-level models may underestimate the potential habitats of species when failing to account for local adaptation (e.g., Ikeda et al., 2017; Oney et al., 2013; Pearman et al., 2010; Razgour et al., 2019; Zhang et al., 2021). However, in our study, we found that the species model overestimated the potential distribution of the WP by assuming that this population could tolerate all the climatic conditions tolerated by the species as a whole. This implies that intraspecific genetic variation will not always lessen the impacts of climate change on species habitat suitability (Cacciapaglia and Woesik, 2018; Hu et al., 2021; Lecocq et al., 2016).

Although they have important implications for the conservation and management of Pacific cod, our SDMs have some limitations. The occurrence data of Pacific cod were primarily obtained from the online datasets. Less data for the WP were uploaded to the datasets by relevant organizations, resulting in a difference in the number of occurrence records between the WP and EP. Because of the long temporal and large spatial scales of data sampling, the acquired data for the WP were likely to represent the realized niche adequately, and the disparity in the amount of data between the two populations may not bias the niche differentiation measures. This inference was supported by similar studies on the other species (Hu et al., 2021; Zhang et al., 2020a,b). However, the SDMs based on a larger dataset can produce more accurate predictive results (Collart et al., 2021). Due to lack of availability of the data, substrate variables were not included in the SDMs, despite the fact that these variables have been proven to have important influences on

the distribution of Pacific cod (Abookire et al., 2006; Dean et al., 2000; Sakurai and Hattori, 1996). In subarctic ecosystems, the extent of sea ice and the timing of sea ice formation and retreat have strong effects on the distribution of prey and indirectly affect the potential distribution of Pacific cod (Stevenson and Lauth, 2019). Pacific cod is extremely sensitive to temperature changes, and ice thickness is closely correlated with water temperature. We did not include sea ice thickness in the model to avoid the impact of collinearity of predictors. We used the multiyear average values of environmental factors to represent current climate conditions, making it difficult to explore annual sea ice changes in the Pacific cod distribution. Our SDMs can only predict the horizontal two-dimensional distribution and cannot predict the vertical distribution of species because this represents a shift from the current niche. However, Pacific cod is a benthic species, so the range shift of WP from nearshore to offshore areas implies a shift in suitable areas to greater depths in the face of changing climates. This is consistent with previous studies and our initial hypothesis (Dulvy et al., 2008; Kleisner et al., 2016, 2017). Furthermore, based on the available evidence, Pacific cod was divided into only two populations on a large spatial scale (Grant et al., 1987; Canino et al., 2010), although the more detailed classification is expected to yield more precise predictions. With further genetic research on the Pacific cod, we will test this hypothesis in future work.

4.2. Impacts of climate change on the Pacific cod

The niche differentiation between the WP and EP was mainly due to niche shift, to which water temperature and chlorophyll concentration contributed most. As a cold-water species, water temperature affects all the life history processes of Pacific cod (Stevenson and Lauth, 2019). Meanwhile, this species appears to be an indiscriminate predator, and chlorophyll concentration is likely to have an important influence on the prey distribution (Cohen et al., 1990; Spies et al., 2020). Climate-induced changes to these factors led the species to alter the current distribution patterns to trace the ecological niches. The difference in the niche spaces occupied by the WP and EP implied the different responses of these populations to climate changes. Our population-level SDMs predicted that the EP will colonize new areas northward while retaining most of the current suitable areas, indicating the resilience of the population to climate change. Stevenson and Lauth (2019) discovered a northern shift of the EP by analyzing bottom survey data at a more precise temporal scale; results which are consistent with the predictions of our models. On the other hand, the SDMs predicted that the WP will lose a large amount of suitable areas in the nearshore areas by colonizing some new areas in the offshore waters of the Japanese Sea, indicating the vulnerability of this population to climate change. Dispersal ability is a critical factor limiting the potential distribution of species. The projection from SDMs can be diverse depending on different assumptions regarding dispersal ability. Araújo et al. (2006) found that more than half of European amphibians and reptiles will expand their potential distribution under future climate change scenarios based on the assumption of unlimited dispersal ability. However, the potential distribution of most species will contract assuming no dispersal ability. A previous study found that marine species are better at tracking the movement of isotherms than terrestrial species and do so at a rate that is almost six times faster (Lenoir et al., 2020). However, Pacific cod is a high-fidelity species with an average dispersal distance of less than 100 km per generation (Spies, 2012). Therefore, assuming unlimited dispersal ability, it is likely that we overestimated the potential distribution of Pacific cod.

In addition to habitat loss, habitat fragmentation also threatens species survival. The combined effects of habitat loss and fragmentation can lead to a decrease in gene flow between populations (Lino et al., 2019), ultimately resulting in a substantial decline in population size (Koskimäki et al., 2014) and loss of genetic diversity (Gibbs, 2001). By combining species distribution models and landscape pattern analysis, Mondanaro et al. (2021) found that extinct mammals experienced

considerable habitat fragmentation during the last glacial age. We observed considerable habitat fragmentation in the Okhotsk Sea caused by habitat loss, which will exacerbate the negative impact of climate change on the populations in this area.

4.3. Implication for conservation and management

Pacific cod is one of the most productive commercial species, with global catches stable at approximately 450,000 tons (FAO, 2020). Atlantic cod, the same genus (*Gadus*) as Pacific cod, was listed as vulnerable by the International Union for Conservation of Nature in 1996 due to the collapse of this population as a result of overfishing (IUCN, 1996). To prevent the same outcome for Pacific cod, it is important to design adaptive conservation and management strategies in the face of anthropogenic and climatic stresses. Conservation of the WP is a high priority, considering the vulnerability of this population to climate change, especially in the Okhotsk Sea, where climate-induced habitat loss and habitat fragmentation threaten its survival. Pacific cod is one of the most important edible fishes in China and Korea. The northern Yellow Sea and coastal waters of Korea are important habitats for this species but have suffered intense anthropogenic stresses, such as environmental pollution and overfishing. Climate impacts will expedite the decline of Pacific cod unless more conservation actions are focused in these areas. We suggest that regular surveys of fishery resources be conducted and that more targeted management measures, such as the adjustment of fishing intensity and area and the conservation of important spawning grounds, be implemented for the sustainability of Pacific cod in these areas.

5. Conclusion

In conclusion, this is the first attempt to explore the response of Pacific cod to climate change considering intraspecific genetic variation. The different responses of the two Pacific cod populations to environmental predictors imply that population-level SDMs produce more reliable projections than the species-level SDM. Based on the models, the EP will expand its distribution northward while retaining much of the current distribution and shows resilience to climate change. However, the WP will lose most of its current distribution in the nearshore areas and colonize some new habitats in the offshore areas of the Japanese Sea and shows vulnerability to climate change. We suggest that adaptive conservation and management strategies such as the protection of important spawning and breeding grounds are necessary for the sustainability of Pacific cod, especially the WP.

CRediT authorship contribution statement

Linjie Li: Methodology, Software, Data curation, Writing – original draft. **Linlin Zhao:** Conceptualization, Methodology, Writing – review & editing. **Jinbo Fu:** Methodology, Software. **Bin Sun:** Software, Validation. **Changdong Liu:** Conceptualization, Methodology, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

The authors are unable or have chosen not to specify which data has been used.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecolind.2022.109248>.

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