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Original Article

Modeling habitat suitability for *Trichiurus lepturus* Linnaeus, 1758 under climate change scenarios using ensemble approaches

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Abstract: The impact of climate change on fish distribution has drawn increasing attention worldwide. Studying habitat suitability trends of *Trichiurus lepturus*, a commercially valuable circum-global species, is significant for climate-adaptive fisheries management. Using an ensemble species distribution model with 11,632 occurrence records and six environmental predictors (Sea bottom temperature, Salinity, Current Velocity, Depth, Primary production, pH) from Bio-ORACLE (v3.0), we assessed global habitat suitability of *T. lepturus* under current (2010-2020) and future (2040-2050, 2090-2100) scenarios (SSP2-4.5 and SSP5-8.5). Ensemble Model performance was high (AUC = 0.964, TSS = 0.830). Primary production (39.0%), sea bottom temperature (32.3%), and pH (17.1%) were the most influential drivers. Currently, suitable habitat covers 8.80 million km², concentrated in the tropical/subtropical shelves of the western Pacific and Indian Oceans. Future projections show a slight contraction: total suitable habitat declines by 0.1-0.2% under SSP2-4.5 and by 1.4% under SSP5-8.5 by 2100. Paired t-tests on 20 ensemble layers showed no significant changes in total suitable area (P>0.05). Classifying habitat suitability into three quality classes (high, moderate, and low) shows that highly suitable areas remain largely stable (from 8.41 to 8.33 million km²), while moderate-suitability areas decrease by 15.4% and low-suitability areas increase correspondingly. Under the moderate SSP2-4.5 pathway, habitat quality remains stable throughout the century, whereas under the high-emission SSP5-8.5 pathway, the shift by 2100 indicates increased vulnerability of *T. lepturus* to future climate change. This study underscores how climate change affects species' habitat distributions and provides a scientific basis for future habitat protection.

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Introduction

Climate change has emerged as one of the most pervasive drivers of change in marine ecosystems, fundamentally altering ocean temperature, oxygen levels, acidity, and circulation patterns over the past century (Levitus et al., 2000; Doney et al., 2012; Gattuso et al., 2015). Human-induced climate change has driven a northward shift in isotherms, with much more pronounced effects in the oceans than on land (Burrows et al., 2011; Lenoir et al., 2020). Among these changes, ocean warming, acidification, and shifts in primary productivity are major stressors affecting marine life (Doney et al., 2012; Gattuso et al., 2015). These processes lead to widespread ecological consequences, including shifts in species distributions, changes in community composition, altered phenology, disruption of trophic interactions, habitat loss, and species invasions (Beaugrand et al., 2002; Perry et al., 2005; Dulvy et al., 2008; Poloczanska et al., 2013). Collectively, these changes reflect a large-scale reorganization of marine ecosystems in response to ongoing climate forcing.

Marine ectotherms, particularly fish, are highly sensitive to temperature variability because narrow thermal safety margins constrain metabolic performance, growth, and reproductive success (Addo-Bediako et al., 2000; Roessig et al., 2004; Pinsky et al., 2019). Rising ocean temperatures accelerate fish metabolic rates, leading to shorter growth cycles, reduced body size, enhanced motility, and faster evolutionary rates (Daufresne et al., 2009; Ohlberger, 2013). As a result, marine species have

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shown distributional shifts up to seven times faster than those observed in terrestrial systems, commonly tracking warming isotherms toward higher latitudes and greater depths (Poloczanska et al., 2013; Burrows et al., 2011; Chaikin et al., 2022). Such rapid climate-driven redistributions have important implications for biodiversity patterns (e.g., reduced biodiversity in tropical regions and intensified polar invasions), ecosystem functioning, and fisheries-dependent societies, with potential consequences for food security and socio-economic stability under continued ocean warming (Cheung et al., 2013; Payne et al., 2021; Pecl et al., 2022). Understanding these redistribution patterns is particularly urgent for widely distributed, commercially valuable species whose habitats span multiple ocean basins.

Within this context, *Trichiurus lepturus* (Linnaeus, 1758) is a benthopelagic predator of high ecological and commercial importance, occupying a key trophic position in coastal and continental shelf ecosystems (Chiou et al., 2006; Rohit et al., 2015). As a high-level carnivore, it plays a crucial role in controlling the abundance of lower trophic-level organisms (Martins and Haimovici, 1997). The species exhibits a nearly circum-global distribution across non-polar oceans, ranging from temperate waters of the Northern Hemisphere to southern temperate regions (FAO, 2018). Despite its broad geographic range, *T. lepturus* abundance varies markedly by region, with highest concentrations typically occurring in tropical and subtropical waters, particularly in the western Pacific and Indian oceans (Martins and Haimovici, 1997; De la Cruz Torres et al., 2014). The genus *Trichiurus* supports major fisheries worldwide, and *T. lepturus* is a prime example, recognized as the most important commercially caught species in its family, ranking among the top marine species landed globally (FAO, 2017). For example, in the Indian Exclusive Economic Zone alone, average annual landings of *T. lepturus* exceeded 209,000 tonnes between 2014 and 2019, yet the species is considered overexploited, with landings surpassing the maximum sustainable yield (Ghosh et al., 2024). Similarly, in Indonesian waters (southern Java), the species faces high fishing pressure, with fishing mortality (1.16 $year^{-1}$) exceeding natural mortality and the spawning potential ratio dropping to 26 %, indicating overexploitation (Prihatiningsih et al., 2025). The genus *Trichiurus* and related Trichiuridae also support major fisheries across East Asia; in Chinese waters, hairtail species consistently rank first in single-species production, highlighting their immense commercial value (He et al., 2022).

Research on how *T. lepturus* responds to climate change in terms of distribution is still scarce (FAO, 2018). Most existing studies have focused on regional ecology, such as distribution and biological interactions in the Southwest Atlantic (Martins and Haimovici, 1997), feeding habits in the Northwest Pacific (Chiou et al., 2006), and biological aspects in the Gulf of Mexico (De la Cruz-Torres et al., 2014). Even the most recent investigation on habitat suitability under climate scenarios, though using an ensemble approach, was restricted to the congeneric *T. japonicus* and to the northern South China Sea (Zhang et al., 2024). Consequently, ensemble modeling frameworks combined with the latest Shared Socioeconomic Pathways (SSPs; SSP2-4.5 and SSP5-8.5) have rarely been applied to project *T. lepturus's* global distribution. Therefore, a global, multi-scenario assessment of climate-driven distributional shifts remains missing – a gap that the present study seeks to address.

Species distribution models (SDMs) are widely used to quantify species–environment relationships and predict habitat suitability under current and future climate scenarios (Guisan and Thuiller, 2017; Elith and Leathwick, 2009; Araújo et al., 2019). In marine systems, SDMs have become essential tools for assessing climate impacts on fish distributions, supporting ecosystem-based management and conservation planning (Robinson et al., 2011; Cheung et al., 2013; Briscoe et al., 2019). The biomod2 package provides a comprehensive framework for constructing and evaluating multiple SDM algorithms, including generalized linear models (GLMs), maximum entropy models (MaxEnt), generalized additive models (GAMs), and others (Thuiller et al.,

2016; Thuiller et al., 2025). However, predictions from single-algorithm SDMs can vary widely and be highly sensitive to model choice, creating uncertainty in projections (Thuiller et al., 2019). To reduce this uncertainty, ensemble forecasting – which combines multiple algorithms – has been shown to improve predictive accuracy, robustness, and generalization capacity (Araújo and New, 2007; Zhang et al., 2024). Recent advances have integrated ensemble SDMs with high-resolution benthic environmental layers and future Shared Socioeconomic Pathway (SSP) scenarios, enabling more reliable projections of habitat redistribution for marine species (Assis et al., 2024). Despite these methodological improvements, ensemble-based global assessments for many commercially important fish, including *T. lepturus*, remain scarce.

In this study, we assessed the impacts of climate change on the global habitat distribution of *T. lepturus* using an ensemble modeling framework implemented in biomod2. Specifically, we aimed to identify the most influential environmental drivers shaping the current global distribution, map current habitat suitability and quantify its global extent, project future changes in suitable habitat area and its quality under different climate scenarios, and determine whether *T. lepturus* is likely to experience net habitat expansion, net contraction, or relative stability (i.e., a climate "winner", "loser", or "resistant" species). By delivering the first global ensemble projections for this species under SSP scenarios, this study addresses a critical knowledge gap and provides actionable insights for climate-adaptive fisheries management and transboundary conservation planning.

Materials and Methods

Species occurrence data: Occurrence records for this species were obtained from the Global Biodiversity Information Facility (GBIF; https://www.gbif.org/occurrence/; accessed on 4 October 2025), the Ocean Biodiversity Information System (OBIS; https://obis.org/search/; accessed on 15 October 2025), and published geo-referenced field surveys. Data from the three sources were merged, then cleaned and quality-controlled in QGIS (version 3.12). Cleaning involved removing duplicate records, excluding points outside the study area or on land, and eliminating records with missing coordinates. To minimize spatial sampling bias, we applied spatial thinning using the spThin R package (version 0.2.0; Aiello-Lammens et al., 2015), retaining only one occurrence point within a 10 km radius. After thinning, the final dataset comprised 11,632 presence records, which we exported as CSVs and saved as R objects to ensure full reproducibility of subsequent analyses (Chamberlain et al., 2017; Provoost and Bosch, 2022). All cleaned occurrence data were stored with the World Geodetic System 1984 (WGS84) geographic coordinate system.

Environmental data source: We used environmental data from the Bio-ORACLE (version 3.0) database (https://www.biooracle.org/, accessed on 20 December 2025) to predict the potential distribution of *T. lepturus*. Present-day variables (2010-2020) and future projections under two climate scenarios (SSP2-4.5 and SSP5-8.5) were obtained for two time periods: mid-century (2040-2050) and end-century (2090-2100). As *T. lepturus* is a benthic-pelagic species, we extracted the mean of seven benthic environmental layers at a spatial resolution of 0.083°, restricted to its ecological depth range of 2-400 m based on FishBase and FAO reports (FAO, 2018; Froese and Pauly, 2024). The selection of ecologically relevant environmental variables was guided by data availability and established biological knowledge. Accordingly, we included Sea Bottom Temperature as a primary constraint on ectothermic metabolism (Chiou et al., 2006), Primary production as a proxy for prey availability (Rohit et al., 2015), and pH to account for ocean acidification. We added salinity, current velocity, and depth to capture osmoregulatory constraints, dispersal dynamics, and vertical habitat partitioning, respectively. The study area was global, covering all marine waters within the species' depth range (2-400 m).

To reduce overfitting, we performed multicollinearity analysis using Pearson correlation coefficients (corrplot R package) (Naimi et al., 2014).

Variables with $|r| > 0.7$ were excluded. After filtering, dissolved oxygen was excluded due to $|r| > 0.7$, and six variables were retained: sea bottom temperature, salinity, current velocity, depth, primary production, and pH. All raster layers were resampled to 0.083° using bilinear interpolation to reduce computational demand; preliminary tests showed this coarsening did not qualitatively affect the predicted patterns (Assis et al., 2024). For full reproducibility, we performed all analyses in R version 4.5.0 using the biomod2 package version 4.2.6.2 (Thuiller et al., 2025). Validation using occurrence points showed that over 99% of points fell on valid (non-NA) cells, with the remaining NAs corresponding to land or areas outside the study region. For future projections, environmental layers were prepared for the 2050s (representing the 2040-2050 period) and 2100s (2090-2100) under SSP2-4.5 and SSP5-8.5, similarly harmonized, masked to the depth range, and saved in. grd and .rds formats.

Species distribution modeling (SDM): In recent decades, numerous models have been developed to analyze relationships between species distributions and environmental variables (Rathore et al., 2023). In this study, we used the cleaned distribution data and selected environmental predictors to perform Species Distribution Modeling (SDM). To minimize uncertainties associated with single-model predictions (Romera et al., 2017), we employed an ensemble approach using six algorithms implemented in the biomod2 R package, version 4.2.6.2 (Ahmadi et al., 2023; Thuiller et al., 2025): Generalized Boosted Models (GBM), Flexible Discriminant Analysis (FDA), Generalized Additive Models (GAM), Generalized Linear Models (GLM), Maximum Entropy (MaxEnt), and Multivariate Adaptive Regression Splines (MARS). To reduce overfitting, we applied algorithm-specific regularization: tuned parameters for GBM, appropriate penalization for FDA, reduced complexity for GAM and MARS, constrained interactions for GLM, and optimized regularization for MaxEnt.

The study area for pseudo-absence generation included all marine grid cells with depths between 2 and 400 m (i.e., the species' known vertical range), excluding land. This was ensured by applying a depth mask to all environmental layers before sampling, so random pseudo-absence points were drawn only from ecologically accessible areas rather than the entire global ocean. To ensure robustness and assess variability, five independent pseudo-absence datasets (PA1-PA5), each containing 10,000 points, were generated within this study area using the randomPoints function of the dismo package (Hijmans et al., 2017). For each pseudo-absence dataset, we applied 10 bootstrap replicates to randomly partition occurrence records and corresponding pseudo-absence points into training (80%) and testing (20%) subsets. Finally, an ensemble model (EMwmean) was constructed by averaging the predictions of all individual models weighted by their validation AUC scores. All analyses were performed in R version 4.2.6.2 (Thuiller et al., 2025).

Model performance was evaluated using two complementary metrics: the threshold-independent area under the receiver operating characteristic curve (AUC) and the threshold-dependent True Skill Statistic (TSS). AUC values range from 0 to 1, with >0.9 indicating excellent performance, 0.8-0.9 good, 0.7-0.8 fair, and <0.5 worse than random (Fielding and Bell, 1997). TSS values range from −1 to 1, with values close to 1 denoting high accuracy and values < 0.5 indicating poor predictive power (Allouche et al., 2006). To assess overfitting, we calculated the difference between training and testing AUC/TSS scores across replicates; low differences confirmed generalization capacity. Only models with AUC ≥ 0.8 were used in the ensemble to ensure robust results. These models were combined using a weighted average based on their validation AUC values. Additionally, permutation-based variable importance was calculated for each algorithm across three replicates to identify the relative contribution of each environmental predictor.

Ensemble models predicted *T. lepturus* distribution ranges under current conditions and four future scenarios across two climate pathways (SSP2-4.5 and SSP5-8.5). Predictions were generated for two projection periods: mid-century (2040-2050) and late-

century (2090–2100). Binary presence–absence maps were generated using an optimal TSS threshold of 0.418, which was derived by maximizing the True Skill Statistic from the cross-validation replicates of the ensemble model (EMwmean). To assess whether observed changes in suitable habitat area between current and future scenarios were significant, we performed paired t-tests using the 20 ensemble layers (5 PA runs × 4 ensemble algorithms) for each scenario. A P-value < 0.05 was considered statistically significant. All analyses were conducted in R, and output raster layers (GeoTIFF format) were exported for visualization. Continuous suitability values were normalized between 0 and 1, and multi-panel maps were generated using R packages (terra, sf, ggplot2, cowplot) with a consistent color gradient, then exported as high-resolution PNG files.

Using the percentile thresholds derived from the current suitability distribution (33rd and 66th percentiles), the continuous suitability values were classified into three categories. The class boundaries were: Low suitability (0-0.212), Moderate suitability (0.212-0.498), and High suitability (0.498-1). These same breaks were then applied to all future scenarios to ensure comparability. Accordingly, the three classes are referred to as (a) highly suitable, (b) moderately suitable, and (c) low suitability.

Results

Selection of environmental predictors: The correlation analysis among the six environmental variables showed that most pairwise correlations were weak ($|r| < 0.4$), indicating no significant multicollinearity (Table 1). These results confirm that the predictor set is statistically independent and suitable for species distribution modeling. The six variables retained after multicollinearity analysis – namely, Sea Bottom Temperature (SBT), Salinity, Current Velocity, Depth, Primary production, and pH - were used as key environmental factors for modeling the current and future habitat suitability of *T. lepturus* (Table 1).

Model performance: The performance assessment of individual algorithms showed close agreement between calibration and validation scores, indicating limited overfitting across all models (Fig. 1). Differences between calibration and validation means (Mean Diff) were generally small for most algorithms, particularly for FDA, GAM, GLM, and the ROC scores of MAXENT, highlighting the stability and generalizability of the models. Among single algorithms, MAXENT and GBM exhibited the highest predictive performance. MAXENT achieved a mean ROC of 0.963 and a mean TSS of 0.847, while GBM attained a mean ROC of 0.965 and a mean TSS of 0.818 (Fig. 1). All selected models obtained high scores (ROC > 0.8, TSS > 0.6), indicating strong predictive ability. FDA and GAM showed the smallest differences between calibration and validation (Mean Diff near zero), reflecting highly consistent behavior. MARS and GBM showed moderately higher TSS deviations (0.029 and 0.039, respectively), though still within acceptable ranges.

To reduce uncertainty from single-model predictions, we used an ensemble approach combining the six algorithms via a weighted average based on their AUC values (EMwmean). The final ensemble model showed robust, reliable predictive performance across five pseudos-absence datasets (PA1-PA5). The ensemble achieved a mean ROC of 0.964 (±0.0004) and a mean TSS of 0.830 (±0.0026), indicating strong generalization capacity. The optimal threshold for binary mapping was consistently close to 0.418, confirming the appropriateness of the selected cutoff for habitat gain/loss assessments. These results confirm the ensemble model's suitability for projecting current and future habitat suitability of *T. lepturus*.

Variable importance and ecological drivers: The ensemble model analysis identified primary production as the dominant environmental driver, with a mean importance score of 0.390 (34.6% contribution). This was followed by Sea Bottom Temperature (SBT) (0.363, 32.3%) and pH (0.192, 17.1%). Physical factors, including salinity (0.094, 8.4%), depth (0.08, 7.1%), and current velocity (0.006, 0.6%), exhibited low to minor importance (Table 2).

Table 1. Pairwise Pearson correlation matrix among environmental predictors (baseline period 2010-2020).

Variable	Primary production	Current Velocity	pH	Salinity	SBT	Depth
Primary production	1.000	0.034	0.307	-0.318	0.273	0.556
Current Velocity	0.034	1.000	0.172	0.112	0.236	0.070
pH	0.307	0.172	1.000	0.193	0.338	0.245
Salinity	-0.318	0.112	0.193	1.000	0.179	-0.230
SBT	0.273	0.236	0.338	0.179	1.000	0.376
Depth	0.556	0.070	0.245	-0.230	0.376	1.000

Table 2. Relative importance of environmental predictors based on ensemble variable contribution analysis.

Rank	Environmental Variable	Mean Weighted Importance (EMwmean)	% Contribution
1	Primary production	0.390	34.6 %
2	Sea Bottom Temperature (SBT)	0.363	32.3 %
3	pH	0.192	17.1 %
4	Salinity	0.094	8.4 %
5	Depth	0.080	7.1 %
6	Current Velocity	0.006	0.6 %

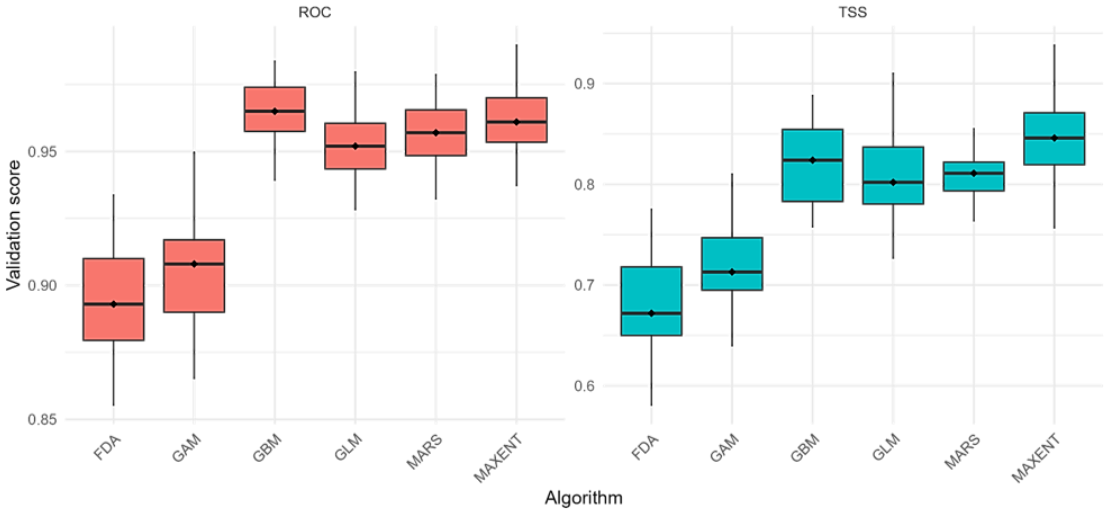


Figure 1. Performance metrics of individual algorithms based on cross-validation results.

Response curves (Fig. 2) show the following patterns: the SBT curve peaks between 16°C and 26°C; primary production displays a threshold increase above 3-4 mmol/m³; pH shows a preference between 7.0 and 7.6 with a decline at higher values; salinity and depth indicate optima around high-salinity waters and shallow zones (0 to −50 m); current velocity contributes moderately across the range.

Current distribution and future projections of habitat suitability for *T. lepturus*

Current distribution: The continuous habitat suitability maps (Fig. 3) show that *T. lepturus* is mainly confined to coastal and shallow continental shelf waters of the western Pacific and Indian Oceans. Highly suitable regions are located in tropical and subtropical waters, with peak suitability around the Indonesian and Philippine archipelagos, northern Australia, and the southern coasts of China and Japan (Fig. 3). These habitats fall primarily within the exclusive economic zones (EEZs) of Indonesia, the Philippines, Australia, China, and Japan. Moderately suitable areas extend across broader shelf margins, while low-suitability regions occupy peripheral parts of the species' range. Beyond the western Pacific and

Table 3. Projected changes in total suitable habitat area for *Trichiurus lepturus* under current and future climate scenarios (0.418 threshold, million km²).

Scenario	Total Habitat Area	Area Lost	Area Gained
Current	8.80	0	0
SSP2-4.5 – 2050	8.79	18,109.98	4,713.86
SSP5-8.5 – 2050	8.80	7,482.27	4,554.48
SSP2-4.5 – 2100	8.78	34,465.28	7,400.33
SSP5-8.5 – 2100	8.68	127,908.77	292.60

Table 4. Area of each suitability class under current and future climate scenarios (million km^2)

Scenario	High suitability	Moderate suitability	Low suitability
Current	8.41	8.34	7.26
SSP2-4.5 – 2050	8.39	8.35	7.26
SSP5-8.5 – 2050	8.40	8.33	7.27
SSP2-4.5 – 2100	8.39	8.34	7.29
SSP5-8.5 – 2100	8.33	7.06	8.62

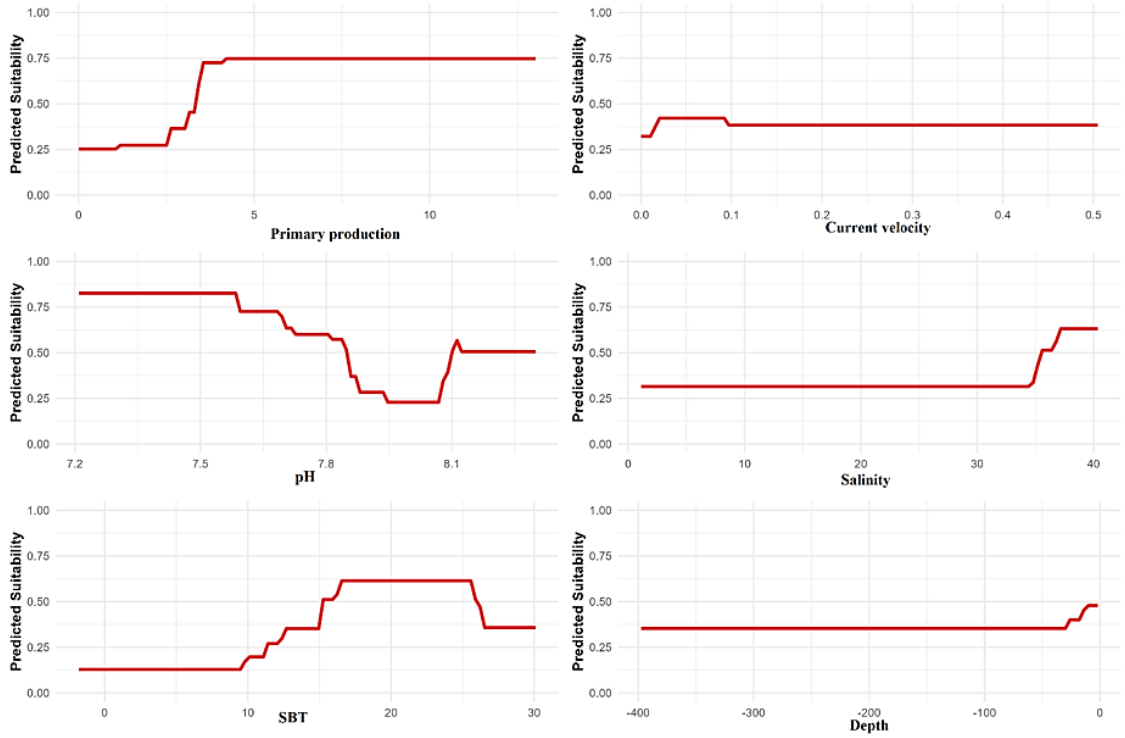


Figure 2. Response curves indicating the relationship between environmental variables and the probability of predicted occurrence for *Trichiurus lepturus*. The six environmental variables include Primary production, Current velocity, pH, Salinity, sea-bottom temperature (SBT), and Depth.

Indian Oceans, the model identifies suitable habitats in other parts of the species' known distribution, including the Gulf of Mexico and Caribbean Sea, the Atlantic coasts of South America and West Africa, the Mediterranean and Red Seas, the Persian Gulf and Arabian Sea, as well as the Andaman Sea and the South China Sea. The total currently suitable habitat area is estimated at 8.80 million km² (Table 3).

Future projections under climate change scenarios: Future habitat suitability was projected under two emission scenarios (SSP2-4.5 and SSP5-8.5) for mid-century (2040-2050) and end-of-

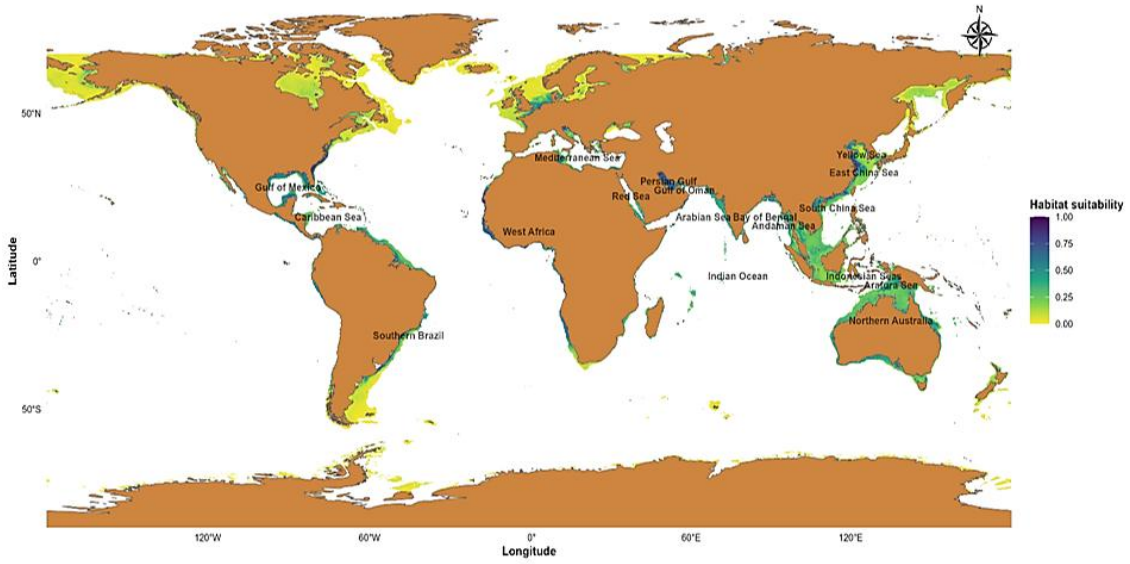


Figure 3. Current global habitat suitability for *Trichiurus lepturus* predicted by the ensemble model. Colors indicate suitability values ranging from 0 (low) to 1 (high).

century (2090–2100), using an optimal TSS threshold of 0.418 to define suitable areas (Table 4). Under mid-century projections, total suitable habitat remains relatively stable, with a slight contraction: under SSP2-4.5 it decreases slightly to 8.79 million km² (–0.15%) and under SSP5-8.5 to 8.80 million km² (–0.03%). By the end of the century, a clearer decline is projected, especially under SSP5-8.5, where suitable habitat shrinks to 8.68 million km² (–1.5% relative to current). Newly suitable areas are mainly in higher-latitude waters and offshore zones, while localized contractions occur in parts of the current tropical range.

By the end of the century, changes become more pronounced. Under SSP2-4.5, suitable habitat contracts to 8.78 million km² (–0.227% relative to current), with a loss of approximately 34,465 km² and a gain of 7,400 km². Under the more extreme SSP5-8.5 scenario, suitable habitat declines further to 8.68 million km² (–1.36% relative to current), characterized by a large loss of 127,909 km² and a very limited gain of only 293 km². The lost areas extend across parts of the current tropical range, while small newly suitable areas are mainly located in higher latitude waters and offshore zones (Figs. 5, 6).

To further examine qualitative shifts in habitat quality, we classified suitability values using percentile thresholds (33rd and 66th) derived from the current suitability distribution, as described in the materials and methods section. The area of each suitability class was calculated for all scenarios (Table 4). Under current conditions, high suitability areas cover the largest extent (8.41 million km²), followed by moderate (8.34 million km²) and low suitability (7.26 million km²). By 2100 under the extreme scenario SSP5-8.5, low suitability areas expand to 8.62 million km², while moderate suitability shrinks considerably (7.06 million km²) and high suitability declines slightly to 8.33 million km² (Fig. 4). Under SSP2-4.5 by 2100, changes remain modest: low suitability increases marginally to 7.29 million km², moderate and high classes show slight contractions. These results indicate a deterioration of habitat quality under the high-emission scenario by the end of the century, with a notable shift from moderate to low suitability, rather than an upward shift in quality. The trends confirm a redistribution of *T. lepturus* suitability, but do not support a poleward expansion in absolute terms under SSP5-8.5.

To evaluate the statistical significance of projected changes in suitable habitat area, we performed paired t-tests using the 20 ensemble layers for each scenario. No significant changes were detected between current conditions and any future scenario (SSP2-4.5 2050:

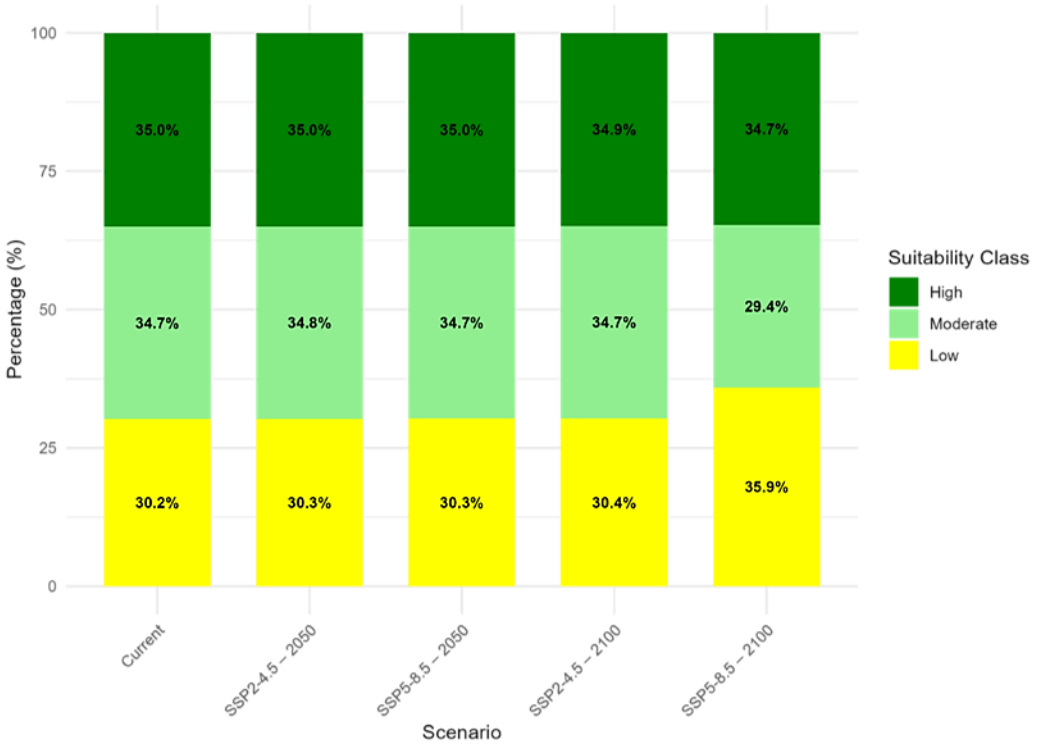


Figure 4. Percentage of each suitability class under current and future climate scenarios (%).

P=0.053; SSP5-8.5 2050: *P*=0.065; SSP2-4.5 2090: *P*=0.200; SSP5-8.5 2090: *P*=0.312). These results confirm that the observed slight contractions in total suitable habitat (maximum 1.5% under SSP5-8.5 2090) are not significant, indicating high resilience of *T. lepturus* to projected climate change through the end of the century.

Discussions

Model performance and current distribution: This study applied an ensemble modeling framework to predict the global distribution of *T. lepturus* under current and future climate scenarios. The model achieved robust predictive performance, comparable to that of ensemble models used for other marine species in previous studies (Ahmadi et al., 2023; Shi et al., 2023; Zhang et al., 2024; Nneji et al., 2025). This confirms the practical value of the ensemble method for predicting *T. lepturus*'s global distribution. The ensemble model predicts that the currently suitable distribution of *T. lepturus* is mainly confined to coastal and shallow continental shelf waters of the western Pacific and Indian Oceans, with highly suitable habitats concentrated in tropical and subtropical waters, particularly around the Indonesian and Philippine archipelagos, northern Australia, and the southern coasts of China and Japan. Beyond these regions, the model also identifies suitable habitats in other parts of the species' known global distribution, including the Gulf of Mexico and Caribbean Sea, the Atlantic coasts of South America and West Africa, the Mediterranean and Red Seas, the Persian Gulf and Arabian Sea. This broad distribution pattern aligns with global distribution records from FishBase and FAO reports (FAO, 2018; Froese and Pauly, 2024).

These findings further highlight the accuracy of using the ensemble model to simulate *T. lepturus* habitat distribution and provide strong support for predicting its habitat distribution under climate change. The species occurrence data used in this study were compiled from GBIF, OBIS, and published field surveys; although they came from multiple sources, the data were carefully cleaned and spatially thinned to reduce sampling bias and improve prediction reliability. Individual algorithms showed minimal overfitting, with close agreement between calibration and validation scores across runs, supporting the reliability of the ensemble projections. This aligns

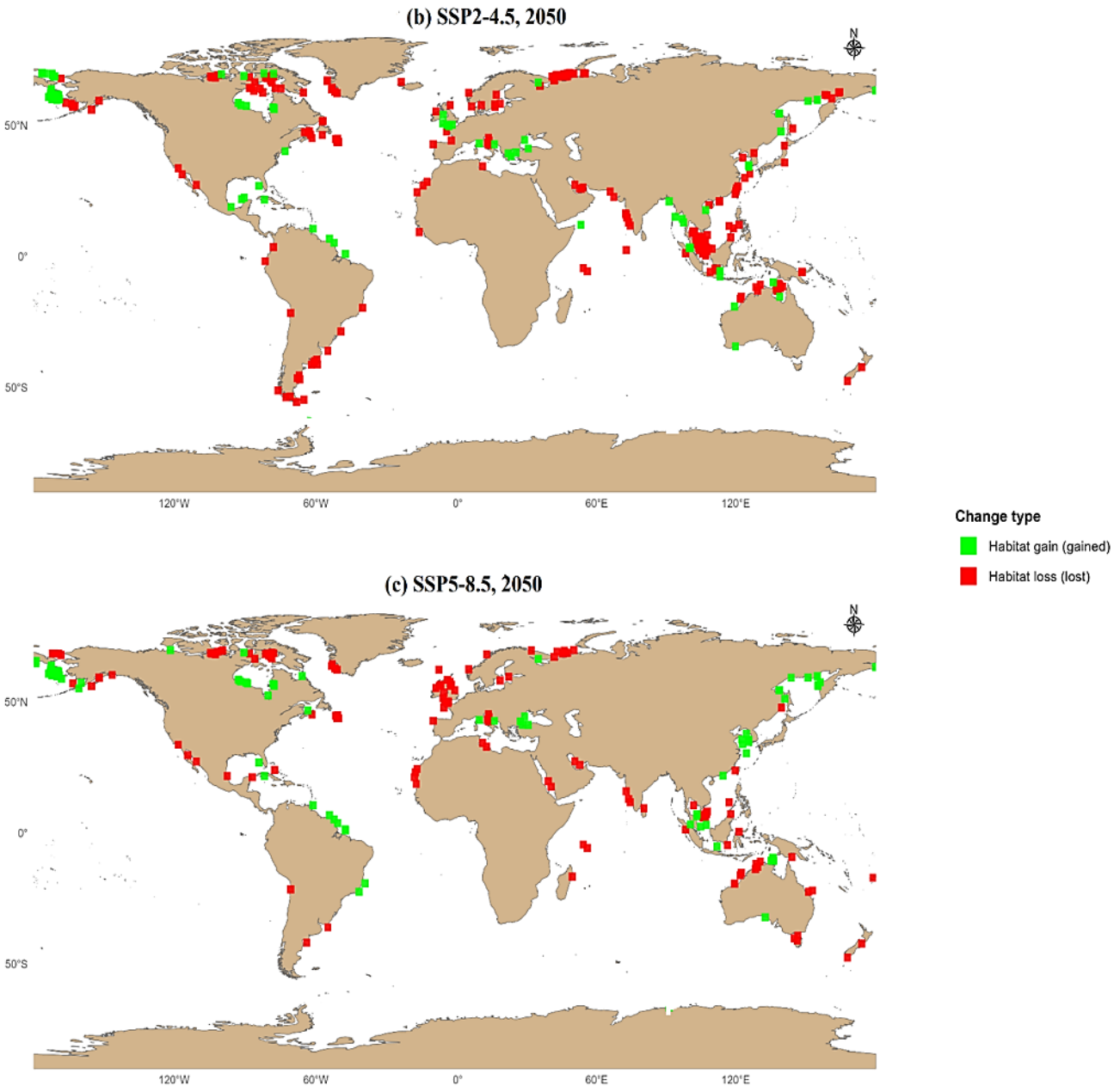


Figure 5. Projected changes in habitat suitability for *Trichiurus lepturus* by 2050 under the SSP2-4.5 and SSP5-8.5 scenarios relative to the current period. Panels (b) and (c) show habitat losses (red) and gains (green) under SSP2-4.5 and SSP5-8.5, respectively. Green indicates areas where suitability is projected to increase, and red indicates areas where it is projected to decrease.

with contemporary species distribution modeling practices that emphasize cross-validation stability and ensemble consensus for marine species (Mainali et al., 2015).

The marine environment is complex and dynamic, with multiple interacting factors shaping species distributions (Mamun et al., 2018). Among the six environmental predictors examined, primary production was the dominant driver (34.6%), reflecting the species' trophic dependence on productive feeding grounds. The threshold increases in suitability above 3-4 mmol/m³ indicate that areas with elevated phytoplankton biomass support higher prey availability, particularly for a benthopelagic predator that relies on crustaceans and small fish (Chiou et al., 2006; Rohit et al., 2015). This relationship between primary productivity and habitat distribution has been explicitly demonstrated in the

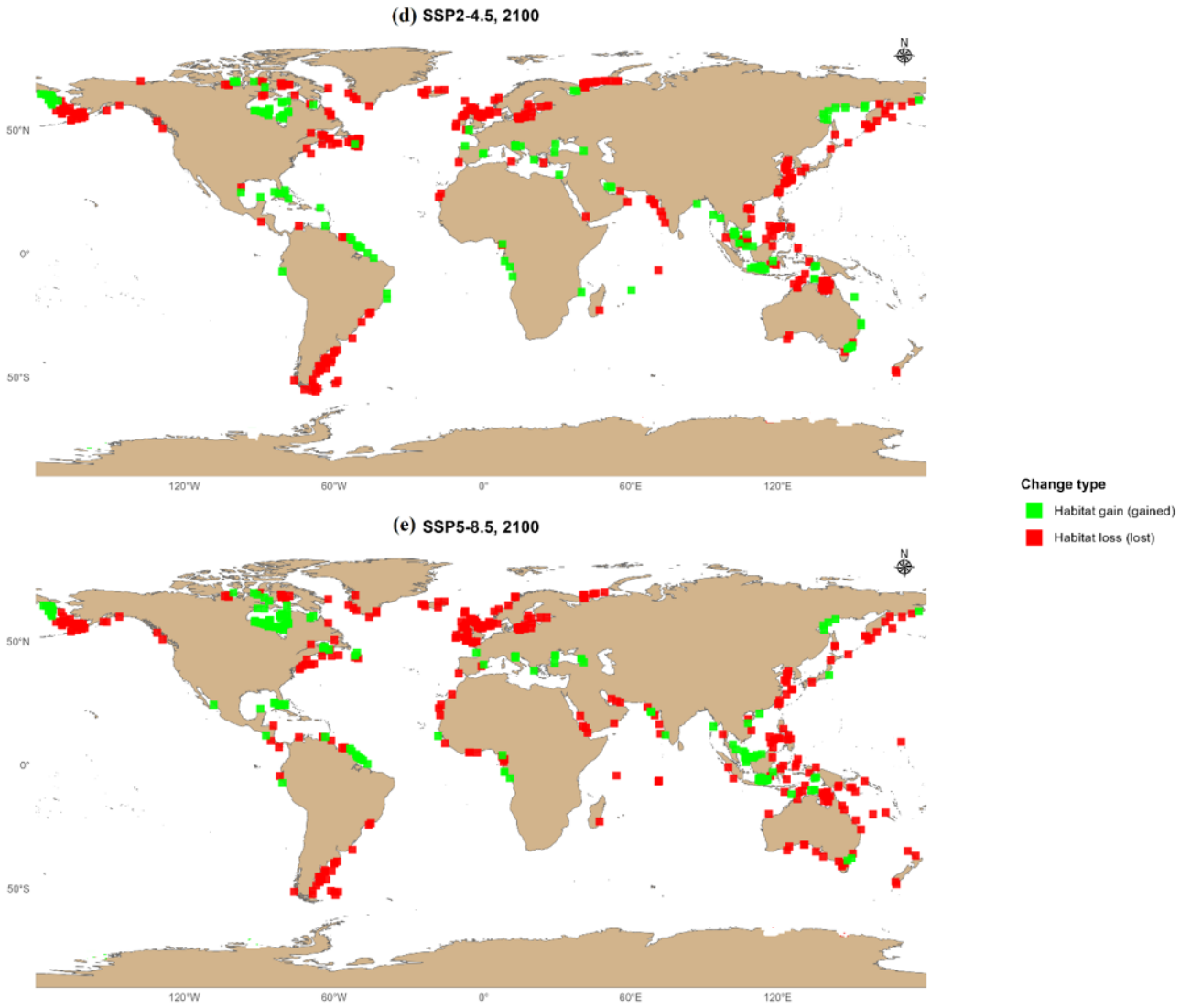


Figure 6. Projected changes in habitat suitability for *Trichiurus lepturus* by 2100 under the SSP2-4.5 and SSP5-8.5 scenarios relative to the current period. Panels (d) and (e) show habitat losses (red) and gains (green) under SSP2-4.5 and SSP5-8.5, respectively. Green indicates areas where suitability is projected to increase, and red indicates areas where it is projected to decrease.

congeneric species *T. japonicus*, where chlorophyll levels influence food availability and subsequently determine habitat distribution patterns (Zhang et al., 2022; Shi et al., 2023). Seasonal patterns further support this threshold mechanism: primary productivity peaks in summer and autumn – promoting foraging activity – while low productivity in spring reduces habitat suitability (Chen et al., 2006; Liu et al., 2019). Independently, a spatial analysis of *T. lepturus* catch distribution in Korean waters found that Chl-a (a proxy for phytoplankton biomass) exhibited significant positive effects on catch volumes – both locally and in neighboring areas – suggesting a diffusion-based distribution mechanism whereby productive regions enhance hairtail abundance in adjacent waters through spillover (Apriliani et al., 2018; Nam et al., 2025). Coastal upwelling systems often sustain these productive areas by transporting nutrient-rich waters into the euphotic zone, increasing phytoplankton biomass and supporting higher trophic levels (Carr et al., 2003; Chavez et al., 2009). Similar nutrient-enrichment processes driven by monsoon-induced rainfall and coastal currents have been documented in the northern South China Sea, where increased primary productivity enhances foraging opportunities for *T. japonicus* (Cloern, 2001; Yin, 2002). Climate-driven intensification and geographic shifts of coastal upwelling (the Bakun

effect) are expected to further expand these nutrient-enriched habitats (Bakun et al., 2015; Wang et al., 2015), potentially increasing foraging opportunities for *T. lepturus* in newly suitable areas. This result echoes findings from other marine fish studies, where primary production or chlorophyll-*a* often serve as key proxies for food supply and habitat quality (Brown et al., 2016; Champion et al., 2021).

Sea bottom temperature was the second most important variable (32.3%). Consistent with our findings, Ren et al. (2025) identified temperature as the most influential driver for *T. lepturus* distribution patterns among the environmental factors examined. This finding aligns with the well-established sensitivity of ectothermic marine fishes to thermal regimes, as temperature directly governs metabolic rates, growth, reproduction, and survival (Pinsky et al., 2019; Sunday et al., 2023). The SBT response curve showed a clear thermal optimum between 16 and 26°C, with distribution boundaries tightly linked to warm temperate and subtropical waters. Complementary threshold responses for *T. lepturus* have been reported in the northern China Seas, where spawning-related otolith growth showed strong responses to nearshore surface temperatures of approximately 14°C, nearshore bottom temperatures of 15°C, and offshore surface temperatures of 18°C (Sun et al., 2020). This pattern is consistent with previous observations for congeneric species, where bottom temperature was identified as the primary constraint on habitat suitability. For instance, studies on *T. japonicus* – a congeneric species distributed in the northern South China Sea – have demonstrated that it is significantly affected by SBT as a demersal fish (Xiong et al., 2023; Zhang et al., 2024).

pH contributed 17.1% to the model, highlighting the species' sensitivity to ocean acidification. The preference for neutral to slightly alkaline conditions (pH 7.0-7.6) suggests that ongoing decreases in surface and bottom pH under climate change (IPCC, 2019) could directly affect physiological processes, although further experimental studies are needed to confirm causal mechanisms. Recent advances in deep learning-based species distribution modeling further support pH as a key driver of marine species distribution. In a study covering 38 marine taxa – ranging from pelagic fishes to marine mammals – pH was identified as one of the most influential environmental variables in predicting species occurrence (Morand et al., 2024). This independent finding, derived from a completely different modeling framework, reinforces our conclusion that pH plays a significant role in shaping the habitat suitability of *T. lepturus*.

Salinity (8.4%) and depth (7.1%) played notable roles, while current velocity (0.6%) contributed negligibly. The preference for high-salinity waters within the range of 31-35 ‰ aligns with the species' predominantly marine distribution, although *T. lepturus* can occasionally enter estuarine environments. This finding is independently corroborated by a spatial analysis of *T. lepturus* catch distribution in the southern coastal waters of South Korea, which identified salinity as an influential positive driver, with fish aggregating in high-salinity water masses ranging from 33.7 to 34.5 PSU (Nam et al., 2025). Concurrently, the species' strong affinity for shallow (0 to −50 m), soft-bottom continental shelf zones reflects its benthopelagic habit and reliance on shelf topography for feeding and reproduction (Martins and Haimovici, 1997; FAO, 2018). A study on the congeneric species *T. japonicus* in the northern South China Sea also identified continental shelf habitats as highly suitable, with optimal depths reported between 40 and 200 m (Xiong et al., 2023; Zhang et al., 2024). Although the preferred depth range differs slightly from our findings for *T. lepturus* (0-50 m), this discrepancy may reflect regional or seasonal variations in habitat availability, or differences in sampling design and modeling resolution. Nevertheless, both studies consistently highlight the fundamental importance of shelf-associated, soft-bottom benthic environments for species of the genus *Trichiurus*. Notably, Nam et al. (2025) also reported a negative spatial spillover effect for salinity, suggesting a substitution mechanism whereby fish concentrate in favorable local habitats, thereby reducing resource density in

neighboring areas – a finding that supports the view that *T. lepturus* distribution is regulated by fine-scale ecological dynamics. Current velocity contributed the least (0.6%), suggesting that while *T. lepturus* tolerates some hydrodynamic variability, its distribution is primarily constrained by trophic conditions, temperature, and pH.

The influence of future climate scenarios on the habitat of *T. lepturus:* The reliability of future projections depends heavily on the accuracy of the environmental data used (Han et al., 2023). High-resolution future environmental data from Bio-ORACLE can capture regional climate patterns and reduce prediction deviations compared with coarser datasets (Tyberghein et al., 2012; Assis et al., 2024), thereby improving model accuracy. In contrast to the earlier Representative Concentration Pathways (RCPs), the Shared Socioeconomic Pathways (SSPs) comprehensively integrate socio-economic factors such as population growth, economic development, and policy responses (Van Vuuren et al., 2014). This broader consideration helps policymakers better understand climate challenges under alternative development paths and formulate more targeted policies. High-resolution environmental data are particularly important for capturing the thermal and productivity gradients that drive the distribution of *T. lepturus*. All projections were based on two Shared Socioeconomic Pathways (SSP2-4.5 and SSP5-8.5), which represent moderate and high greenhouse gas emission scenarios, respectively.

Our mid-century projections show that total habitat area remains almost unchanged under both scenarios (SSP2-4.5 and SSP5-8.5), with a net loss of <0.1% relative to current conditions. However, turnover is relatively considerable, with losses (7,500-18,100 km^2) exceeding gains (4,500-4,700 km^2). More importantly, mean suitability values for high, moderate, and low habitat classes show virtually no shift from current levels (deviations <0.02). This stability in habitat quality, despite ongoing spatial replacement, suggests that at mid-century, climatic pressures have not yet crossed thresholds that would alter the intrinsic value of different suitability classes. Ren et al. (2025) projected a northward shift in the center of gravity and reduced population densities for *T. lepturus* under RCP8.5 by 2050, while Xiong et al. (2023) reported only a minor range extension in the winter of the RCP370-2050 scenario for the congeneric species *T. japonicus* in the Beibu Gulf, along with contractions in other seasons and scenarios. Differences in scenario frameworks (SSP vs. RCP), geographic scales (global vs. regional), and seasonal studies may explain the potential discrepancies in the modeled outputs among the studies examined.

In contrast, our end-of-century projections show that under SSP2-4.5 the total habitat area decreases slightly relative to current conditions, whereas under SSP5-8.5, this decrease is more pronounced. The underlying turnover of these net changes differs considerably between scenarios: under SSP2-4.5, habitat loss is partially offset by gains, while under SSP5-8.5 a very large loss occurs against a negligible gain. However, this reduction in habitat area was not significant compared to current conditions. Regarding habitat quality, under SSP2-4.5 the mean suitability values for all three classes remain stable (deviation <0.02). Under SSP5-8.5, however, the high- and moderate-suitability classes show a decreasing trend, while the low-suitability class increases. These global-scale projections can be compared with regional studies on congeneric species and the same species. Zhang et al. (2024), using an ensemble species distribution model for *T. japonicus* in the northern South China Sea, projected that by the 2090s the area of highly suitable habitats would decrease by approximately 30.54% under SSP1-2.6 and by 53.67% under SSP5-8.5. Ren et al. (2025) projected for *T. lepturus* in the northern China seas under RCP2.6 and RCP8.5 that by the end of the century, population densities would decrease, spatial patterns would be altered, and spatial overlap among species would decrease significantly by 2100.

Classifying habitat suitability into three quality classes reveals distinct temporal dynamics. Under current conditions, mean suitability is highest for the high-suitability class (8.41), followed by moderate (8.34) and low (7.26). By mid-century (2050), both

SSP2-4.5 and SSP5-8.5 show only minor deviations from current values across all three classes (all changes <0.02), indicating relative stability in habitat quality under both scenarios in the near term. By the end of the century (2100), the patterns diverge strongly between scenarios. Under SSP2-4.5, mean suitability values remain close to current levels (high: 8.39, moderate: 8.34, low: 7.29), with all deviations still below 0.03. Under the high-emission SSP5-8.5 scenario by 2100, however, a marked shift occurs: the high-suitability class declines slightly to 8.33, the moderate-suitability class drops sharply from 8.34 to 7.06, and the low-suitability class increases substantially from 7.26 to 8.62. This indicates a deterioration of moderate-suitability areas and a relative expansion of low-suitability values, rather than an upward shift in habitat quality. Because *T. lepturus* is a benthic-pelagic species and depends on bottom temperature and benthic productivity, climate-driven changes may still force redistribution toward deeper waters and higher latitudes, as documented for marine fishes (Pinsky et al., 2013; Sunday et al., 2023; Dahms and Killen, 2023). However, under SSP5-8.5 by 2100, such redistribution does not translate into improved habitat suitability. Finally, these range shifts may still influence benthic-pelagic coupling and trophic dynamics in newly colonized shelf ecosystems (Gaines et al., 2018; Pinsky et al., 2019), even without qualitative habitat gains. Therefore, our findings indicate that *T. lepturus* exhibits remarkable resilience under the moderate emission pathway (SSP2-4.5), where habitat quality remains stable throughout the century, but becomes climate-vulnerable under the high emission pathway (SSP5-8.5), where moderate-suitability habitats collapse, and low-suitability areas expand by 2100.

Although the ensemble model provides robust projections, several areas for improvement remain. The model did not incorporate the impact of human activities (e.g., fishing pressure and pollution) into the simulations; therefore, actual habitat suitability may be lower than predicted in heavily fished areas. Furthermore, this study did not consider several ecological and oceanographic factors – such as seafloor topography, thermocline depth, and ocean currents – that may influence the spatial distribution of *T. lepturus*. Omitting these unobserved variables may bias the estimated effects of the included covariates. Hence, future research should acquire and integrate high-resolution oceanographic data to enable a more comprehensive, ecologically informed understanding of hairtail distribution dynamics. Nevertheless, the strong performance of our ensemble model (mean ROC = 0.964, mean TSS = 0.830) and the consistency of our projections with global and regional studies provide a solid foundation for climate-adaptive fisheries management and marine spatial planning for *T. lepturus*.

Conclusions

Understanding how climate change affects the sustainable management of fishery resources is crucial to ensuring long-term environmental and economic stability. This study developed an ensemble species distribution model to analyze the global habitat suitability of *T. lepturus*, incorporating six benthic environmental predictors (sea bottom temperature, salinity, current velocity, depth, primary production, and pH) to assess spatial distribution patterns under current and future climate scenarios (SSP2-4.5 and SSP5-8.5) for mid-century (2050) and end-century (2100). Our findings indicate that climate-driven changes in marine environments will alter the spatial distribution and habitat quality of *T. lepturus*, shifting habitats from moderate to low suitability under the high-emission scenario by 2100, despite no significant net loss in total suitable area. To address such future environmental challenges, policymakers must prioritize science-based, climate-resilient management frameworks. This includes reducing fishing pressure in areas where moderate-suitability habitats are projected to degrade, establishing marine protected areas in stable high-suitability zones, and adopting ecosystem-based approaches to fisheries governance. The results of this study offer a scientific foundation for the climate-adaptive management and sustainable development of *T. lepturus* resources

worldwide. However, this study has limitations, including the omission of human activities (e.g., fishing pressure, pollution), simplified ecological interactions, and uncertainties in climate projections. Future research should refine these analyses by incorporating more complex ecological processes and exploring the potential mechanisms of species adaptation to climate change.

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References

Addo-Bediako A., Chown S.L., Gaston K.J. (2000). Thermal tolerance, climatic variability and latitude. Proceedings of the Royal Society B: Biological Sciences, 267: 739-745.

Ahmadi A., Imanpour Namin J., Sharifian S., Daliri M. (2023). Habitat suitability projections for the black pomfret (*Parastromateus niger*) under climate change: an ensemble modeling approach. Iranian Journal of Ichthyology, 10: 215-224.

Aiello-Lammens M.E., Boria R.A., Radosavljevic A., Vilela B., Anderson R.P. (2015). spThin: An R package for spatial thinning of species occurrence records for use in ecological niche models. Ecography, 38: 541-545.

Allouche O., Tsoar A., Kadmon R. (2006). Assessing the accuracy of species distribution models: prevalence, kappa and the true skill statistic (TSS). Journal of Applied Ecology, 43: 1223-1232.

Apriliani I.M., Nurrahman Y.A., Dewanti L.P., Herawati H. (2018). Determination of potential fishing ground for hairtail (*Trichiurus* sp.) fishing based on chlorophyll-a distribution and sea surface temperature in Pangandaran waters, West Java, Indonesia. AACL Bioflux, 11: 1047-1054.

Araújo M.B., Anderson R.P., Barbosa A.M., Beale C.M., Dormann C.F., Early R., Rahbek C. (2019). Standards for distribution models in biodiversity assessments. Science Advances, 5: eaat4858.

Araújo M.B., New M. (2007). Ensemble forecasting of species distributions. Trends in Ecology and Evolution, 22: 42-47.

Assis J., Fernandez Bejarano S.J., Salazar V.W., Schepers L., Gouvêa L., Fragkopoulou E., Leclercq F., Vanhoorne B., Tyberghein L., Serrão E.A. (2024). Bio-ORACLE v3.0. Pushing marine data layers to the CMIP6 Earth System Models of climate change research. Global Ecology and Biogeography, 33: e13813.

Bakun A., Black B.A., Bograd S.J., Garcia-Reyes M., Miller A.J., Rykaczewski R.R., Sydeman W.J. (2015). Anticipated effects of climate change on coastal upwelling ecosystems. Current Climate Change Reports, 1: 85-93.

Beaugrand G., Reid P.C., Ibanez F., Lindley J.A., Edwards M. (2002). Reorganization of North Atlantic marine copepod biodiversity and climate. Science, 296: 1692-1694.

Briscoe N.J., Elith J., Salguero-Gómez R., Lahoz-Monfort J.J., Camac J.S., Giljohann K.M., Holden M.H., Hradsky B.A., Kearney M.R., McMahon S.M., Phillips B.L., Regan T.J., Rhodes J.R., Vesk P.A., Wintle B.A., Yen J.D.L., Guillera-Arroita G. (2019). Forecasting species range dynamics with process-explicit models: matching methods to applications. Ecology Letters, 22: 1940-1956.

Brown C.J., O'Connor M.I., Poloczanska E.S., Schoeman D.S., Buckley L.B., Burrows M.T., Duarte C.M., Halpern B.S., Pandolfi J.M., Parmesan C., Richardson A.J. (2016). Ecological and methodological drivers of species' distribution and phenology responses to climate change. Global Change Biology, 22: 1548-1560.

Burrows M.T., Schoeman D.S., Buckley L.B., Moore P., Poloczanska E.S., Brander K.M., Brown C., Bruno J.F., Duarte C.M., Halpern B.S., Holding J., Kappel C.V., Kiessling W., O'Connor M.I., Pandolfi J.M., Parmesan C., Schwing F.B., Sydeman W.J., Richardson A.J. (2011). The pace of shifting climate in marine and terrestrial ecosystems. Science, 334: 652-655.

Carr M.E., Kearns E.J. (2003). Production regimes in four Eastern Boundary Current systems. Deep-Sea Research Part II: Topical Studies in Oceanography, 50: 3199-3221.

Chaikin S., Riva F., Marshall K.E., Lessard J.P., Belmaker J. (2024). Marine fishes experiencing high-velocity range shifts may not be climate change winners. Nature Ecology and Evolution, 8: 936-946.

Chamberlain S.A., Boettiger C. (2017). R, Python, and Ruby clients for GBIF species occurrence data. Available from: https://doi.org/10.7287/peerj.preprints.3304v1. Retrieved 5/31/2017.

Champion C., Brodie S., Coleman M.A. (2021). Climate-driven range shifts are rapid yet variable among recreationally important coastal-pelagic fishes. Frontiers in Marine Science, 8: 622299.

Chavez F.P., Messie M. (2009). A comparison of Eastern Boundary upwelling Ecosystems. Progress in Oceanography, 83: 80-96.

Chen Y.F.L., Chen H.Y. (2006). Seasonal dynamics of primary and new production in the northern South China Sea: The significance of river discharge and nutrient advection. Deep-Sea Research Part I: Oceanographic Research Papers, 53: 971-986.

Cheung W.W., Watson R., Pauly D. (2013). Signature of ocean warming in global fisheries catch. Nature, 497: 365-368.

Chiou W.D., Chen C.Y., Wang C.M., Chen C.T. (2006). Food and feeding habits of ribbonfish *Trichiurus lepturus* in coastal waters of south-western Taiwan. Fisheries Science, 72: 373-381.

Cloern J.E. (2001). Our evolving conceptual model of the coastal eutrophication problem. Marine Ecology Progress Series, 210: 223-253.

Dahms C., Killen S.S. (2023). Temperature change effects on marine fish range shifts: A meta-analysis of ecological and methodological predictors. Global Change Biology, 29: 4459-4479.

Daufresne M., Lengfellner K., Sommer U. (2009). Global warming benefits the small in aquatic ecosystems. Proceedings of the National Academy of Sciences of the United States of America, 106: 12788-12793.

De la Cruz-Torres J., Martínez-Pérez J., Franco-Lopez J., Ramírez-Villalobos A. (2014). Biological and ecological aspects of *Trichiurus lepturus* Linnaeus, 1758 (Perciformes: Trichiuridae) in Boca Del Rio, Veracruz, Mexico. American Journal of Environmental Sciences, 14: 1058-1066.

Doney S.C., Ruckelshaus M., Emmett Duffy J., Barry J.P., Chan F., English C.A., Galindo H.M., Grebmeier J.M., Hollowed A.B., Knowlton N., Polovina J. (2012). Climate change impacts on marine ecosystems. Annual Review of Marine Science, 4: 11-37.

Dulvy N.K., Rogers S.I., Jennings S., Stelzenmuller V., Dye S.R., Skjoldal H.R. (2008). Climate change and deepening of the North Sea fish assemblage: A biotic indicator of warming seas. Journal of Applied Ecology, 45: 1029-1039.

Elith J., Leathwick J.R. (2009). Species distribution models: ecological explanation and prediction across space and time. Annual Review of Ecology, Evolution, and Systematics, 40: 677-697.

FAO (2017). FAO Global Capture Production database updated to 2015 - Summary information. Rome: Food and Agriculture Organization of the United Nations. Available from: http://www.fao.org/3/I9540EN/i9540en.pdf. Retrieved 4/25/2026.

FAO (2018). The State of World Fisheries and Aquaculture 2018 – Meeting the sustainable development goals. Rome: Food and Agriculture Organization of the United Nations. Available from: http://www.fao.org/3/I9540EN/i9540en.pdf. Retrieved 4/25/2026.

Fielding A.H., Bell J.F. (1997). A review of methods for the assessment of prediction errors in conservation presence/absence models. Environmental Conservation, 24: 38-49.

Froese R., Pauly D. (2024). FishBase. Available from: www.fishbase.org. Retrieved 5/31/2024.

Gaines S.D., Costello C., Owashi B., Mangin T., Bone J., Molinos J.G., Burden M., Dennis H., Halpern B.S., Kappel C.V., et al. (2018). Improved fisheries management could offset many negative effects of climate change. Science Advances, 4: eaao1378.

Gattuso J.P., Magnan A., Billé R., Cheung W.W., Howes E.L., Joos F., Allemand D., Bopp L., Cooley S.R., Eakin C.M., Hoegh-Guldberg O. (2015). Contrasting futures for ocean and society from different anthropogenic CO2 emissions scenarios. Science, 349: aac4722.

Ghosh S., Rohit P., Muthurathinam A.M., Rajesh K.M., Koya M., Anulekshmi C., Nakhwa A.D., Surya S., Manas H.M., Roul S.K., Azeez P.A., Kumar R.V. (2024). Fishery and stock dynamics of ribbonfish *Trichiurus lepturus* (Linnaeus, 1758) in the Indian Exclusive Economic Zone. Indian Journal of Fisheries, 71: 8-17.

Guisan A., Thuiller W., Zimmermann N.E. (2017). Habitat suitability and distribution models: with applications in R. Cambridge University Press. Cambridge. 462 p.

Han H.B., Yang C., Jiang B.H., Shang C., Sun Y.Y., Zhao X.Y., Xiang D.L., Zhang H., Shi Y.C. (2023). Construction of chub mackerel (*Scomber japonicus*) fishing ground prediction model in the northwestern Pacific Ocean based on deep learning and marine environmental variables. Marine Pollution Bulletin,

193: 16.

He X., Luo Z., Zhao C., Huang L., Yan Y., Kang B. (2022). Species composition, growth, and trophic traits of hairtail (Trichiuridae), the most productive fish in Chinese marine fishery. Animals, 12: 3078.

Hijmans R.J., Phillips S., Leathwick J., Elith J. (2017). dismo: Species Distribution Modeling. R package version 1.1-4. Available from: https://CRAN.R-project.org/package=dismo. Retrieved 1/9/2017.

IPCC (2019). Managing the risks of extreme events and disasters to advance climate change adaptation. A Special Report of Working Groups I and II of the Intergovernmental Panel on Climate Change. Field C.B., Barros V., Stocker T.F., Dahe Q., Dokken D.J., Ebi K.L., Mastrandrea M.D., Mach K.J., Plattner G.-K., Allen S.K., et al. (Eds.). Cambridge University Press. Cambridge, UK; New York, NY, USA. 582 p.

Lenoir J., Bertrand R., Comte L., Bourgeaud L., Hattab T., Murienne J., Grenouillet G. (2020). Species better track climate warming in the oceans than on land. Nature Ecology and Evolution, 4: 1044.

Levitus S., Antonov J.I., Boyer T.P., Stephens C. (2000). Warming of the world ocean. Science, 287: 2225-2229.

Liu D.Z., Zhao Q.L. (2019). Study on the spatial and temporal distribution of chlorophyll a concentration in Beibu gulf. Journal of Marine Sciences, 37: 95.

Mainali K.P., Warren D.L., Dhileepan K., McConnachie A., Strathie L., Hassan G., Karki D., Shrestha B.B., Parmesan C. (2015). Projecting future expansion of invasive species: comparing and improving methodologies for species distribution modeling. Global Change Biology, 21: 4464-4480.

Mamun M., Kim S., An K.-G. (2018). Distribution pattern prediction of an invasive alien species, largemouth bass, using a maximum entropy model (MaxEnt) in the Korean Peninsula. Journal of Asia-Pacific Biodiversity, 11: 516-524.

Martins A.S., Haimovici M. (1997). Distribution, abundance and biological interactions of the cutlassfish *Trichiurus lepturus* in the southern Brazil subtropical convergence ecosystem. Fisheries Research, 30: 217-227.

Morand G., Joly A., Rouyer T., Lorieul T., Barde J. (2024). Predicting species distributions in the open ocean with convolutional neural networks. Peer Community Journal, 4: e93.

Naimi B., Hamm N.A.S., Groen T.A., Skidmore A.K., Toxopeus A.G. (2014). Where is positional uncertainty a problem for species distribution modelling? Ecography, 37: 191-203.

Nam J., Park C., Son J., Kwon O., Jeong M., Lee M. (2025). Ecological and anthropogenic drivers of hairtail catch distribution: A spatial analysis of the southern coastal waters of South Korea. Animals, 15: 2472.

Nneji I.C., Mambo W.W., Zheng Z., Oladipo S.O., Zhao H., Lu W., Nneji L.M., Lin J., Liu W. (2025). Predicting Habitat Suitability and Range Dynamics of Three Ecologically Important Fish in East Asian Waters Under Projected Climate Change. Biology, 14: 1476.

Ohlberger J. (2013). Climate warming and ectotherm body size – from individual physiology to community ecology. Functional Ecology, 27: 991-1001.

Payne M.R., Kudahl M., Engelhard G.H., Pinnegar J.K. (2021). Climate risk to European fisheries and coastal communities. Proceedings of the National Academy of Sciences of the United States of America, 118: e2018086118.

Pecl G.T., Araújo M.B., Bell J.D., Blanchard J., Bonebrake T.C., Chen I.-C., Clark T.D., Colwell R.K., Danielsen F., Evengård B., Falconi L., Ferrier S., Frusher S., Garcia R.A., Griffis R.B., Hobday A.J., Janion-Scheepers C., Jarzyna M.A., Jennings S., … Williams S.E. (2017). Biodiversity redistribution under climate change: Impacts on ecosystems and human well-being. Science, 355: eaai9214.

Perry A.L., Low P.J., Ellis J.R., Reynolds J.D. (2005). Climate change and distribution shifts in marine fishes. Science, 308: 1912-1915.

Pinsky M.L., Eikeset A.M., McCauley D.J., Sunday J.M. (2019). Greater vulnerability to warming of marine versus terrestrial ectotherms. Nature, 569: 108-111.

Pinsky M.L., Worm B., Fogarty M.J., Sarmiento J.L., Levin S.A. (2013). Marine taxa track local climate velocities. Science, 341: 1239-1242.

Poloczanska E.S., Brown C.J., Sydeman W.J., Kiessling W., Schoeman D.S., Moore P.J., Brander K., Bruno J.F., Buckley L.B., Burrows M.T., Duarte C.M., Halpern B.S., Holding J., Kappel C.V., O'Connor M.I., Pandolfi J.M., Parmesan C., Schwing F., Richardson A.J. (2013). Global imprint of climate change on marine life. Nature Climate Change, 3: 919-925.

Prihatiningsih P., Tirtadanu T., Taufik M., Rosmiati R., Nurdin E., Panggabean A.S., Kembaren D.D., Nurulludin N., Chodrijah U., Mahulette R.T., Nugraha B. (2025). Unveiling the status of *Trichiurus lepturus* (Actinopterygii, Scombriformes, Trichiuridae) stocks in

the southern Java waters, Indonesia: A biological and length-based assessment approach. Acta Ichthyologica et Piscatoria, 55: 31-43.

Provoost P., Bosch S. (2022). robis: R Client for the OBIS API. Available from: https://github.com/iobis/robis. Retrieved 5/31/2026.

Rathore M.K., Sharma L.K. (2023). Efficacy of species distribution models (SDMs) for ecological realms to ascertain biological conservation and practices. Biodiversity and Conservation, 32: 3053-3087.

Ren J., Liu Q., Ma Y., Ji Y., Xu B., Xue Y., Zhang C. (2025). Spatio temporal distribution of four trophically dependent fishery species in the northern China Seas under climate change. Biology, 14: 168.

Robinson L.M., Elith J., Hobday A.J., Pearson R.G., Kendall B.E., Possingham H.P., Richardson A.J. (2011). Pushing the limits in marine species distribution modelling: Lessons from the land present challenges and opportunities. Global Ecology and Biogeography, 20: 789-802.

Roessig J.M., Woodley C.M., Cech J.J., Hansen L.J. (2004). Effects of global climate change on marine and estuarine fishes and fisheries. Reviews in Fish Biology and Fisheries, 14: 251-275.

Rohit P., Rajesh K.M., Sampathkumar G., Karamathulla P. (2015). Food and feeding of the ribbonfish *Trichiurus lepturus* Linnaeus off Karnataka, south-west coast of India. Indian Journal of Fisheries, 62: 58-63.

Romera R., Gaertner M.A., Sanchez E., Dominguez M., Gonzalez-Aleman J.J., Miglietta M.M. (2017). Climate change projections of medicanes with a large multi-model ensemble of regional climate models. Global and Planetary Change, 151: 134-143.

Shi Y.C., Kang B., Fan W., Xu L.L., Zhang S.M., Cui X.S., et al. (2023). Spatio-temporal variations in the potential habitat distribution of Pacific sardine (*Sardinops sagax*) in the northwest Pacific Ocean. Fishes, 8: 86.

Sun P., Chen Q., Fu C., Zhu W., Li J., Zhang C., Yu H., Sun R., Xu Y., Tian Y. (2020). Daily growth of young of the year largehead hairtail (*Trichiurus japonicus*) in relation to environmental variables in the East China Sea. Journal of Marine Systems, 201: 103243.

Sunday J.M., Bates A.E., Dulvy N.K. (2023). Thermal tolerance and the global redistribution of animals. Nature Climate Change, 13: 103-110.

Thuiller W., Georges D., Engler R., Breiner F. (2016). biomod2: Ensemble platform for species distribution modeling. R package version 3.3-7. Available from: https://CRAN.R-project.org/package=biomod2. Retrieved 12/31/2016.

Thuiller W., Georges D., Gueguen M., Engler R., Breiner F., Lafourcade B., Patin R., Blancheteau H. (2025). biomod2: Ensemble Platform for Species Distribution Modeling. R package version 4.2-6-2. Available from: https://CRAN.R-project.org/package=biomod2. Retrieved 5/31/2025.

Thuiller W., Guéguen M., Renaud J., Karger D.N., Zimmermann N.E. (2019). Uncertainty in ensembles of global biodiversity scenarios. Nature Communications, 10: 1446.

Tyberghein L., Verbruggen H., Pauly K., Troupin C., Mineur F., De Clerck O. (2012). Bio-ORACLE: a global environmental dataset for marine species distribution modelling. Global Ecology and Biogeography, 21: 272-281.

Van Vuuren D.P., Kriegler E., O'Neill B.C., Ebi K.L., Riahi K., Carter T.R., Edmonds J., Hallegatte S., Kram T., Mathur R. (2014). A new scenario framework for climate change research: Scenario matrix architecture. Climatic Change, 122: 373-386.

Wang D., Gouhier T.C., Menge B.A., Ganguly A.R. (2015). Intensification and spatial homogenization of coastal upwelling under climate change. Nature, 518: 390-394.

Xiong P.L., Xu Y.W., Sun M.S., Zhou X.X., Jiang P.W., Chen Z.Z., Fan J.T. (2023). The current and future seasonal geographic distribution of largehead hairtail *Trichiurus japonicus* in the Beibu Gulf, South China Sea. Frontiers in Marine Science, 9: 14.

Yin K. (2002). Monsoonal influence on seasonal variations in nutrients and phytoplankton biomass in coastal waters of Hong Kong in the vicinity of the Pearl River estuary. Marine Ecology Progress Series, 245: 111-122.

Zhang J., Li J., Zhang K., Xu Y., Xu S., Chen Z. (2024). Spatial and temporal distribution of habitat pattern of *Trichiurus japonicus* in the northern South China Sea under future climate scenarios. Fishes, 9: 488.

Zhang M., Wang X.H., Cai Y.C., Du F.Y., Sun D.R., Wang Y.Z., et al. (2022). Spatial aggregation and dispersion characteristics of *Trichiurus haumela* in the Beibu Gulf, northern South China Sea. Journal of Fishery Sciences of China, 29: 1647-1658.