



Projected changes in seasonal potential distribution of chub mackerel *Scomber japonicus* under continued ocean warming in Korean waters

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ABSTRACT: Chub mackerel *Scomber japonicus* (subsequently referred to as mackerel), a commercially important small pelagic fish in Korea, is highly sensitive to environmental changes and has shifted its spatial distribution owing to climate change in recent decades. This study examined projected changes in the seasonal potential distribution of mackerel in Korean waters in the 2050s. Three species distribution models — a maximum entropy model, a generalised additive model, and boosted regression trees — were fitted using mackerel presence and 5 skillful environmental variables (temperature, salinity, current velocity, and chlorophyll concentration at the surface, and mixed layer depth) over 18 yr (1998–2015) and projected under 3 CMIP6 future scenarios. The distribution models projected future changes in mackerel habitat with high seasonal and regional variability. Mackerel habitat was projected to increase by 13.35–42.01% throughout the year in the East Sea and decrease by up to 12.73% in the northern East China Sea and by 5.28–20.93% in the Yellow Sea in spring and summer. The habitat gains and losses of mackerel were mainly driven by the predicted temperature increases and salinity decreases. The habitat contraction in spawning areas — mainly in the Yellow and northern East China Seas — contributes to the loss of spawning habitats, which could considerably change the abundance and timing of spawning and, in turn, fisheries productivity. Our findings suggest that future changes in the seasonal potential distribution of mackerel and their potential impacts on fishing communities should be considered to effectively plan future management strategies, particularly for environmentally sensitive species such as mackerel.

KEY WORDS: Chub mackerel · *Scomber japonicus* · Habitat distribution · Climate change · Future projection · Korean waters · Species distribution model · CMIP6

1. INTRODUCTION

Global sea surface temperatures have risen since the early 20th century, particularly rapidly in the western Pacific Ocean (IPCC 2021). The recently acceler-

ated pace of warming has intensified interactions in marine ecosystems, affecting species composition and diversity (Collie et al. 2008, Oremus et al. 2020, IPCC 2021), geographic distribution (Perry et al. 2005, Hazen et al. 2013, Pinsky et al. 2013), fish catch

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(Free et al. 2019, Holsman et al. 2020, Whitehouse et al. 2021), and human–wildlife conflicts (Abrahms 2021, Abrahms et al. 2023). Fish are projected to migrate poleward at approximately 40–50 km decade⁻¹ due to climate change (Hobday 2010, Cheung et al. 2011), impacting marine ecosystems and communities reliant on fish for protein. Anticipating these shifts can lead to proactive management strategies, balancing economic and conservation goals.

Small pelagic species such as chub mackerel *Scomber japonicus* (subsequently referred to as mackerel), anchovy *Engraulis japonicus*, and Pacific flying squid *Todarodes pacificus* contribute significantly to Korea's commercial fish catches (>45.5% for 1970–2022) and show considerable variability in abundance and distribution due to environmental changes. These fluctuations can economically impact fisheries and national food security. Surveys indicate that Korean fishers have observed changes in water temperature and negative effects on yields, including reduced landings, increased fishing effort, and lower quality of catches (Han et al. 2018a,b). Over the past 57 yr, Korea's fish community structure has shifted from demersal to pelagic dominance due to climate change (Zhang & Kim 1999, Jin et al. 2003), with a notable shift in the dominant species from filefish *Thamnaconus modestus* to mackerel near Jeju Island off the southern coast of Korea (Jung et al. 2013). Impact of climate change on fisheries structure and dependability of fisheries resources poses economic challenges for fisheries and communities (Han et al. 2018a,b). Therefore, understanding the current and future distribution of key fisheries resources is critical for predicting the potential biological responses and consequent socio-ecological impacts of climate variability and change.

Chub mackerel—a small pelagic fish found in the temperate and subtropical Pacific—is heavily fished by Korea, China, and Japan. In Korea, it represents 12% of total catches, ranking third from 2006 to 2021 (Statistics Korea 2024). In the Northwest Pacific, there are 2 mackerel populations—the Tsushima and Pacific stocks—distinguished by their distribution, migration, and spawning areas (Yamada et al. 1986). This study focused on the Tsushima stock, which inhabits Korean waters, including the Yellow Sea (YS), East China Sea (ECS), and East Sea (ES), spawning from March to June, with peak spawning activity from April to May (Cha et al. 2002). Post-spawning, it migrates north to the YS and ES for feeding and south to the northern ECS (NECS) and Jeju Island for wintering (Choi et al. 2003), leading to seasonal distribution changes. Extensive fishery-dependent data on

mackerel production and distribution exist because of its commercial significance (Sassa & Tsukamoto 2010, Lee et al. 2016, Lee et al. 2018). Historically, large purse-seine vessels primarily targeted the NECS and southern ES (1983–1985), but by 2001–2005, fishing expanded to the YS, likely due to warmer waters increasing suitable habitat (S. Kim et al. 2012).

Given the expectations of significant shifts in mackerel distribution due to climate-driven environmental change in Korean waters, few studies have explored the timing and extent of these future changes. The release of the Coupled Model Intercomparison Projects' 6th phase (CMIP6) data prompts the need to assess future projections using shared socioeconomic pathways (SSPs), which are newly proposed climate scenarios in CMIP6. In this study, we investigated future seasonal changes in the potential distribution of mackerel in Korean waters using 3 of the latest climate scenarios from CMIP6. This study marks a crucial step in understanding how small pelagic fish may respond to future climate change, offering valuable insights for management strategies and supporting informed proactive policy-making.

2. METHODS

2.1. Input data for distribution model construction

We obtained the mackerel presence data required for model construction from large purse-seine commercial fisheries data provided by the National Institute of Fisheries Science, Korea (see the 'Data availability' section, below). The purse-seine fishery accounted for the majority of the mackerel catch in Korea, ranging from 85 to 96%, with an average of 91% in 2006–2021 (Statistics Korea 2024). Monthly catch data offer insights into fishing locations and landings, with a spatial resolution of 0.5° for the years between 1982 and 2018. Any positive catches were treated as indicating the presence of mackerel, while catches of other fish or no catch being considered as a potential absence of mackerel from the fisheries data. For projecting the distribution of mackerel on a seasonal timescale, a period from January to March was defined as winter, April to June as spring, July to September as summer, and October to December as autumn. The presence of mackerel in the fishery was mainly concentrated along the southern coast of Korea in winter and spring and expanded northward along the coast of the YS in summer and autumn, reflecting their seasonal migratory range (Fig. 1).

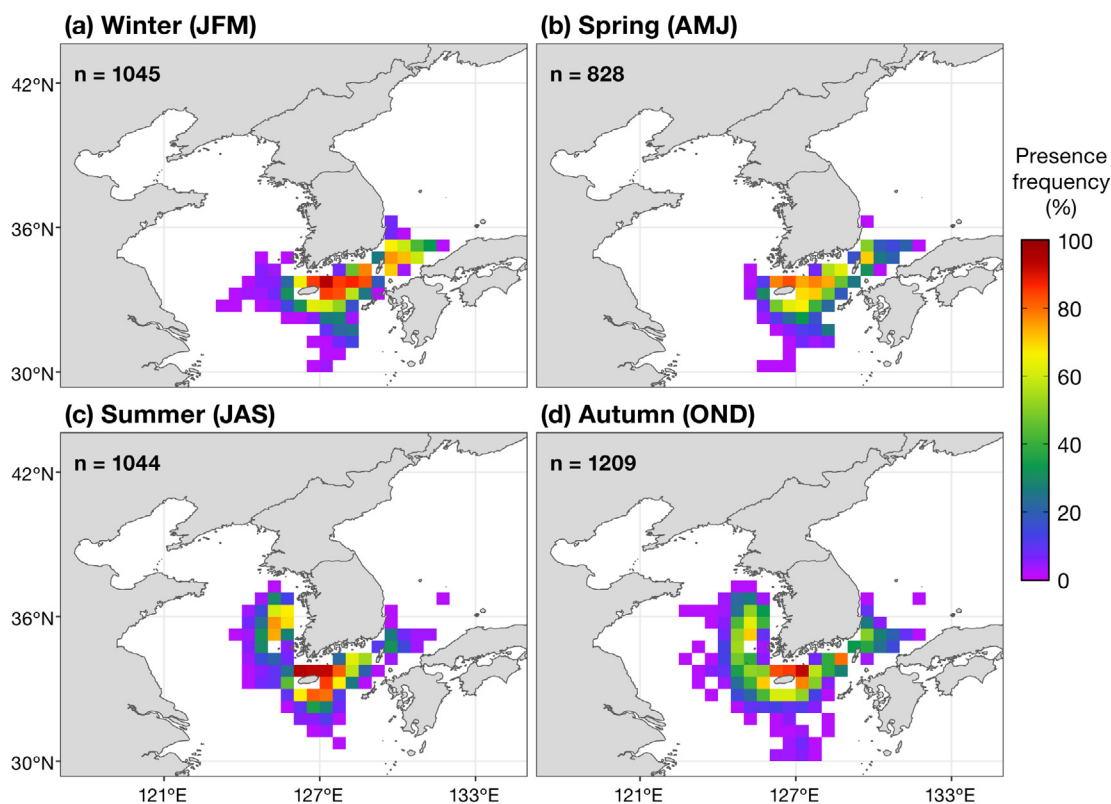


Fig. 1. Seasonal distribution of the presence of chub mackerel *Scomber japonicus* in Korean waters during 18 yr (1998–2015). The presence points were regarded as positive catches from large purse-seine fisheries (data source: The National Institute of Fisheries Science). A maximum value of 100% indicates mackerel presence every 3 mo (per season) for 18 yr

Notably, 1045 (winter), 828 (spring), 1044 (summer), and 1209 (autumn) presence points from 1998 to 2015 were used for the model construction. Based on the data distribution, the model domain was established to cover the YS, the NECS, and the ES within 200 km of the presence points (Fig. 2).

Five environmental variables—sea surface temperature (SST), sea surface salinity (SSS), sea surface current speed (SSV), chlorophyll *a* concentration (CHL) at the surface layer, and mixed layer depth (MLD)—from 1998 to 2015 were used in the model construction (Table 1). Only pelagic variables were considered in this study, based on findings from previous studies. Mackerel exhibit vertical migration behaviour (seasonal and diel changes) and can reach a depth of >200 m in the Korea Strait in the ES (Yasuda et al. 2023). However, the YS and ECS—where mackerel are mainly present—are shallow (<200 m), and previous studies have shown that mackerel distribution is associated with environmental variables in the upper layers of the YS and ECS (Chen et al. 2009, Li et al. 2014, Yu et al. 2018, 2021).

The environmental data were obtained from the Global Ocean Forecasting System 3.1 of the HYbrid

Coordinate Ocean Model (HYCOM) reanalysis data (<https://www.hycom.org>) and the Ocean Colour Climate Change Initiative project (OC-CCI) 5.0, which compiles multi-sensor global satellite data (<https://www.oceancolour.org>). The MLD was defined using a threshold method with a density criterion, setting the density change from a near-surface value at a 10 m depth ($\Delta\sigma_\theta = 0.03 \text{ kg m}^{-3}$; de Boyer Montégut et al. 2004), which has been widely used in regional seas around Korea (Jang et al. 2011, Park et al. 2011, Lim et al. 2012). SSV was calculated using the northward (*v*) and eastward (*u*) water velocities. To correspond with the mackerel presence data, the environmental data were spatially interpolated bilinearly into a 0.5° grid and temporally averaged on a monthly basis. Considering the availability periods of both the presence data and environmental data, the model construction period was set to 18 yr, from 1998 to 2015.

2.2. Species distribution modelling

Three species distribution models (SDMs)—the Maximum Entropy model (MaxEnt), Generalised Ad-

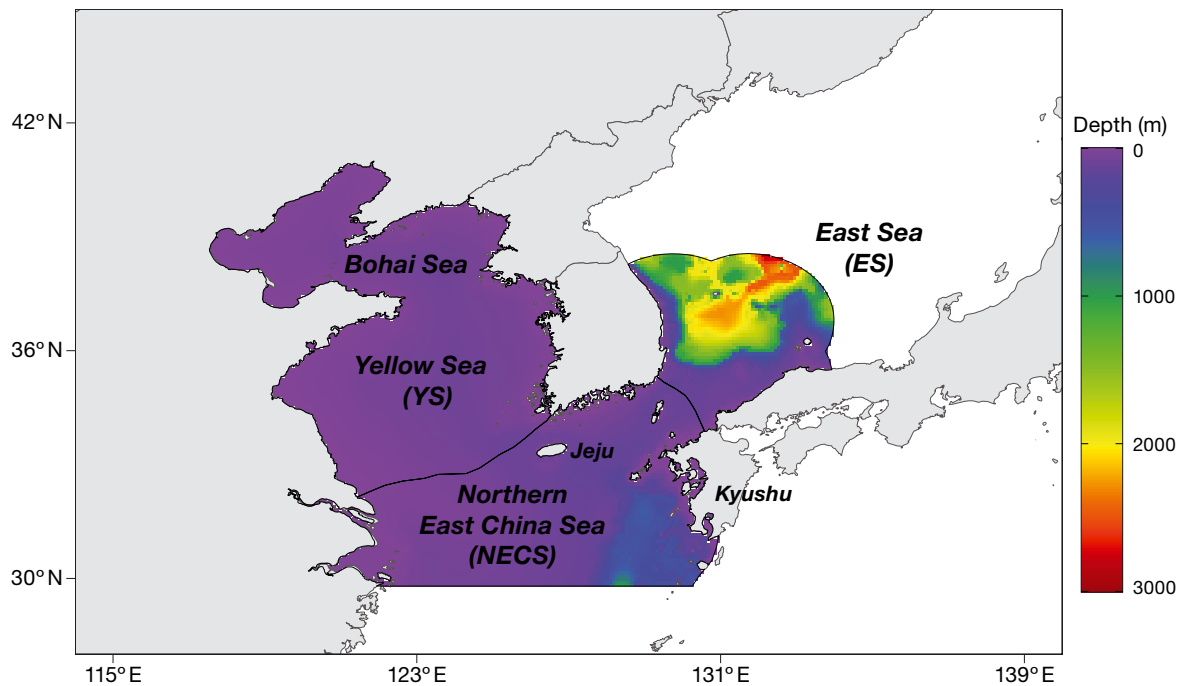


Fig. 2. Study area: the Yellow Sea (YS) with the Bohai Sea, the northern East China Sea (NECS), and part of the East Sea (ES). Colours show depth (m) based on ETOPO5 from the National Oceanic and Atmospheric Administration. The boundaries between the regional oceans were defined by the Large Marine Ecosystem (Large Marine Ecosystems Hub 2023)

Table 1. Environmental dataset for constructing the chub mackerel *Scomber japonicus* distribution model in Korean waters. HYCOM: HYbrid Coordinate Ocean Model; OC-CCI: Ocean Colour Climate Change Initiative project

Environmental variables	Abbreviation	Unit	Source	Temporal resolution	Spatial resolution (km)	Temporal coverage
Sea surface temperature	SST	°C	HYCOM	3 h	8.8	1994.01–2015.12
Sea surface salinity	SSS	psu	HYCOM	3 h	8.8	1994.01–2015.12
Sea surface current speed	SSV	m s ⁻¹	HYCOM	3 h	8.8	1994.01–2015.12
Mixed layer depth	MLD	m	HYCOM	3 h	8.8	1994.01–2015.12
Chl <i>a</i> concentration	CHL	mg m ⁻³	OC-CCI	1 mo	4.0	1997.09–present

ditive Models (GAMs), and Boosted Regression Trees (BRTs, also known as 'gradient boosting machines') — have been increasingly applied in fish distribution research (Rodrigues et al. 2023) and were used in this study. The 3 SDMs require both presence and absence data; in cases where absence data is unavailable, pseudo-absence data can be used instead of absence data. Presence data from 1998–2012 and 2013–2015 were used for model training and testing, respectively. Although SDMs constructed using presence–absence data can have better predictive performance than those constructed with presence-only or presence (Fiedler et al. 2018), the commercial catch data we used did not have sufficient absence

information recorded. Pseudo-absence data were randomly selected from grids with no catch records. The number of pseudo-absence points was set to 3 times the number of presence points (the ratio of presence to pseudo-absence was 1:3), and this sampling process was repeated 30 times. The models were run iteratively 30 times, maintaining the training presence data while replacing the pseudo-absence data to assess the effect of pseudo-absence selection on overall inference.

MaxEnt is a machine learning-based SDM that estimates species distribution by finding a probability distribution with maximum entropy (Phillips et al. 2006). MaxEnt requires 2 main parameters: feature

and multiplier regularisation. The feature is a model-fitting function that allows different possible shapes of response curves to environmental factors: linear (L), product (P), quadratic (Q), hinge (H), threshold (T), and categorical (C). The regularisation multiplier is a smoothing parameter that affects how focused or closely fitted the output distribution is, and a larger regularisation multiplier provides a more spread-out and less localised prediction (default = 1; Phillips 2017). For model construction, a total of 60 combinations consisting of 6 feature classes (L, H, LQ, LQH, LQHP, and LQHPT) and 10 regularisation multipliers from 0.5 to 5 with intervals of 0.5 were used, as in Muscarella et al. (2014). The combinations with the highest area under the curve of the receiver operating characteristic (AUC) were then selected for each season. The feature types were LQHP in spring and summer and LQHPT in autumn and winter. The regularisation multipliers were 0.5 in winter, spring, and summer, and 3.5 in autumn. The MaxEnt modelling was performed using the 'dismo' package version 1.3-5 (Hijmans et al. 2021) in R version 4.0.2 statistical programming environment (R Core Team 2020).

BRTs are machine-learning-based SDMs that combine classical regression trees and boosting (Elith et al. 2008). The BRTs have 2 main parameters: tree complexity and learning rate. Tree complexity reflects the complexity of the interactions: a value of 1 fits an additive model, 2 fits a 2-way interaction, and 3 fits a 3-way interaction between variables (Elith et al. 2008). The learning rate, also known as the shrinkage parameter, determines the contribution of each tree to a growing model, and in general, smaller learning rates are conditionally preferable (Elith et al. 2008). Since the optimal values of tree complexity and learning rate depend on the size of the dataset, 3 tree complexities (1, 2, and 3) and 5 learning rates (0.05, 0.01, 0.005, 0.001, and 0.0005) were considered for the model construction. The model with the slowest learning rate and highest tree complexity was selected for each season and penalised according to the number of trees as a function of deviance explained. Using this combination, a model of 10 000 trees showing the best deviances was selected from among 50 to 10 000 trees in 50 increments. BRTs modelling was implemented using the 'gbm' package version 2.1.8 (Greenwell et al. 2020) in R.

GAM is a nonlinear modelling approach that uses a smoothing function that is not restricted to linear relationships (Hastie & Tibshirani 1990). To estimate the presence probability of mackerel (P), the model was fitted using a binomial family with a logit link function, and all explanatory variables were considered

using tensor product smooths (s). This smooth term was controlled to set the basis dimension, k , to 10.

$$P(\text{mackerel presence}) \sim s(\text{SST}) + s(\text{SSS}) + s(\text{SSV}) + s(\text{MLD}) + s(\text{CHL}) \quad (1)$$

The GAM was implemented using the 'mgcv' package version 1.8-39 (Wood 2011) in R version 4.0.2 statistical programming environment (R Core Team 2020).

We also explored the effect of a multi-model ensemble (MME) of the 3 SDMs, as the choice of SDM can have an equally significant effect as climate change scenarios on projected species distributions (Brodie et al. 2022). The MME was calculated by averaging the outputs of the selected models in each SDM for each season.

2.3. Model evaluation: area under the curve and true skill statistic

An AUC and true skill statistic (TSS) were used to evaluate the predictive skill of each model, as these are widely used evaluation indices for the SDMs. The receiver operating characteristic curve is a graph that compares the true positive rate to the false positive rate derived from the confusion matrix across various thresholds (a threshold-independent method). The AUC, the area under this curve, ranges from 0 to 1, indicating a model's discriminative ability, with a random model at 0.5. As ecological models with an AUC value >0.7 indicate good performance (Swets 1988, Phillips & Dudík 2008), a SDM with an AUC of >0.7 can be considered reliable in this study. The AUC has the advantage of accounting for the prediction accuracy of both the presence and absence of species, making it one of the most widely used metrics for SDM validation.

TSS is a measure of both sensitivity and specificity. Sensitivity is the probability that the model will correctly classify a presence, while specificity is the probability that the model will correctly classify an absence. Like AUC, TSS includes accuracies of both presence and absence and is not affected by the presence-absence ratio or the area and shape of the data distribution (Allouche et al. 2006, Shabani et al. 2018). The TSS ranges from 0 and 1, indicating the model's discriminative ability, and a SDM with a TSS of >0.4 can be considered reliable (Landis & Koch 1977). As TSS depends on a threshold, we choose the threshold that maximises the sum of sensitivity and specificity, which is suitable for presence-only data

(Liu et al. 2013). The thresholds chosen were different seasonally: 0.46 (winter), 0.38 (spring), 0.35 (summer), and 0.45 (autumn).

To calculate AUC and TSS of SDMs, the 'dismo' package version 1.3-5 (Hijmans et al. 2021) and the 'ENMeval' package version 2.0 (Kass et al. 2021) of R were used.

2.4. Future projection: CMIP6

CMIPs are products of the World Climate Research Programme's Working Group of Coupled Modelling, and are the latest global climate model outputs used in the Assessment Reports of the Intergovernmental Panel on Climate Change. New global model experiments, CMIP6, were released in 2021 (<https://esgf-node.llnl.gov/projects/cmip6/>). The technical differences between CMIP5 and CMIP6 include an upgraded ocean circulation model, a general increase in horizontal and vertical resolutions, and complexity of marine ecosystem descriptions and related parameterisations (Séférian et al. 2020). In addition, CMIP6 employs new climate change scenarios called SSPs, compared to the representative concentration pathways (RCPs) in CMIP5. RCPs consider only Earth's radiative forcing, whereas SSPs consider socio-economic factors such as human population, economic growth, education, and urbanisation.

To investigate future changes in mackerel presence probabilities using the constructed SDMs, 5 CMIP6 models—ACCESS-ESM1.5, CanESM5, CMCC-ESM2, MPI-ESM1.2-HR, and MPI-ESM1.2-LR—providing 3-dimensional water temperature, salinity, current speed, and CHL for the historical (1998–2015) and projected future (the 2050s) periods under 3 SSPs (SSP1-2.6, SSP2-4.5, and SSP5-8.5) were used (Table 2). The monthly model data were re-gridded onto a regular horizontal resolution of 0.5°, coinciding with the mackerel presence data,

using bilinear interpolation. The MLD and SSV were calculated using the same formulas as those for the model inputs.

For future environmental changes, the delta method (Navarro-Racines et al. 2020), a simple bias correction method, was employed. The correction method operates by adding the difference between the future and historical mean values of a climate variable from CMIP6 to the reanalysis/observations. The delta method was applied for each month as follows:

$$\Delta X_m = X_m^F - \bar{X}_m \quad (2)$$

$$X_m^C = X_m^O - \Delta X_m \quad (3)$$

where ΔX_m is the delta change in month m , \bar{X}_m is the 15 yr (2000–2014) mean of the variable in the current climate for month m , and X_m^F is the 10 yr mean of the variable in the future climate of each global circulation model (GCM) for month m (Eq. 2). X_m^C is the bias-corrected GCM and X_m^O is the current climate from the reanalysis for month m (i.e. HYCOM and OCCCI; Eq. 3). The bias correction was applied to each GCM, and the presence probabilities derived from the 5 GCMs were averaged to produce an ensemble projection for the future.

In addition, to determine the partial effect of each environmental variable on future changes in the mackerel presence probability, each historical covariate was iteratively replaced with projected future data. For example, to assess the partial effect of SST, only SST was replaced with future data from the historical environmental variable to project mackerel presence probabilities.

2.5. Estimators of range and shift in mackerel habitat distribution

The loss (gain) of the potential distribution area and the centre of the potential distribution of mackerel

Table 2. List of the Coupled Model Intercomparison Project Phase 6 (CMIP6) models used for projecting the chub mackerel *Scomber japonicus* distribution in the future (2050s)

CMIP6	Modelling group	Country	Horizontal resolution (no. grids, lon × lat)
ACCESS-ESM1.5	Commonwealth Scientific and Industrial Research Organisation	Australia	360 × 300
CanESM5	Canadian Centre for Climate Modelling and Analysis	Canada	260 × 291
CMCC-ESM2	The Euro-Mediterranean Centre on Climate Change	Italy	362 × 292
MPI-ESM1.2-HR	Max Plank Institute for Meteorology	Germany	802 × 404
MPI-ESM1.2-LR			256 × 220

were calculated for the historical and future periods under each future scenario. The mackerel distribution range was calculated as the geographical area with a presence probability above the threshold that maximises the sum of sensitivity and specificity, as described in Section 2.3. The calculated distribution ranges were expressed as the coverage percentage of the study area. In addition, this study assessed changes in the geographical area of mackerel habitat distribution nearshore where fish are mainly harvested, within 1.5° (approximately 150 km) from land.

The centre of the mackerel distribution range was estimated using the centre of gravity, a conventional abundance-weighted average estimator for the centre of species distribution (Thorson et al. 2016), with abundance replaced by the presence probability as follows:

$$(\bar{X}, \bar{Y}) = \left(\frac{\sum_{i=1}^n X_i \times P_i}{\sum_{i=1}^n P_i}, \frac{\sum_{i=1}^n Y_i \times P_i}{\sum_{i=1}^n P_i} \right) \quad (4)$$

Where \bar{X} and \bar{Y} are the longitude and latitude of the centre of gravity, respectively. X_i and Y_i are the longitude and latitude of the i^{th} grid, respectively. P_i is the presence probability of mackerel in the i^{th} grid, and n is the number of grids. These estimators can be affected by missing values that vary by season; therefore, the missing data in the OC-CCI and satellite observations of CHL were filled by using distance-weighted interpolation and extrapolation, with missing rates of 29, 8, 3, and 21% from winter to autumn, respectively (Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m751p133_supp.pdf). Subsequently, the filled data were applied to the delta method.

3. RESULTS

3.1. Model evaluation

The 3 different mackerel SDMs and the ensemble of SDMs had a test AUC >0.70 (0.77–0.97), and most of the test TSS, except for 3 summer cases (2 MaxEnt and 1 BRT), were >0.40 (0.36–0.87) in all seasons, indicating that the mackerel SDMs could produce reliable predictions (Fig. 3). Similarly, point-biserial correlations between predicted presence probability and presence with pseudo-absence data in train and test data showed a significant correlation (Pearson's correlation coefficient = 0.44–0.84, $p < 0.001$). These highly significant correlations support the fact that the mackerel SDMs can pro-

vide accurate predictions. Minor differences of <0.1 between the train and test AUC values (up to 0.07 for BRT in summer) show a low impact on the selection of pseudo-absence on model inference (Warren & Seifert 2011). The ensemble prediction performed superior to the single model predictions, especially in summer and autumn, whereas the single models showed no significant performance differences. As a result, we present the ensemble SDM as the representative model in this study.

3.2. Historical presence probability

The mackerel distribution predicted by the ensemble of SDMs during the historical period shows strong seasonality. The high presence probability is concentrated in the coastal area of the NECS in spring, expands along the coast of the Korean side in the YS in summer, extends beyond the central YS to the entrance of the Bohai Sea in autumn, and then shrinks back to the NECS in winter (Fig. 4). The simulations of the 3 SDMs and the ensemble show significant positive spatial correlations ($r = 0.905$ – 0.997 in all seasons, $p < 0.001$).

3.3. Future changes in mackerel distribution

Although all scenarios were applied for the future projection, the 3 SSPs resulted in minor differences in the spread of the future projection for the presence probability. Therefore, only SSP5-8.5, the highest emission scenario, is examined here, and projections for the remaining scenarios, SSP1-2.6 and SSP2-4.5, are presented in Figs. S2 & S3. Based on the MME, ensemble projection of the 3 SDMs with 5 CMIP6 models, the presence probability was projected to decrease mainly in the NECS in winter and spring and in the YS in summer and autumn under the SSP5-8.5. However, an increase in the presence probability was also projected in the ES in all seasons and in the western part of the NECS in winter (Fig. 5a). Future changes in the mackerel presence probability projected by the 3 SDMs showed a highly significant positive spatial correlation ($r = 0.931$ – 0.996 across the MME under the 3 SSPs in all seasons, $p < 0.001$).

The mackerel distributions were projected to contract noticeably in the NECS in winter and spring and in the YS in summer and autumn (Fig. 5b). In winter, the habitat was historically distributed along the Korean Strait, but through the contraction of the

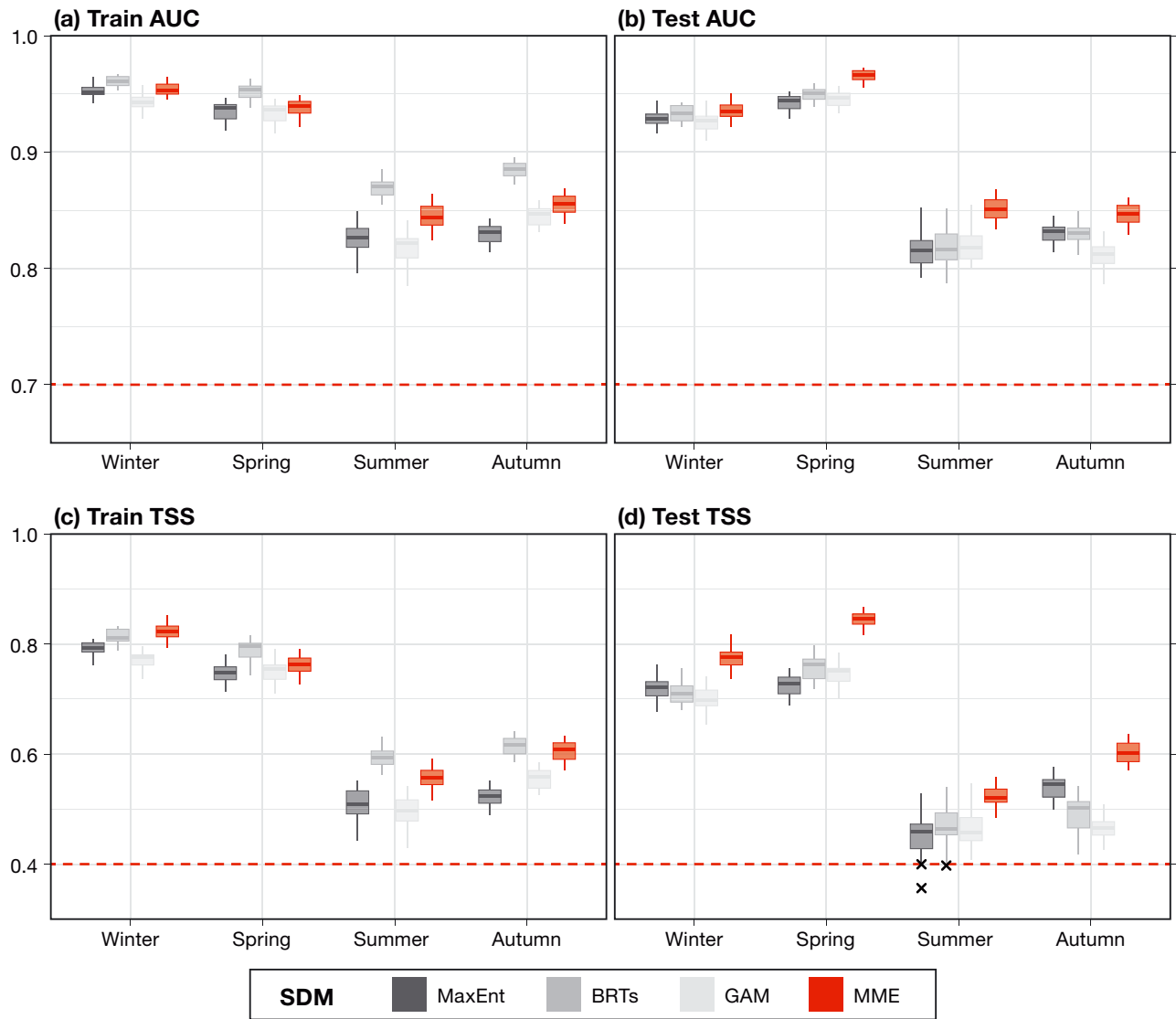


Fig. 3. Performance measures of the maximum entropy model (MaxEnt), boosted regression trees (BRTs), generalised additive model (GAM), and multi-model ensemble (MME): (a) train area under the curve (AUC), (b) test AUC, (c) train true skill statistic (TSS), and (d) test TSS. Dashed red lines: 0.7 AUC for (a) and (b) and 0.4 TSS for (c) and (d); black cross: models that do not meet the criteria (>0.7 AUC or >0.4 TSS), indicated by the dashed red line. Boxes: interquartile ranges (25th to 75th percentile); horizontal line within the boxes: median; whiskers: smallest and largest values within 1.5× the interquartile range; points: outliers

southern boundaries of the range, it was instead concentrated on the southern coast of Korea and expanded northward on the ES. In spring, the distribution range reduced slightly in the southern NECS and expanded in the ES. In summer, the range, which historically spread to the central YS, was limited to the southern YS and was expanded in the ES. In autumn, the distribution, which spread to the central YS during the historical period, was concentrated in the southern YS, similar to summer but with the smallest change under the future scenarios.

For quantifying these distribution changes, the medians of the distribution ranges derived from 5 GCMs and 3 SDMs were provided (Fig. 6). The mackerel habitat was projected to increase by 0.07–8.79% throughout the year in the future compared to the study area under the SSP5-8.5 (Fig. 6a). These increases reflect a considerable expansion of the habitat area in the ES ranging from 13.35 to 42.01% in all seasons (Fig. 6b). However, in the YS, the habitat availability was projected to decrease by 20.93% in spring and 5.28% in summer (Fig. 6c); in the NECS,

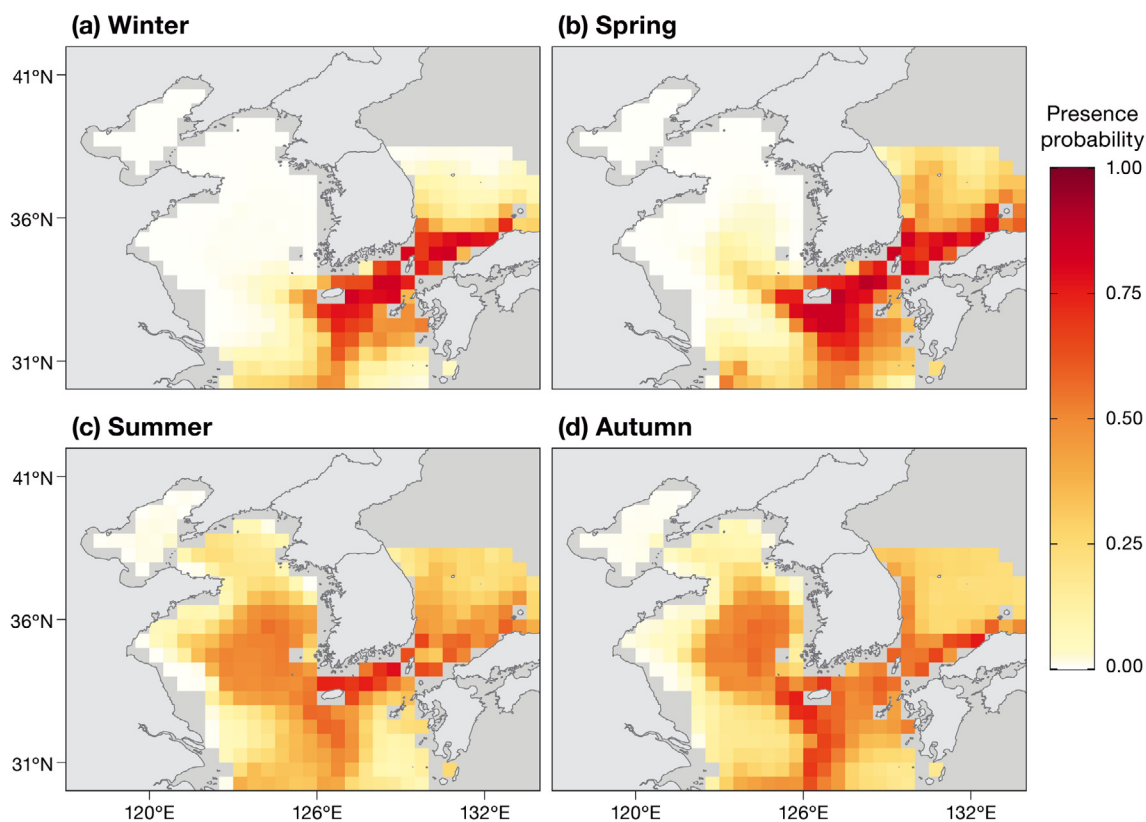


Fig. 4. Seasonal distribution of the presence probability for chub mackerel *Scomber japonicus* in Korean waters, simulated by the multi-model ensemble and averaged over 18 yr (1998–2015)

the habitat distribution was projected to decrease in all seasons, with a small decrease of less than 1.40% from autumn to spring, and a considerable decrease of 12.73% in summer (Fig. 6d).

The availability of mackerel habitat, especially within nearshore waters where fish are mainly harvested, has a significant impact on socioeconomic benefits, due to its role as a key commercial species. The mackerel habitat area in the nearshore, which is defined as 150 km from land in this study (Fig. 7a), was projected to increase in the ES throughout the year (Fig. 7c) and to decrease in the YS during summer and autumn (Fig. 7d), and this pattern was consistent across the model domain. In the NECS, where available habitats are primarily in the coastal region, most potential fishing grounds encompass mackerel habitats, showing no significant differences in habitat area between historical and future periods, indicating minimal offshore distribution changes (Fig. 7e). However, given that mackerel is currently harvested in the YS and NECS, the stability and decrease of the projected mackerel habitat in these regions is likely to have a greater impact on the mackerel fishery than the increase in habitat availability in the ES.

Furthermore, the centre of the mackerel distribution in Korean waters is also projected to change in the future. In winter and spring, the distribution centre moves northeast, with distances ranging 50.6–85.3 km for winter and 91.5–105.8 km for spring between the historical and future periods. In summer, the centre shifts eastward, ranging 58.1–66.9 km, while in autumn, it moves slightly to the east, ranging 14.2–18.0 km between the historical and future periods across different SSPs. Typically, the centre tends to shift further under the highest emission scenario (SSP5-8.5), except in autumn. However, given the resolution of the dataset used in this study ($0.5^\circ \sim 50$ km), the changes in autumn, showing a 20 km shift, indicate an insignificant change of $<0.5^\circ$.

3.4. Differences among climate change scenarios (SSPs)

Overall, the differences in the spatial distribution of the projected presence probability under the 3 climate change scenarios were subtle. However, non-linear changes were exhibited, varying seasonally

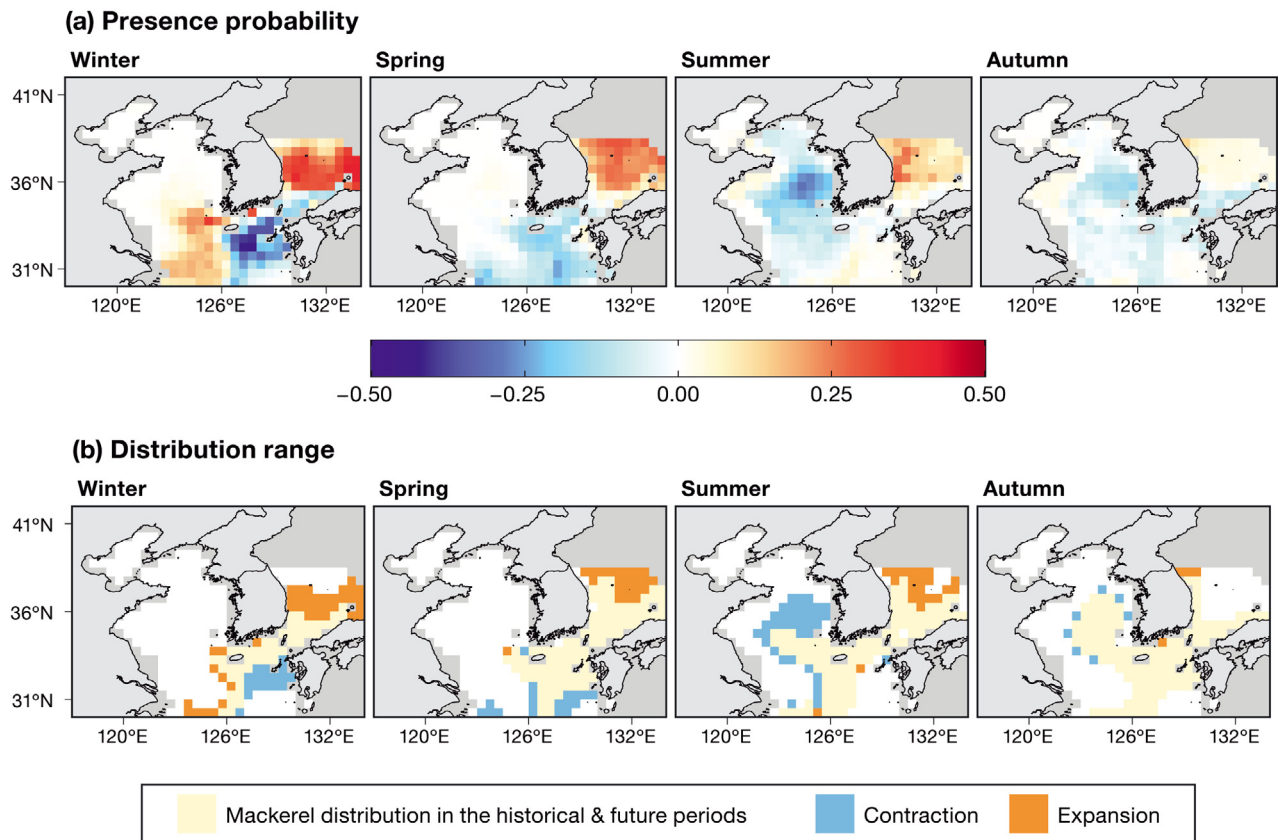


Fig. 5. Future seasonal changes in the (a) presence probability and (b) spatial distribution range of chub mackerel *Scomber japonicus* in the 2050s under the SSP5-8.5 scenario projected by the multi-model ensemble. In (a), the change is a simple subtraction of the mackerel presence probability in the historical period (1998–2015) from the future period. In (b), the potential distribution is defined as areas with presence probabilities above thresholds

and regionally (Fig. 8). For example, in winter, the projection under the SSP1-2.6 showed the smallest change (Fig. 8a), while SSP5-8.5 showed the largest change (Fig. 8i). In contrast, in spring, the largest change in the ES was projected for SSP2-4.5 (Fig. 8f), highlighting the seasonal and non-linear variations between the 3 future scenarios. In addition, in summer, the scenarios do not differ considerably in the ES, while the largest decrease in the YS was projected for SSP5-8.5 (Figs. 8c, 8g, and 8k), suggesting that the differences between scenarios may also vary by regional ocean.

The area occupied by mackerel exhibited non-linear changes under the 3 climate change pathways. Based on the MME, in the model domain, differences of 0.5–1.4%, 0.3–1.0%, 1.0–2.3%, and 0.3–2.2% across the scenarios from winter to autumn, respectively, were not considerable. In contrast, considerable differences were observed among the scenarios on a regional ocean scale. In the ES, the sce-

nario differences in the geographical area of mackerel habitat distribution were 8.0–24.1%, 0.0–1.6%, 1.6–4.8%, and 0.0–9.6% from winter to autumn, respectively, compared with the ES as projected by MME. In the YS, the scenario differences in mackerel habitat coverage were 3.8–9.6% for summer and 0.0–0.7% for autumn, and in the NECS, these differences were 1.9–10.3%, 1.9–3.8%, 0.1–1.9%, and no difference from winter to autumn, respectively. Therefore, the distribution of mackerel in the regional ocean is expected to be variable in response to the rate of climate change. For example, the regional oceans where the scenario differences account for >5% of the area are the ES in winter and autumn, the YS in summer, and the NECS in winter. Furthermore, if habitats are projected beyond the 2050s, as the effects of global warming become greater than natural variability, the differences among scenarios are expected to diverge and increasingly influence mackerel distribution.

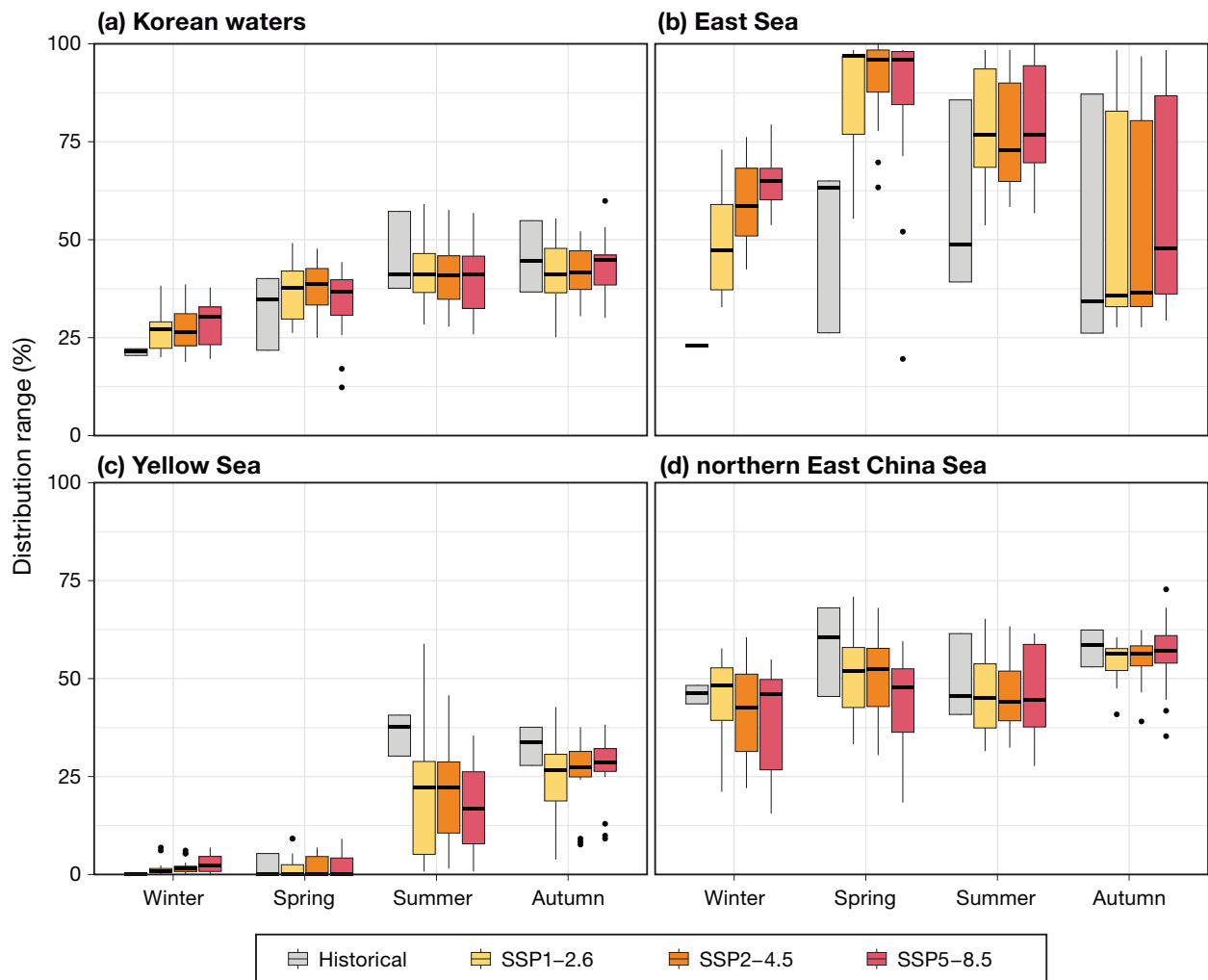


Fig. 6. Boxplot for the relative habitat range of the chub mackerel *Scomber japonicus* projected by the multi-model ensemble. The geographical coverage was calculated as the percentage of habitat in the historical (1998–2015) and future (2050s) periods under the 3 different future climate scenarios (red shade: warmest pathway): (a) Korean waters, (b) East Sea, (c) Yellow Sea, and (d) northern East China Sea. Boxes: interquartile range (25th to 75th percentile); horizontal line within the boxes: median; whiskers: smallest and largest values within 1.5× the interquartile range; points: outliers

3.5. Key drivers of future changes in mackerel distribution

We further tested the effects of each variable on future changes in the probability of presence. The GCMs used in this study represented a range of future conditions and varied in the degree of predicted changes among the SSPs. To estimate future environmental changes in current mackerel habitats, kernel density, a method for estimating the probability density function for each environmental variable at the historical presence points of mackerel, was estimated (Fig. S4). The greatest changes in the future were estimated for SST and SSS. Based on the MME of the 5 CMIP6 models, the predicted mack-

erel habitat encompassed SST increases of 1.26, 1.49, 1.88, and 1.44°C, and SSS decreases of 0.20, 0.17, 0.30, and 0.25 psu from winter to autumn, respectively, under the SSP5-8.5 in the future. On the other hand, the other covariates (SSV, MLD, and CHL) are expected to have a minor influence on future distribution changes. In other words, mackerel would experience unprecedented environmental conditions with respect to SST and SSS.

To assess the impacts of climate change on the distribution patterns of mackerel and evaluate the major drivers of future changes in mackerel distribution, we examined how each environmental predictor influenced our predictions. SST and SSS had the largest impact on future mackerel distribution

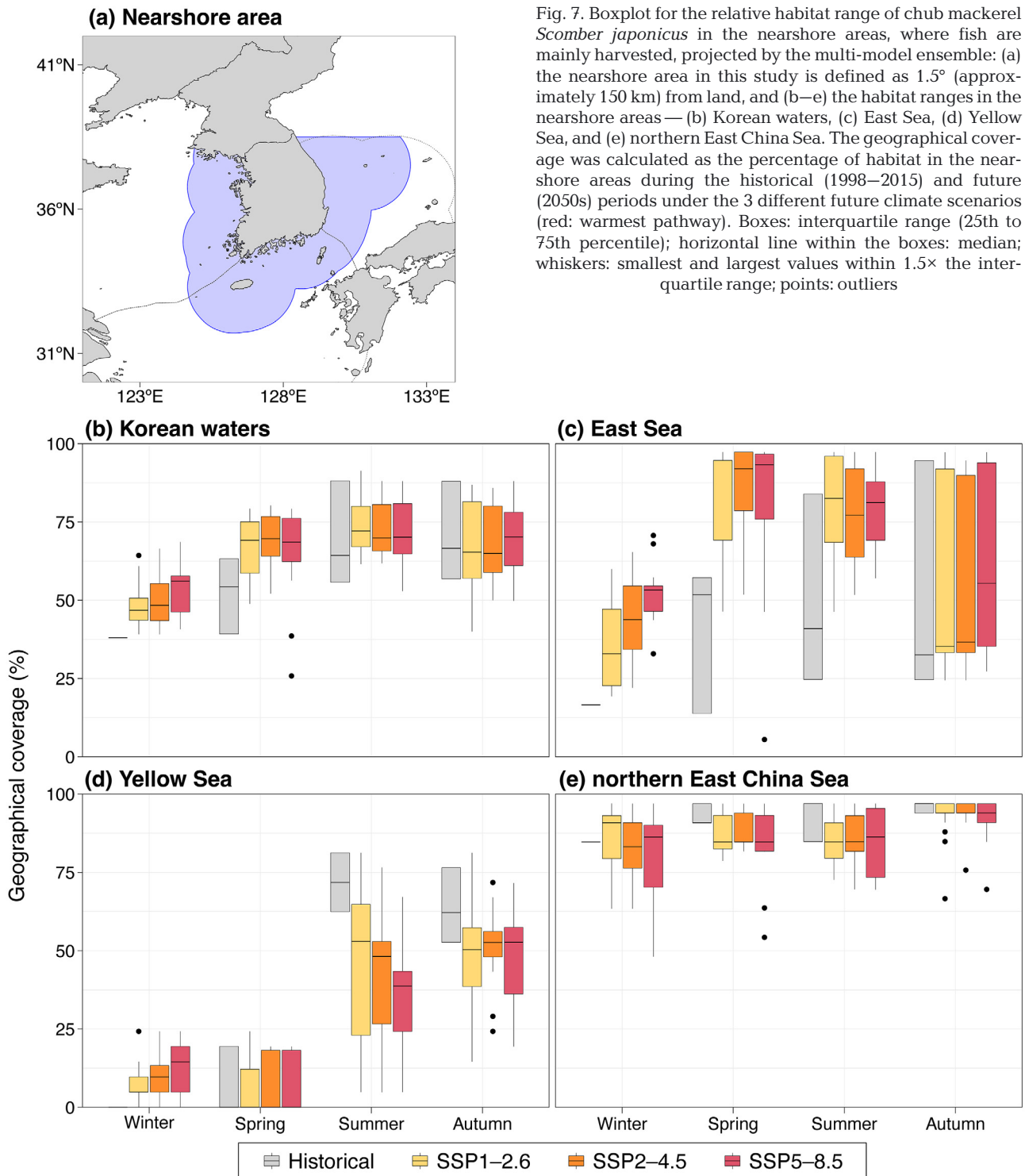


Fig. 7. Boxplot for the relative habitat range of chub mackerel *Scomber japonicus* in the nearshore areas, where fish are mainly harvested, projected by the multi-model ensemble: (a) the nearshore area in this study is defined as 1.5° (approximately 150 km) from land, and (b–e) the habitat ranges in the nearshore areas — (b) Korean waters, (c) East Sea, (d) Yellow Sea, and (e) northern East China Sea. The geographical coverage was calculated as the percentage of habitat in the nearshore areas during the historical (1998–2015) and future (2050s) periods under the 3 different future climate scenarios (red: warmest pathway). Boxes: interquartile range (25th to 75th percentile); horizontal line within the boxes: median; whiskers: smallest and largest values within 1.5× the interquartile range; points: outliers

changes (Fig. 9), and their effects varied by season. As SST was predicted to increase in the future, the presence probability was projected to decrease considerably in the NECS, increase in the ES in spring and winter, and decrease slightly across the

southern YS and the NECS in summer and autumn. As SSS was predicted to decrease in the future, the presence probability was projected to decrease in the YS and the western NECS from spring to autumn, with this change being more pronounced

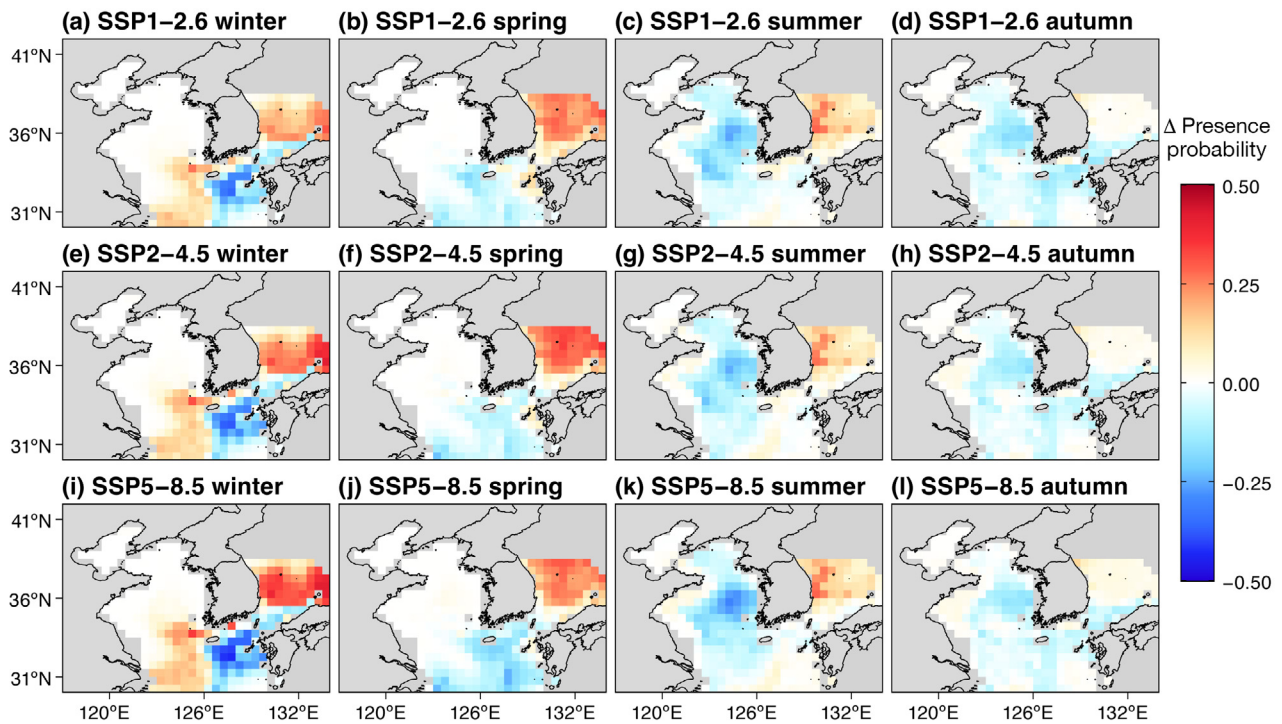


Fig. 8. Future seasonal changes in the presence probability of chub mackerel *Scomber japonicus* in the 2050s under the 3 climate change scenarios (SSP1-2.6, SSP2-4.5, and SSP5-8.5). The change is a simple subtraction of the mackerel presence probability in the historical period (1998–2015) from the future period

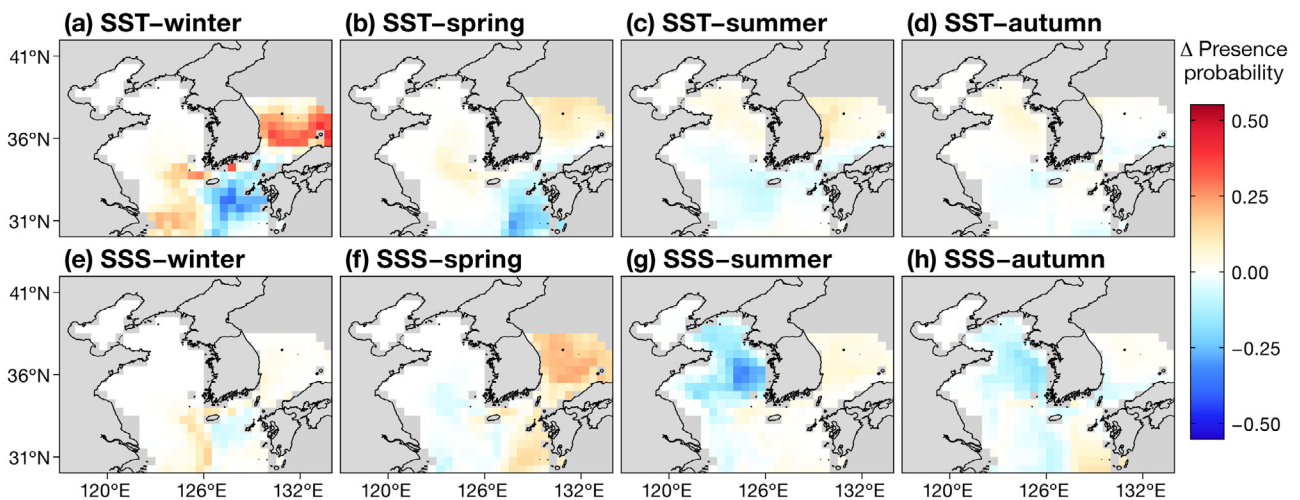


Fig. 9. Effects of each environmental variable (SST: sea surface temperature; SSS: sea surface salinity) on future changes in the presence probability of chub mackerel *Scomber japonicus* in the 2050s under the SSP5-8.5 scenario projected by the multi-model ensemble. The partial effect was estimated by replacing each future variable with data from the historical dataset. The change is a simple subtraction of the mackerel presence probability in the historical period (1998–2015) from the partial effects

in summer. Regarding the spatial distribution, SST changes were closely related to a decrease in habitat suitability in the NECS in winter and spring, whereas SSS changes were more closely related to

a probability of decrease in the YS in summer and autumn. The similarity in projections by the 3 SDMs strengthens our findings, as opposed to if the expected responses had differed.

4. DISCUSSION

4.1. Assessing uncertainty in future projections

Uncertainty in the future projections may come from various sources, including imperfect sampling (positional uncertainty), statistical methods, and future forcing (Naimi et al. 2014, Brodie et al. 2022). An ensemble projection provides integrated results, but it must be accompanied by a thorough understanding of the associated uncertainty. The future projections of the presence probability of mackerel

are an ensemble of 450 outputs — 30 pseudo-absence datasets, 5 CMIP6 models, and 3 SDMs — per year in each season and scenario. To quantify the uncertainty in this large ensemble, the SDs of the projections under the SSP5-8.5 derived from variations in the factors are presented (Fig. 10). Of the 3 factors, CMIP6 shows the largest variation in the projected probability, followed by the SDMs and the pseudo-absence dataset. The spatial distribution of the variability from CMIP6 shows seasonal variability: in winter and spring, SDs are generally higher in the NECS and ES, whereas in summer and autumn, they are noticeably

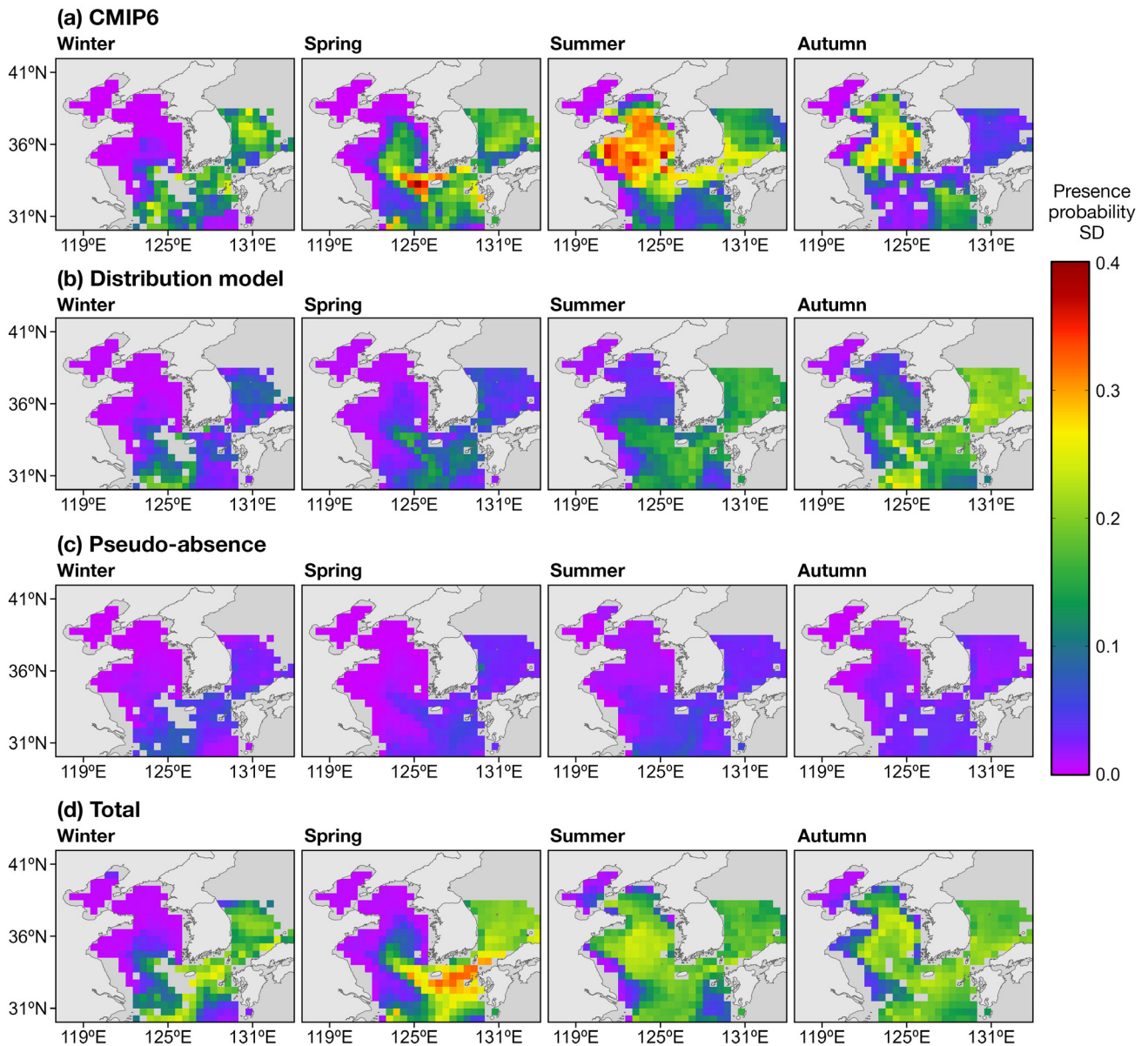


Fig. 10. SDs of future projections of the presence probability for chub mackerel *Scomber japonicus* under the SSP5-8.5, derived from (a) CMIP6 (n = 5), (b) species distribution models (n = 3), (c) pseudo-absence datasets (n = 30), and (d) the entire ensemble (n = 450)

higher in the YS (Fig. 10a). The SDs from the SDMs were mainly high in the NECS and ES across all seasons, with increases in the southern YS in summer and autumn (Fig. 10b). The SDs from the 30 pseudo-absence datasets were relatively high in the NECS and ES; however, these values were notably low, remaining below 0.1 (Fig. 10c). Thus, considering all these factors, the uncertainties are relatively high in the NECS and the ES in winter and spring (0.08 for the YS, 0.14 for the NECS, and 0.17 for the ES), while the uncertainties become more evenly distributed across the study area in summer and autumn, with spatial averages of 0.15 and 0.16, respectively (Fig. 10d).

The accuracy of the projections for each environmental covariate can influence model uncertainty. While SST and SSS are typically modelled with higher accuracy in CMIP6, in contrast, CHL has greater uncertainty due to the complexity of biogeochemical interactions. Consequently, the projection performance of each variable could contribute to the overall projection uncertainty.

4.2. Changes in distribution: the cul-de-sac effect

Although migratory species like mackerel adapt quickly to environmental changes (Hughes et al. 2014), our findings indicate a future distribution contraction for mackerel in the YS and NECS. This pattern of displacement, driven by climate change, mirrors observations in other bodies of water. For instance, in the ECS, mackerel habitat expanded and moved north-westward, along with spatial shifts in preferred water temperatures driven by negative Pacific decadal oscillations, which resulted in warm water temperatures (Yu et al. 2021). Similar trends have been documented for other seas, such as on the Northeast US continental shelf, where both larval and adult Atlantic mackerel *Scomber scombrus* moved northeast due to global warming (Overholtz et al. 2011, McManus et al. 2018), with adults previously unable to inhabit the continental shelf due to low winter temperatures now finding suitable conditions as ocean temperatures rise. This warming has also led to a shallower distribution, moving from depths >100 m to approximately 70 m (Overholtz et al. 2011). Furthermore, since 2007, the Northeast Atlantic mackerel stock has migrated and spawned further north and west as a result of global warming (Nøttestad et al. 2016). These shifts in the distribution have led to an intergovernmental conflict, commonly referred to as the 'Mackerel War' regarding the size and allocation of fishing quotas, primarily involving

Iceland, the Faroe Islands, the European Union, and Norway (Spijkers & Boonstra 2017, Østhagen 2020).

Global warming raises concerns in semi-enclosed areas (Pozdnyakov et al. 2007, Albouy et al. 2012), such as the YS, where geographic range contractions of mackerel may present a 'cul-de-sac' effect, such that species are unable to find climate refuges, potentially impacting populations and leading to species extinction (Ben Rais Lasram et al. 2010). Predictions indicate that several major fish species in the YS may suffer from the 'cul-de-sac' effect due to climate change (Hu et al. 2022, Liu et al. 2023), which could shrink mackerel distribution ranges, alter species composition, introduce new ecological interactions, and consequently affect fisheries productivity and economic outcomes.

4.3. Potential effects of future distribution changes on reproduction

As the early life stages of marine species are especially sensitive to environmental shifts, the survival rate of mackerel in the early stages influences its recruitment in the succeeding years (Kim et al. 1999, Sassa & Tsukamoto 2010). Post-spawning and hatching significantly impact population dynamics, including survival and mortality. Our results indicate an expected decline in mackerel distribution in all seasons, particularly during spring and summer, which are vital for their early life stages. Mackerel spawning occurs in regions like northern Taiwan, western Kyushu in Japan, and around Tsushima and Jeju Island (Kim et al. 2019). Our projections suggest that some areas — specifically the northwestern Jeju Island and areas west of Kyushu — might become inappropriate habitat for future spawning. As spawning grounds require specific environmental conditions distinct from those for feeding or migration, losing access to these critical areas could have greater consequences than the anticipated habitat range reduction.

Unfavourable spawning conditions can lead to population decline, but changes in the spawning ground location or timing of spawning can mitigate climate effects. Recent studies have described changes in the spawning season and grounds in response to climate variability and changes in mackerel populations. In Korean waters, mackerel spawn approximately 2 mo earlier than they historically spawned in the 1960s (Kim et al. 2020). Along the Pacific coast of Japan, the Pacific mackerel stock that traditionally spawned around the Izu Islands has expanded spawning grounds northward since the 2000s. The spawning period was also extended, and a delay of the peak

spawning time was observed from 1978 to 2017 (Kanamori et al. 2019). In Western Europe, Atlantic mackerel shifted their peak spawning northward, which was associated with SST changes from 1977 to 1998 (Beare & Reid 2002). Their spawning locations moved further north in association with regional warming from 1977 to 2010 (Hughes et al. 2014), with projections indicating a continued northward shift of spawning grounds by the middle and end of the 21st century under RCP 4.5 and RCP 8.5 scenarios (Bruge et al. 2016). Therefore, climate-induced changes in mackerel distribution may result in unforeseen changes in the spawning grounds and timing.

4.4. Potential effects of mackerel distribution changes on prey–predator interactions

Prey distribution is another important factor in determining the distribution of marine species. CHL has often been used as a proxy for ocean productivity in species distribution studies, including this study; however, it has limitations in representing the complete preyscape of forage species. Mackerel mainly feed on small fish (e.g. anchovy) and zooplankton (e.g. salpa, euphausiids, and amphipods), with anchovy being the most dominant prey, as indicated through stomach content analysis (Yoon et al. 2008, Seong et al. 2021). The future distribution of anchovies is projected to expand in the YS and decrease in the ECS during winter and spring and to decrease markedly in the YS and ECS during summer and autumn (Bang et al. 2022). In addition, future zooplankton biomass in the YS and NECS is projected to increase in all seasons, particularly in coastal regions, according to the ocean physics-lower trophic ecosystem coupled model for Korean waters (NIFS 2022). This change in prey communities could result in shifts in diet or further population responses compared to the distributional and phenological shifts discussed here.

Mackerel is an important prey resource for predatory species, particularly the Pacific flying squid in Korean waters. These squid are opportunistic carnivores, and are one of the main predators of mackerel in Korean waters, as reported using next-generation sequencing (NIFS unpubl. data). Future spawning grounds of squids assessed based on thermal conditions are projected to contract in the NECS based on CMIP3 (J. Kim et al. 2012). Using SDM approaches, the squid presence probability in the YS and NECS is projected to increase in winter and spring and decrease in summer and autumn, with a notably large decline in summer, based on CMIP6 (NIFS 2022).

Predator–prey interactions are an essential factor to consider in future distribution studies (Carroll et al. 2019), as climate change is likely to change the distribution and abundance of both prey and predators of the mackerel. In addition, many other predatory fishes consume mackerel besides the squid discussed above. Therefore, an improved understanding of predator–prey dynamics for mackerel could lead to more accurate predictions of future changes in its distribution and abundance.

4.5. Limitations

The main limitations of this study include the low spatio-temporal resolution of future data from CMIP6 and catch-based presence-only data. Although mackerel distribution could be related to mesoscale phenomena, such as sea surface height and eddies (Guan 2008, Li & Chen 2009), the CMIP6 coarse model grids are incapable of resolving these fine-scale spatial features. The use of CMIP6 data rather than downscaling models allows for multiple models and scenarios to be considered; however, this method cannot incorporate mesoscale ocean dynamics, which have been shown to be relevant to mackerel distribution in previous studies (Guan 2008, Li & Chen 2009).

Commercial catch data are more accessible and allow for the consideration of long-term seasonal variability; however, the data have biases due to preferential sampling of commercial fishing vessels (Karp et al. 2023). This preferential sampling could include biases from intense sampling in coastal regions because ports constrain fishing vessel distribution and, in turn, effort. Therefore, presence data may not adequately depict the true presence of mackerel. Fishery-independent data would be powerful for addressing these concerns, but they do not exist for mackerel in this region. Consequently, the offshore environment may not have been as thoroughly incorporated into our study as the nearshore habitat conditions of mackerel. Nonetheless, this study represents an important first step towards proactive planning for fisheries and fishery managers to address climate change-induced impacts on important pelagic fishery resources.

Our results also have limitations regarding inter-seasonal variations in mackerel habitat preferences, as the distribution models were constructed for each season separately. For example, with ongoing global warming, mackerel may encounter warmer temperatures in summer that they have not historically experienced, whereas in winter, they might not experi-

ence a novel environment due to already experiencing similar temperatures in summer and autumn. If considerable warming occurs in winter, the current preference of mackerel could shift to resemble more closely their autumn preferences. Despite the potential for such inter-seasonal variations, distribution models might categorise a warmer temperature as a novel environment, overlooking experiences from other seasons. This approach could lead to projections that are more adverse than reality, especially for the winter season.

4.6. Implications

Despite its limitations, this study provides valuable insights into how mackerel distribution may respond to climate change, and identifies the major factors driving these changes. Warming and freshening of the surface ocean are expected to cause a northward shift in suitable habitat in the ES, improving habitat conditions in the ES and contracting suitable habitat in the NECS during winter and spring, as well as in the YS during summer and autumn. Given the projected future contraction of mackerel habitats in the NECS and YS, where the majority of catches have been recorded, immediate action and ongoing monitoring are essential to adapt to these changing ecosystems. Shifting the primary distribution area to the ES could lead to changes in the key factors that determine mackerel habitat. As discussed in the future projection of anchovy distribution in Korean waters (Bang et al. 2022), mackerel spawning typically occurs in coastal areas. Consequently, adaptation to the ES, a coastal environment characterised by a less complex coastline compared to the YS and NECS, and transport to the coast by ocean currents are likely to play crucial roles in determining their habitat. It will also be essential to be prepared to adapt and modify fishing gear and methods in response to potential shifts in mackerel distribution. In the NECS and YS, where the distribution is projected to decline in the future, it will be important to assess whether the fishing gear previously used for mackerel can be adapted to target other fish species; conversely, in the ES, where mackerel catches are currently low but the distribution is projected to expand in the future, the formulation of new fisheries strategies is necessary.

In light of these projected distribution changes, to sustain mackerel catch levels amid shifting distribution, the Korean government must prepare by possibly revising and updating fishery regulations. For example, in Korea, efforts to manage the mackerel

stock have included setting the total allowable catch for the large purse-seine fishery since 1999 and implementing a closed season (one month within the period from April to June) since 2016. These measures have been evaluated positively thus far (Gim et al. 2020). However, as our results indicate a contraction in the geographical range of mackerel, adjusting the total allowable catches and closed seasons dynamically in response to changes in abundance and spawning habitats is vital. Marine protected areas could also be a valuable management strategy, although such measures are not currently in place for mackerel.

Korea is unable to secure a complete 200 nautical mile exclusive economic zone due to its geographical proximity to neighbouring countries. Shared fish stocks, including mackerel, have historically been exploited by many countries, such as South Korea, North Korea, China, and Japan. As shared fish stocks shift in distribution, international conflicts may arise or be exacerbated, potentially affecting local economies and food security.

As our models project that mackerel habitat in the ES will move northwards, the northern countries, such as North Korea and Russia, will then have better access to mackerel stocks. Consequently, ongoing fish conflicts are likely to intensify, and new conflicts may emerge in the future. Furthermore, countries sharing mackerel stocks, including Korea, China, and Japan, are expected to face reductions in the mackerel distribution due to climate change. Despite this shared challenge, no joint scientific or management plan has been designed or prepared to respond to these distribution shifts. It is therefore imperative to establish a multi-national agreement or a multi-national response team tasked with developing and implementing climate-related fishery management strategies.

5. CONCLUSIONS

As ocean warming accelerates in both rate and magnitude, understanding its impact on critical coastal habitats and on fish distribution is imperative. This study investigated the future distribution of chub mackerel, a species of significant commercial and biological importance in Korean waters, for the 2050s. Utilising 3 SDMs—MaxEnt, BRTs and GAMs—a MME, 3 SSPs, and future data from 5 GCMs (CMIP6), we found an expected increase in mackerel habitat in the ES and a maintenance or decrease in the YS and the NECS except in winter. Notably, the most significant changes were projected under the SSP 5-8.5 sce-

nario, with SST and SSS being the primary factors influencing these distributional shifts. The projected contraction of habitat range in the YS and NECS, currently the primary fishing grounds in Korean waters, contrasts with an expansion in the ES. These regional differences can be associated with possible shifts in the location of main fishing grounds or changes in regional catch production in Korea in the future. Additionally, the predicted distributional shrinkage during spring, the main spawning season for mackerel, could adversely impact spawning grounds, potentially leading to alterations in the timing and location of spawning. Our findings suggest that effective resource management, including monitoring and joint management with neighbouring countries sharing mackerel resources, will become increasingly necessary in the future.

Data availability. The fisheries data that support the findings of this study are available from the corresponding author upon reasonable request.

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