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Ensemble projections of fish distribution in response to climate changes in the Yellow and Bohai Seas, China

Yunlong Chen [a], Xiujuan Shan [a,b,*], Harry Gorfine [c], Fangqun Dai [a], Qiang Wu [a,b], Tao Yang [a,b], Yongqiang Shi [a,b], Xianshi Jin [a,b]

[a] *Key Laboratory of Sustainable Development of Marine Fisheries, Ministry of Agriculture and Rural Affairs, Shandong Provincial Key Laboratory of Fishery Resources and Ecological Environment, Yellow Sea Fisheries Research Institute, Chinese Academy of Fishery Sciences, Qingdao 266071, PR China*

[b] *Shandong Changdao Fishery Resources National Field Observation and Research Station, Yantai 265800, PR China*

[c] *School of Biosciences, The University of Melbourne, Parkville, Vic. 3010, Australia*

A R T I C L E I N F O

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A B S T R A C T

Climate change is an important driving force affecting species distribution, so quantifying the influences of climate change on species distributions is necessary for effective fishery management. To identify the geographical distribution pattern and future potential suitable habitat area of fishes in the Yellow and Bohai Seas (YBS), we built ensemble models of spatial distribution for 22 important fish species using 3185 valid distributional records and 9 environmental variables extracted from multiple databases. The constructed ensemble models showed high accuracy with mean AUC, Kappa and TSS values of 0.97, 0.82 and 0.84. Salinity and temperature proximal to the seabed were the main environmental factors affecting the distribution of fishes. Presently, the number of important fish species (NIFS) tends to be low in the Bohai Sea and high in the Yellow Sea. Future projections indicated that there would be obvious interspecific differences in the geographical distribution of fishes, and the number of species with range contractions is predicted to be greater than that of range expansions. Coastal fishes and cold temperate fishes are predicted to narrow their occupied areas. In the future, the NIFS in the YBS is expected to increase overall. Spatially, sporadic areas in the central and southern Yellow Sea will have a reduced NIFS, while the Bohai Sea, coastal waters near the southern Shandong Peninsula and the northern East China Sea may experience increased NIFS. Our results provide a theoretical basis for predicting the climate-driven range shifts of fishes in one of the world's most heavily impacted marine ecosystems, that can be extended to develop climate-adaptive management strategies.

1. Introduction

Climate change is a stark testament to the impact humans are exerting on the natural environment this century and has emerged as the biggest long-term threat to marine ecosystems. Together with overfishing, habitat degradation and pollution, these physio-chemical alterations in aquatic conditions complicate the challenge that global fishery resources are facing (Gaines et al., 2018; Wilson et al., 2018; Carozza et al., 2019). Climate change can impact directly or indirectly on fishery resources over differing ecological scales such as individuals, populations, communities, food webs and large ecosystems (Kortsch et al., 2015; Duffy et al., 2016; Kuczynski et al., 2018; Flannery-Sutherland, 2021). Among these, the study of distribution patterns in fish communities under the influence of climate change is a hot issue in the field of international fisheries ecology, providing a contextual basis for fisheries-related institutions, organizations and governments to formulate relevant climate-fishery policies (Pinsky and Mantua, 2014; Cramer et al., 2018). In 2021, the general office of the CPC Central Committee and the general office of the State Council issued the Opinions on Further Strengthening Biodiversity Conservation and Biodiversity Conservation in China, providing guidance and goals for future biodiversity conservation. Under a global background of biodiversity loss, it is important to enhance our understanding of the current and potential suitable habitats for fishery resources, and this comprehension is

* Corresponding author at: Key Laboratory of Sustainable Development of Marine Fisheries, Ministry of Agriculture and Rural Affairs, Shandong Provincial Key Laboratory of Fishery Resources and Ecological Environment, Yellow Sea Fisheries Research Institute, Chinese Academy of Fishery Sciences, Qingdao 266071, PR China.

E-mail address: shanxj@ysfri.ac.cn (X. Shan).

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necessary for formulating species protection measures which are reasonable and effective for balancing rational utilization with biodiversity conservation.

The Yellow Sea and Bohai Sea (YBS) region is an important fishing area in China with abundant fishery resources. In 2020, commercial catches from the YBS exceeded 2.8 million tons, accounting for 30% of China's total marine fishing production, thereby playing an important role in providing employment opportunities, meeting the human demand for protein, and stabilizing the livelihoods of fishery practitioners (MARA, 2021). Meanwhile, the YBS is also one of the world's most heavily impacted ecosystems by climate change, where the net SST change in the YBS is five times the global average rate of SST warming (Belkin, 2009). Currently, there remains a lack of sufficient scientific cognition about the extent to which climate change will reshape and alter the geographical distribution of fish populations, or lead to potentially irreversible changes in fish community structure and marine ecological processes in this area. It is reported that responses of marine fishes to climate change often vary by area and species (Alabia et al., 2018; Ilarri et al., 2022). What is the current distribution pattern of fishes in the YBS? What are the main environmental factors limiting their geographical distribution? What is the relative importance of these factors? How can the change of these environmental factors further cause distribution shifts of fishes under future climate scenarios? These problems have not been solved, which seriously restricts the protection and utilization of fishery resources in the YBS and limits the agility to mitigate climate change induced risks.

Species distribution models (SDMs) are widely used to study the impacts of climate change on species' distribution (Nekrasova et al., 2021). So far, widely used SDMs include the domain model (DOM), random forest (RF), generalized additive model (GAM), and maximum entropy model (MaxEnt), (Hao et al., 2019). However, the predictive performance of different individual SDMs may be variable across species and regions (Araújo et al., 2006; Pearson et al., 2006). In this context, the ensemble forecasting framework was introduced to address the intermodel variation in species distributions identified by Araújo and New (2007). Due to its comprehensive utilization of information from multiple models, ensemble modeling has become an innovative approach with excellent predictive accuracy (Zhang et al., 2019; Hao et al., 2020).

In this paper, we explored the distribution patterns of fish species in the YBS and their associations with environmental variables using ensemble SDMs. Then, we predicted their future changes in potential suitable habitat areas under different climate scenarios. The results derived provide a theoretical basis for predicting climate-driven range shifts of fishes in one of the world's most heavily impacted marine ecosystems, and can be extended to develop climate-adaptive fishery management measures.

2. Materials and methods

2.1. Occurrence data of fishes in the YBS

Species occurrence of fishes in the YBS (Fig. 1) was obtained from the Global Biodiversity Information Facility (GBIF, https://www.gbif.org/), Ocean Biodiversity Information System (OBIS, https://obis.org/), and fishery-independent species biomass surveys conducted by the Yellow Sea Fisheries Research Institute (YSFRI), Chinese Academy of Fishery Sciences (CAFS). There are many fish species in the YBS, but most occur only rarely or occasionally. In this study, we ranked the relative biomass of fish in the YBS, and selected those species accounting for more than 95 % of the total fish biomass. Finally, 22 species were screened for further analysis, and their ecological traits (habitat, migration type and thermophily) were detailed in Supplemental Table S1. In total, 234,789 records of these 22 fishes were aggregated from multiple sources among which 112,436 records were from GBIF (1752–2022), 119,317 records were from OBIS (1742–2022) and 3036 records were from YSFRI

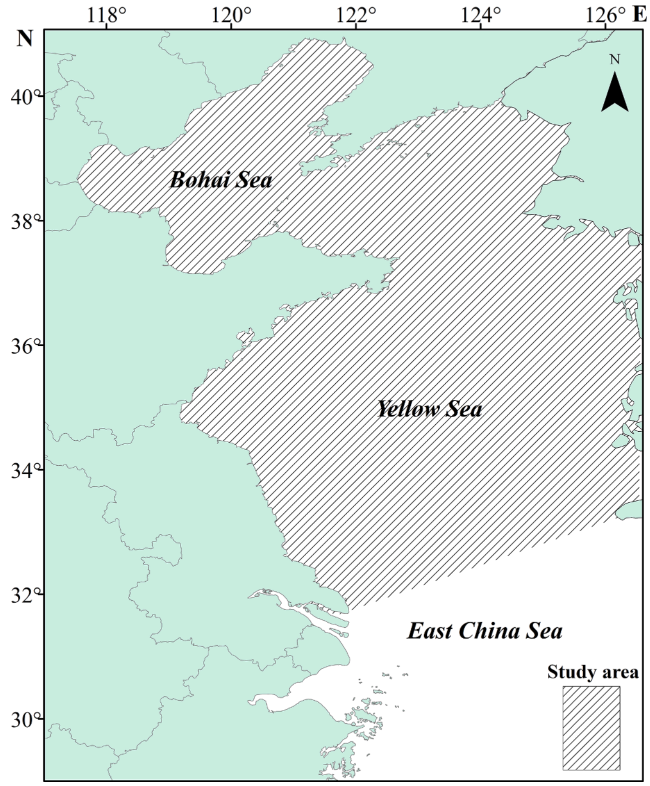

Fig. 1. Location of the study area.

(2015). After that, a secondary screening process was performed to guarantee the quality of the collected data via the following steps: firstly, records before 1990 were excluded to characterize the current distribution of fish in the YBS; secondly, data points with incorrect latitude and longitude information were removed using expert judgment and data properties; thirdly, the study area was divided into geographical units with $5' \times 5'$ spatial resolution and only one record was retained in the same grid to avoid duplication. Finally, 3185 distribution records of the 22 fishes in the YBS were obtained for the subsequent construction of SDMs. The derived dataset of filtered export of GBIF occurrence data is available at https://doi.org/10.15468/dd.h7w4jd. The specific numbers of records of each fish species are detailed in Supplemental Table S1.

2.2. Environmental variables

Considering the data availability for environmental variables and their correlation with fish distribution in the YBS, nine environmental variables (bottom temperature, bottom salinity, current velocity, depth, distance from shore, primary productivity, phytoplankton, dissolved oxygen and chlorophyll) were selected for the follow-up analysis (Table 1). Among them, data for depth and distance from shore were obtained from the Global Marine Environment Datasets (GMED, https://gmed.auckland.ac.nz/index.html) at a spatial resolution of $5' \times 5'$, and the layers of the other seven variables were extracted from the Bio-ORACLE database (https://www.bio-oracle.org/) at a spatial resolution of $5' \times 5'$ (Tyberghein et al. 2012; Assis et al., 2018). Multicollinearity was assessed using Spearman's rank correlation test. When the Spearman coefficient of two environment variables was higher than 0.7, only one variable was retained (Schickele et al., 2020). Finally, five variables (bottom temperature, bottom salinity, current velocity, depth, distance from shore and primary productivity) were selected to further build the SDMs (Supplemental Fig. S1).

Table 1
List of environmental variables used in the YBS species distribution models.

Environmental variables	Abbreviation	Unit	Range	Source
Bottom temperature	BT	°C	8.18–20.05	Bio–ORACLE
Bottom salinity	BS	PSS	29.07–34.55	Bio–ORACLE
Current velocity	CV	m/s	4.7×10^{-03}–0.35	Bio–ORACLE
Depth	Depth	m	0.38–124.94	GMED
Distance from shore	DS	100 km	2.3×10^{-03}–2.65	GMED
Primary productivity	PP	g/m^3/day	4.2×10^{-05}–0.15	Bio–ORACLE
Phytoplankton	Phoyto	μmol/m^3	0.46–14.55	Bio–ORACLE
Dissolved oxygen	DO	μmol/m^3	175.62–354.12	Bio–ORACLE
Chlorophyll	Chl	mg/m^3	0.12–4.23	Bio–ORACLE

2.3. Construction, optimization, and evaluation of ensemble models

We used the biomod2 package in R (Thuiller et al., 2016) to develop nine SDMs and project the current and future geographic distribution of fishes in the YBS. These SDMs were Artificial neural network (ANN), Classification tree analysis (CTA), Flexible discriminant analysis (FDA), GAM, Generalized boosting model (GBM), Generalized linear model (GLM), Multivariate adaptive regression splines (MARS), RF and Surface range envelop (SRE). Default settings of the SDMs were those recommended by Thuiller et al. (2016) and Ruiz-Navarro et al. (2016) (Supplemental Table S2).

In order to evaluate the model's predictive performance, a cross-validation process was performed with 100 repetitions. When constructing the SDMs for each species, 80% of the data were randomly selected as a training dataset, while the remaining 20% of the data were used to validate the model (Chen et al., 2021). Three indices including the Area Under Receiver-operating Characteristic Curve (AUC), the true skill statistic (TSS), and Cohen's Kappa (Kappa) were used to assess the predictive accuracy of the models (Cohen, 1960; Hanley and McNeil, 1982; Allouche et al., 2006). The index values ranged between 0 and 1, with a value closer to 1 indicating a higher prediction accuracy of the model. Before further constructing the ensemble models, it has been recommended to screen the qualified SDMs based on the following guidelines: AUC $\geq$ 0.7, TSS $\geq$ 0.5 and Kappa $\geq$ 0.4 (Chen et al. 2021). Then, the ensemble model was built by weighting these individual models proportionally according to their evaluation values (Thuiller et al., 2016). The importance values for the different environmental variables contributing to the distribution of fishes in the YBS were calculated by the following process. To begin with, reference values were firstly calculated using models constructed with all variables; next, predicted values were obtained using the new models constructed with randomization of individual variables; and then the Spearman coefficient of reference and predicted values were estimated. Lastly, the importance values were obtained by subtracting the Spearman coefficient from 1. The higher the importance value, the greater influence that the variable has on the model results (Thuiller et al., 2016). Clustering analysis was used to compare results across different fish species in combination with environmental variables, and a heatmap was generated with Euclidean distance and the complete linkage method using the pheatmap package in R (Kolde, 2018).

2.4. Current and future predictions of potential suitable habitat area of fishes in the YBS

Possible future climates in the YBS were represented by emission scenarios developed by the Coupled Model Intercomparison Project Phase 5 (CMIP5) of the Intergovernmental Panel on Climate Change (IPCC). A total of four emission scenarios, referred to as representative concentration pathways (RCPs), were put forward. Here, we chose the low RCP2.6, the medium RCP6.0, and the severe RCP8.5 scenarios to project the potential suitable habitat area of fishes in the YBS. Since both RCP4.5 and RCP6.0 are medium stabilization scenarios, here we only included RCP6.0 for projection. In addition, future predictions in the mid-term (2050) and long-term (2100) were both included in each scenario analysis.

When predicting future changes of potential suitable habitat area of fishes in the YBS, bottom temperature, bottom salinity and current velocity were dynamic variables, and forecast data were obtained from the Bio-ORACLE database (https://www.bio-oracle.org/). Distance from shore and primary productivity were treated as static variables. The cut-off value determined by the TSS method was used to convert the results of continuous probabilities projected by the ensemble models into binary values (Guisan et al., 2017). Afterwards, the binary distribution (0/1) matrix for each species under current and future climate scenarios was established. The specific meaning of each matrix is listed in Supplemental Table S3. For each species, the occupied area was represented by the number of geographical units whose binary value was 1, and estimates of the future changes in the occupied area (range expansions/contractions) were based on this number. To explore the potential impacts that climate change may have on fish community, the number of important fish species (NIFS) in each geographical unit was calculated by superimposing binary maps of each species respectively under current and future climate scenarios.

3. Result

3.1. Model performance

Using the selected occurrence data and five environmental variables in the YBS, we successfully built the SDMs of 22 important fish species. Cross-validation results showed that the mean AUC value (averaged by nine individual SDMs) of 20 fish species was greater than 0.7, the mean Kappa value of 20 fish species was greater than 0.4, and the mean TSS value of 17 fish species was greater than 0.5 (Fig. 2). This means that the predictions from single SDMs for most fishes were reliable except for a few species such as whitespotted conger (*Conger myriaster*) and greater pipefish (*Syngnathus acus*). Next, we built the ensemble SDMs of each species by the weighted average method using single SDMs whose values from the evaluation matrix exceeded the criteria. Results showed that the accuracy of ensemble SDMs was greatly improved compared with single SDMs across the 22 fish species, with AUC values of 0.92–0.99 (mean 0.97), Kappa values of 0.69–0.96 (mean 0.82), and TSS values of 0.69–0.96 (mean 0.84).

3.2. Importance analysis of environmental variables

The relative importance that each environmental variable contributed to the distribution patterns of fishes in the YBS is shown in Fig. 3. Clustering analysis indicated that the bottom salinity and bottom temperature were the main environmental variables affecting the geographical distribution of fishes in the YBS, while the relative importance of seawater velocity and primary productivity were low.

Among the 22 species, the geographical distribution of 13 fishes such as Japanese anchovy (*Engraulis japonicus*), smallhead hairtail (*Eupleurogrammus muticus*) and small yellow croaker (*Larimichthys polyactis*) were mainly determined by bottom salinity, accounting for 59.1 % of the total number of studied species; the geographical distribution of 5 fishes such as plaice (*Cleisthenes herzensteini*), Mi-iuy croaker (*Miichthys miiuy*) and Bombay-duck (*Harpadon nehereus*) were mainly determined by bottom temperature, accounting for 22.7 % of the total number of studied species. Distribution of bastard halibut (*Paralichthys olivaceus*) and Chub mackerel (*Scomber japonicus*) were mainly determined by distance from shore. In addition, the geographic distributions of some

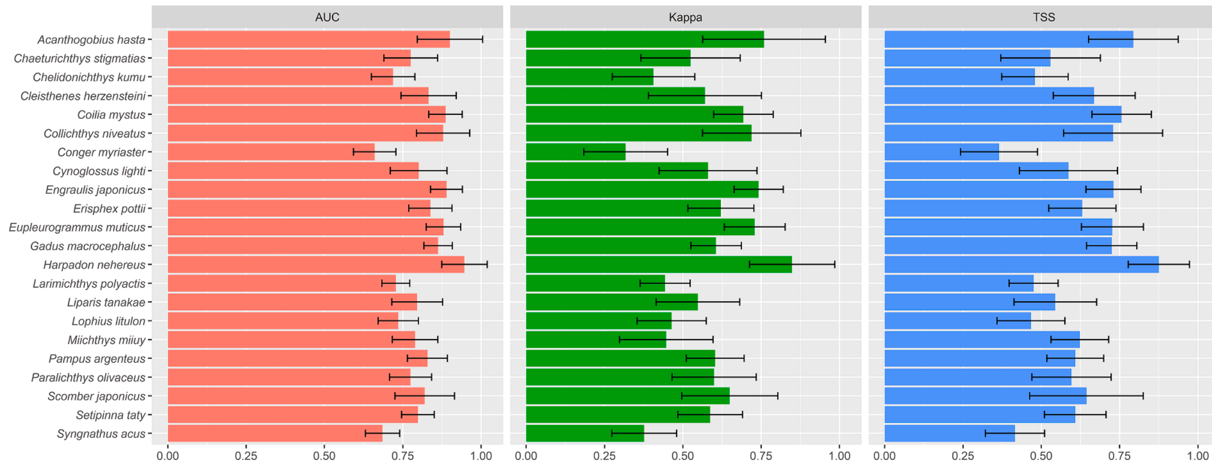

Fig. 2. Summary of the performances for nine individual species distribution models (SDMs) evaluated by the area under the receiver operating characteristic curve (AUC, left), the Cohen's Kappa (Kappa, middle) and the true skill statistics (TSS, right) for 22 fish species in the Yellow and Bohai Seas (YBS). Data are expressed with mean ± standard deviation.

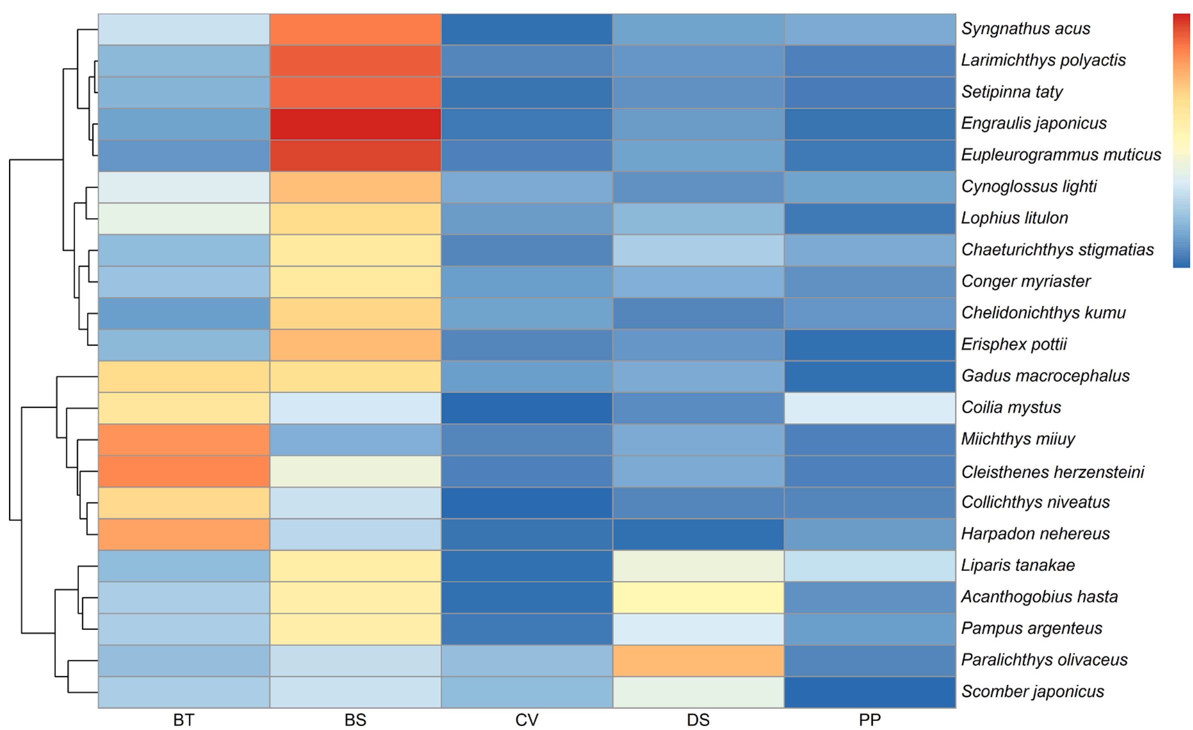

Fig. 3. Clustering analysis for 22 fish species in the YBS with five environmental variables. Environmental variables include bottom temperature (BT), bottom salinity (BS), current velocity (CV), distance from shore (DS) and primary productivity (PP).

species such as Pacific cod (*Gadus macrocephalus*) were influenced by multiple environmental variables.

3.3. Current and future spatial distribution patterns of NIFS in the YBS

We mapped the current spatial distribution of NIFS in the YBS layer upon layer based on the ensemble model results (Fig. 4). Overall, the NIFS in the YBS reflects obvious spatial heterogeneity, tending to be low in the Bohai Sea and high in the Yellow Sea. In the Bohai Sea, the NIFS is relatively low with less than 6 species, except for the north side of the Bohai Sea Strait and sporadically within some waters along the coast. In the Yellow Sea, coastal waters near southern Shandong Peninsula and some of the northern area of the Yellow Sea have lower NIFS, whereas the NIFS in the remaining waters is higher, with generally more than 10 species (Fig. 4). High NIFS areas are mainly distributed in coastal waters near the Hangzhou Bay and the Zhoushan Archipelago, the west coast of the Korean Peninsula, and the southern Yellow Sea area (31.5° –33.5°, 122.5° –125°E).

The predicted spatial distribution of NIFS in the YSB and its potential change showed similar patterns among different climate scenarios, therefore, here we only presented results under the severe Rcp8.5 scenario (see Supplemental Fig. S2 for results of other scenarios). In general, future NIFS in the YBS will undergo an increasing trend in both the mid-term (2050) and long-term (2100), but with changed spatial distribution characteristics compared with the current situation (Fig. 5). At the end of 2100s, NIFS in sporadic areas of the central and southern Yellow Sea may decrease. Meanwhile, the Bohai Sea, coastal waters near the southern Shandong Peninsula and the northern East China Sea may

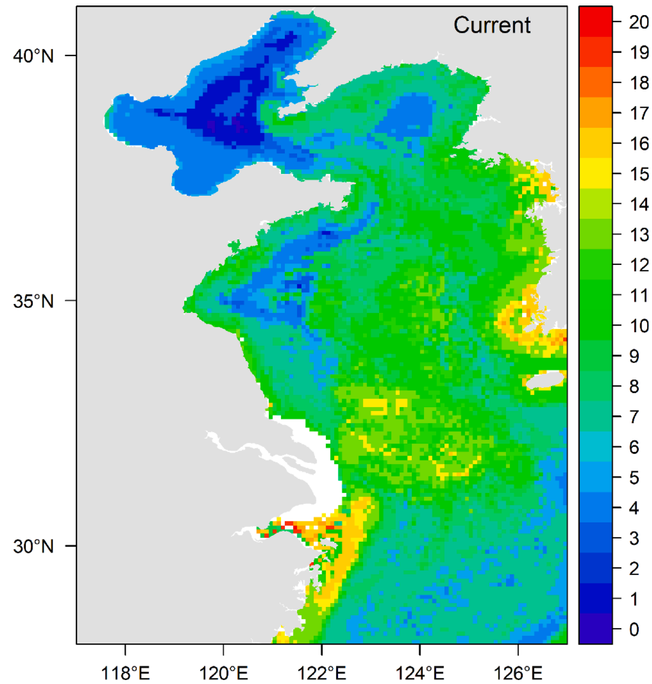

Fig. 4. Current spatial distribution of NIFS in the YBS.

experience increased NIFS.

3.4. *Future range shifts of fish species in the YBS*

In general, there were more species showing range contractions than range expansions under future climate change scenarios. For instance, the number of species expected to shrink their ranges were 14, 13, and 13 under Rcp2.6, Rcp6.0 and Rcp8.5 scenarios, respectively, while those fishes extending their distributions were 8, 9 and 9. There were obvious interspecific differences in the potential suitable habitat area of species in the YBS and similar patterns were found among different climate scenarios, therefore as with 3.3, only the results under the severe Rcp8.5 scenario are presented here (see Supplemental Fig. S3 for results of other scenarios).

Fish species can be divided into three groups according to the changes in the occupied area (Fig. 6). The first group was mainly represented by species such as tonguefish (*Cynoglossus lighti*), *H. nehereus* and osbeck's grenadier anchovy (*Coilia mystus*), which may expand their potential suitable habitat area in the future. The second group consists of species which may narrow their potential suitable habitat area under future climate change such as *S. acus*, *C. herzensteini* and *G. macrocephalus*. The third group mainly includes species like spotted velvetfish (*Erisphex pottii*), bluefin gurnard (*Chelidonichthys kumu*) and *C. myriaster*, whose future potential suitable habitat areas was predicted to be relatively stable.

We also found that there were high consistencies among predictions of future changes in suitable habitat areas across the fish species under different climate scenarios, and this consistency became stronger by 2100 compared with 2050. Taking the Rcp8.5 scenario for example, the predicted suitable habitat area for small yellow croaker would be expected to decrease by 13 % by 2050 and this trend is more pronounced by 50 % by 2100 compared to the current distribution.

3.5. *Future range shifts of fishes for different ecological groups*

Future range shifts of fishes for different ecological groups had similar patterns among different climate scenarios, therefore as with 3.3 and 3.4, only results under the severe Rcp8.5 scenario are presented here (see Supplemental Fig. S4 for results of other scenarios). In terms of habitat, the average predicted change of occupied area for demersal fishes was slightly higher than that of pelagic species. For instance, the average rates of change were predicted to be −3.2 % for demersal species (N = 17) and −1.1 % for pelagic species (N = 5) by 2050, while those were −5.3 % and 4.8 % in 2100 (Fig. 7).

In terms of migration type, as the only open-seas species in this study, Chub mackerel may expand its suitable habitat area in the future and increase in area by up to 25.8 % in 2100. In the future, the average change in the area occupied by sedentary fishes (N = 4) and longshore fishes (N = 8) is unlikely to change much, but the results showed high interspecies differences, indicating different adaptability among fish species in the face of climate change even from the same ecotype. Climate change was predicted to cause somewhat negative consequences for the potential geographical distribution of coastal fishes (N = 9). The average change in the current areas occupied by coastal fishes was predicted to be −10.5 % in 2100 (Fig. 7).

In terms of thermophily, cold temperature fishes (N = 4) will be impacted the most by climate change with a decreasing rate of up to −64.5 % under Rcp8.5 scenarios in 2100. The average change in area occupied by warm temperature fishes (N = 11) will be more likely to exhibit a slight increase of 13.9 % in 2100. It is projected that warm water fishes (N = 7) will be relatively less affected by climate change (Fig. 7).

4. Discussion

4.1. *Spatial distribution pattern of NIFS in the YBS*

The YBS provides ample habitat with high heterogeneity for a diverse range of fish species to potentially inhabit. Our findings revealed that under contemporary climatic conditions, high NIFS areas were mainly distributed in coastal waters near the Hangzhou Bay and the Zhoushan Archipelago, the west coast of the Korean Peninsula, and the southern Yellow Sea area (31.5°–33.5°, 122.5°−125°E), which is generally consistent with previous studies (Chen et al., 2018). This may be closely related to the behavioral habits of fishes in the YBS. In addition to a few settled species (such as spear tail shrimp, gadfly scorpene, etc.), most fish species within the YBS are migratory over short or long distances. In autumn, they begin to migrate southwards to the southern Yellow Sea and the East China Sea for over-wintering and then successively move northward to offshore areas for spawning as the water temperature rises during the ensuing year (Jin and Tang, 1996)..

As a semi-closed sea in China, the Bohai Sea is the northernmost boundary of the geographical distribution of many fish species, providing limited areas for species to move northwards in response to climate-driven warming of its waters. We found that cold temperature species will be more likely to be affected by future climate change, potentially reducing their suitable habitat area by 64.5 % in 2100 under the Rcp8.5 scenario. Studies on fishes in the Mediterranean Sea showed that the Gulf of Lion and the Adriatic Sea, as the coldest areas in the Mediterranean Sea, were projected to become a 'cul-de-sac' for endemic fish species, which means they may first provide a refuge and then consequently facilitate the extinction of the entrapped species (Ben Rais Lasram et al., 2010; Albouy et al., 2012). Although similar in latitude to the Mediterranean Sea, our study did not project the "cul-de-sac" effect in this area for YBS. The Bohai Sea may experience increased NIFS under medium (Rcp6.0) and high (Rcp8.5) emission scenarios by the end of the 21st century.

In the future, potential changes in suitable habitat area of fishes in the YBS are likely to be greater as global rates of greenhouse gas emissions increase. Studies have also shown that despite increases in sea temperature and salinity having less impact on species under low emission scenarios, the increase rates may nevertheless be beyond the thermal and salinity tolerance of fishes, leading to habitat fragmentation and adverse consequences on fish populations (Ben Rais Lasram et al.,

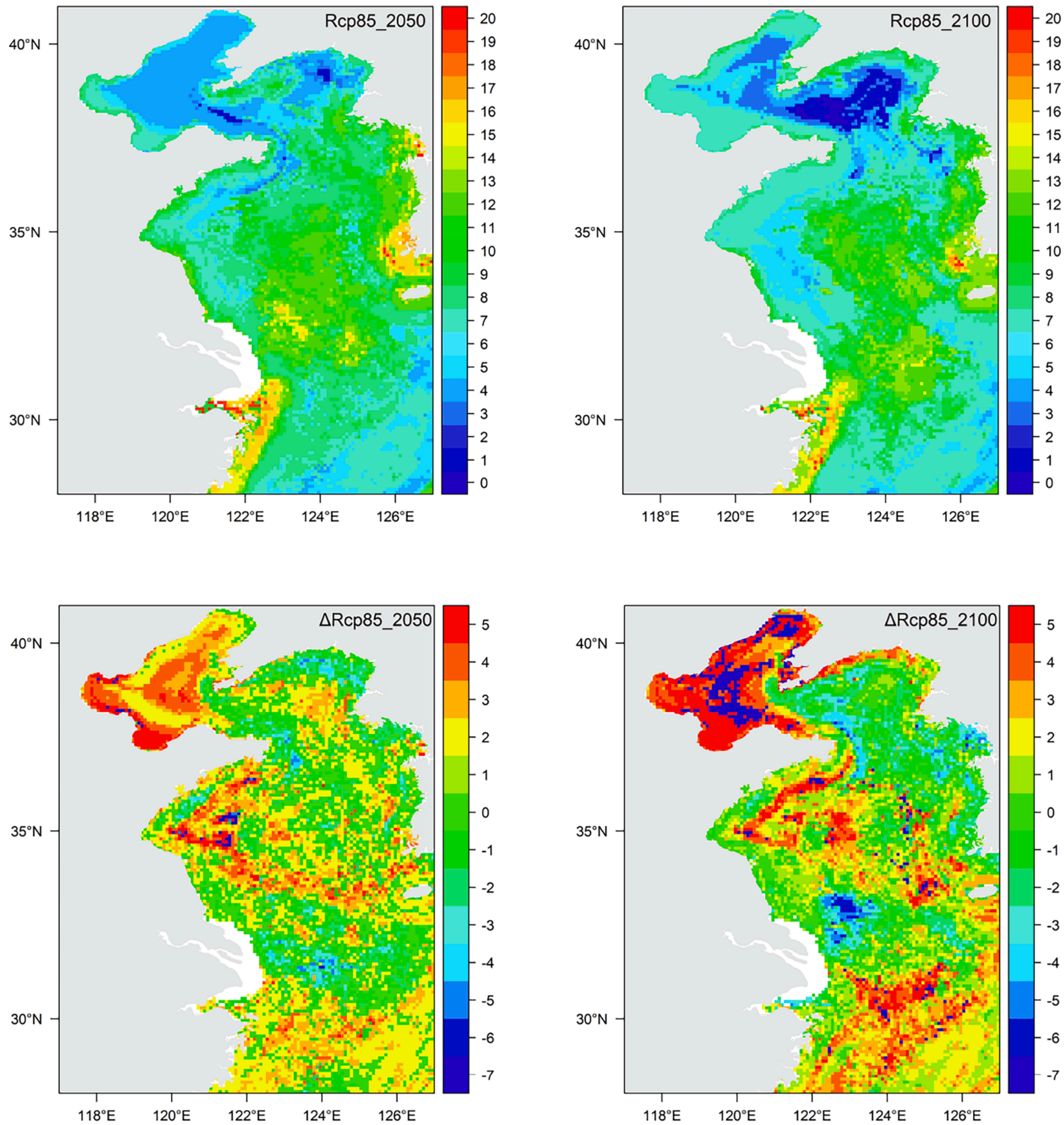

Fig. 5. Future spatial distribution and changes of NIFS in the YBS under Rcp8.5 scenario.

2010; Du Pontavice et al., 2021). Taxanomically, our results suggest that dominant species in the YBS ecosystem such as Japanese anchovy, anglerfish, Tanaka's snailfish, silver pomfret and small yellow croaker (Chen et al., 2018) are likely to contract their ranges in the future. These species are top predators or keystone species for energy conversion within their food webs, exerting a major influence in controlling the abundance of other species in the community. The predicted decreasing changes in their spatio-temporal distribution patterns is likely to alter communities' structure and ecosystem function. Additionally, range shifts among those species which support commercial fisheries will result in profound socio-economic impacts for fishing industries.

4.2. Implications on fish protection and management in the YBS

Under the influence of climatic change, marine ecosystems are undergoing tremendous variations, such as rising sea water temperature, decreasing dissolved oxygen, acidification, glacier melting and rising sea level, as well as hydrodynamic effects on currents, water column stability, and incident wave energy (Doney et al., 2012). Climate change is becoming an increasingly important driver in reshaping the distribution, abundance and diversity of fish species, thereby altering the functions and services of the ecosystem (Brander, 2007; Huang et al., 2021). Studying geographical distribution patterns of fishes and their responses to climate change is critical to predict future spatial and temporal characteristics and scientifically evaluate the impacts on fisheries (Clark et al., 2020).

The implications for fish protection and management in the YBS of our present work can be summarized in the following three recommendations. First, our work provided a spatially-explicit map of NIFS in the YBS and reveals their spatial heterogeneity. As biodiversity conservation has become China's national strategy under its policy of Ecological Civilization (Wu et al., 2019), revealing the current geographical distribution patterns of fishes will significantly improve the spatial management capacity in China (Guan et al., 2020), so as to better cope with the major risks caused by biodiversity loss and ecosystem degradation. Future retention of suitable areas of habitat, such as waters near Hangzhou Bay and Zhoushan archipelago can be used as shelters for fishes in the YBS to mitigate some of the risks posed by climate change, so the management and protection of these areas should be further strengthened. Areas such as the southern Yellow Sea and waters outside the northeast of the Yangtze Estuary, that may be lost in the future, require vigilant monitoring for area-specific environmental changes which can potentially impact upon fish population dynamics.

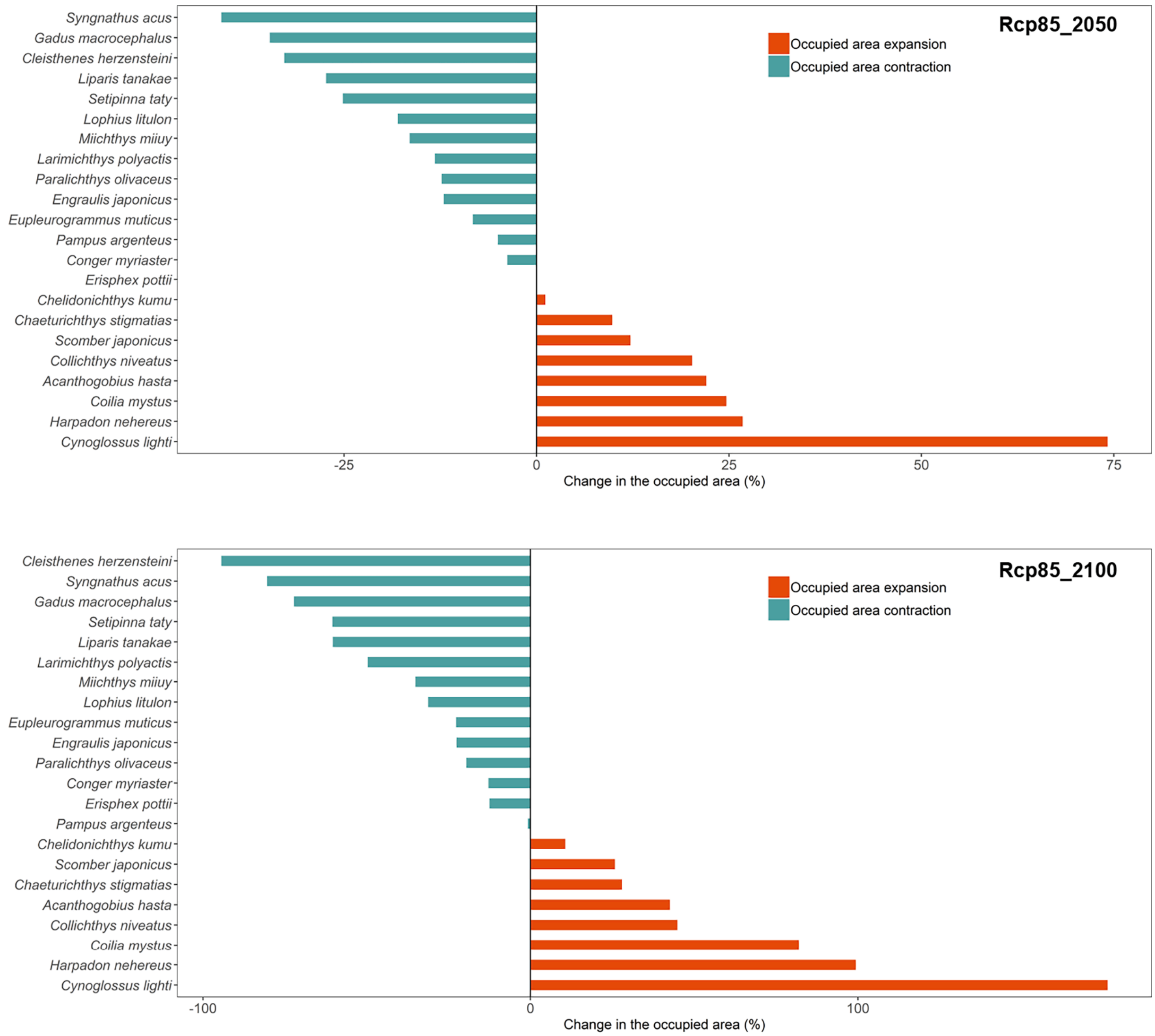

Fig. 6. Changes in the occupied area (%) by 22 fish species in the YBS under Rcp8.5 scenario.

Second, this study identified the interspecific differences among fishes in the YBS in response to climate change in terms of their geographical distribution patterns, revealing the plasticity and adaptability of different fish species or ecotypes. Incorporating interspecific and ecological differences into fish resource assessment and management will therefore be critical to help the fisheries administrators to formulate specific proactive and responsive management measures which can reasonably be expected to improve the management efficiency whether that be for single-species management, multi-species management, or ecosystem-level fishery management (Barnett et al., 2019; Zakharova et al., 2019; Perryman et al., 2021). Our present work can be used to provide scientific support for fishery management administrations, research institutions and other fishery stakeholders to further carry out the fish resources conservation activities such as protected areas planning and stock enhancement.

Third, regional climate change is more complex than global change, involving more influencing factors, and is closely related to the local environment and economic production (Rogers et al., 2019). We projected the future potential distribution of fishes in the YBS using three emission scenarios encompassing mid-term (2050) and long-term (2100) projections. This information can provide support for a variety of protocols that integrate climate change into the future development of fisheries policies, to promote flexibility and adaptability among future fisheries management measures to effectively cope with a changing and more changeable climate.

4.3. Limitations of the present study

In this present study, we successfully established ensemble models for 22 important fishes in the YBS and projected the potential effects of climate change on their geographical distribution and NIFS in this area. We consider that fishes in the YBS are excellent dispersers and benefit from the high level of oceanographic connectivity in the region, enabling fish species to variously select and establish new habitats in seeking suitable environmental conditions. Notwithstanding this, there are limitations to our ensemble models that are described as follows:

i) *Explanatory variables*. We chose nine environmental variables as explanatory variables to construct SDMs for fishes in the YBS. Although the nine variables may well reflect the relationships between the distribution of targeted fishes and their surrounding environment, we ignored the possible influence of biotic factors such as predation and competition. Zhang et al. (2022) argued that ignoring species trophic interactions might lead to biased projection of species distributions and a joint species distribution model could reduce this bias, especially for species with low prevalence. Tekwa et al. (2022) showed that interactions between trophic levels can reduce the number of regional new

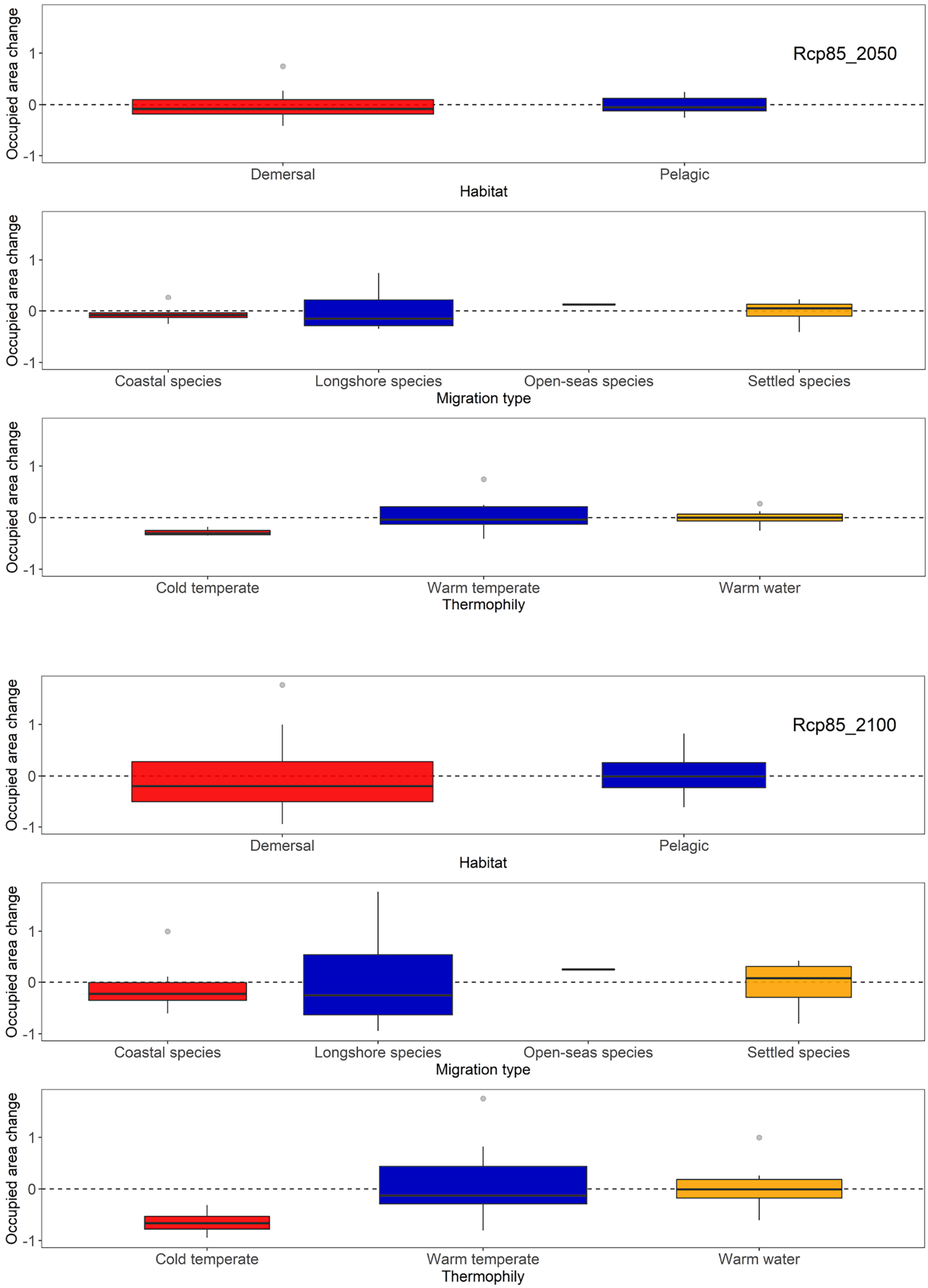

Fig. 7. Changes in the occupied area (%) of different ecological groups classified by habitat, migration type and thermophily for 22 fish species in the YBS under Rcp8.5 scenario.

species, new interaction relationships, and high-yield species, maintain the historical community composition and structure for longer periods, and thus slow down the spatial distribution changes of species caused by climate change. In addition, changes in the fish distribution range may be influenced by the synergistic effects of species and human activity factors (e. g., fishing, Fujiwara et al., 2019). More biological factors need to be considered in future studies to improve the predictive performance of the model.

ii) *Evolutionary factors*. Species often adapt to irreversible climate change in two ways. The first way is to choose an appropriate latitude and depth within their own environmental adaptation range. For example, two thirds of fishes either moved northwards or shifted into deeper water as sea temperatures progressively increased during the past 25 years in the North Sea (Perry et al., 2005; Dulvy et al., 2008). The second way is to undergo local adaptative changes through phenotypic adjustment or micro-evolution (changing the genetic structure of the population). For instance, many species may become vulnerable in the face of climate change and be unable to adjust their physiology to rapid global warming. As to species' thermal limits, it is reported that cold tolerance has evolved faster than heat tolerance in ectotherms and the adaptive responses in upper thermal limits would be limited (Bennett et al., 2021). A study on wild zebrafish (*Danio rerio*) also showed that experimentally observed adaptation rates and existence of an upper thermal tolerance may hinder tropical fishes' evolutionary adaptations (Morgan et al., 2020).

iii) *Climate scenarios*. The climate scenarios evaluated in this study are RCPs from CMIP5, which are comprehensive emission scenarios in accordance with the concentration pathway trajectories and outcomes until 2100 (Moss et al., 2010). There are four scenarios which represent the low (Rcp2.6), intermediate (Rcp4.5 and Rcp6.0) and high (Rcp8.5) pathways, respectively. At present, a series of new emissions scenarios called shared socio-economic pathways (SSPs) were proposed by the IPCC sixth assessment report (AR6), which were further used to drive the climate models (Eyring et al., 2016). The new scenarios include both future changes in demographic, economic development, ecosystems, resources, and social factors, as well as future efforts to mitigate, adapt or cope with climate change. However, we nevertheless investigated the RCPs scenarios in our study for the following two reasons. Firstly, around 40 CMIP6 models have published their results so far while the expected number of models is around 100. Results demonstrate that current models in CMIP6 have higher climate sensitivity than those in CMIP5, for which researchers are still working to identify reasons leading to this situation. Secondly, although new SSPs scenarios provide a wider selection with eight scenarios for researchers to simulate compared to last generation of RCPs scenarios, the four RCPs scenarios have new updated versions in CMIP6 called SSP1-2.6, SSP2-4.5, SSP4-6.0, and SSP5-8.5, respectively, ensuring our results remain pertinent.

5. Conclusions

Our study successfully built the SDMs of 22 important fishes in the YBS using an ensemble modeling technique. Contemporary and future geographical distribution patterns of fishes in the YBS were then projected based on these models. We found that bottom salinity and bottom temperature were the most important environmental variables contributing to the distribution patterns. In addition to our approach, we recommend including more biotic and fishing factors in further studies to enhance the predictive performance of these models. The different responses of fishes and ecological groups facing climate change indicates the necessity of fully considering these differences when developing future climate-related coastal fishery management measures. Although our results may be overestimates due to excluding species interactions, we have made an important first step towards clarifying the potential impacts that climate change on the geographical distribution of fish species in coastal waters of China. Projection under different climate scenarios can provide a variety of protocols supportive of integrating climate change into the future fisheries measures and promoting the flexibility needed to more effectively cope with climate change in the YBS as well as similar marine ecosystems.

CRediT authorship contribution statement

Yunlong Chen: Conceptualization, Methodology, Formal analysis, Visualization, Writing – original draft. **Xiujuan Shan:** Data curation, Writing – review & editing, Supervision, Funding acquisition. **Harry Gorfine:** Methodology, Validation, Writing – review & editing. **Fangqun Dai:** Investigation, Resources. **Qiang Wu:** Investigation, Resources. **Tao Yang:** Investigation, Resources. **Yongqiang Shi:** Writing – review & editing. **Xianshi Jin:** Supervision, 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

Data will be made available on request.

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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.2022.109759.

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