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EDITED BY  
Fan Zhang,  
Shanghai Ocean University, China

REVIEWED BY  
Haiqing Yu,  
Shandong University, China  
Shengyong Xu,  
Zhejiang Ocean University, China

\*CORRESPONDENCE  
Zuozhi Chen  
chenzuozhi@scsfri.ac.cn  
Jiangtao Fan  
jft@scsfri.ac.cn

SPECIALTY SECTION  
This article was submitted to  
Marine Ecosystem Ecology,  
a section of the journal  
Frontiers in Marine Science

RECEIVED 25 October 2022  
ACCEPTED 29 November 2022  
PUBLISHED 12 January 2023

CITATION  
Xiong P, Xu Y, Sun M, Zhou X, Jiang P,  
Chen Z and Fan J (2023) The current  
and future seasonal geographic  
distribution of largehead hairtail  
*Trichiurus japonicus* in the Beibu Gulf,  
South China Sea.  
*Front. Mar. Sci.* 9:1079590.  
doi: 10.3389/fmars.2022.1079590

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# The current and future seasonal geographic distribution of largehead hairtail *Trichiurus japonicus* in the Beibu Gulf, South China Sea

Pengli Xiong<sup>1,2</sup>, Youwei Xu<sup>1,2</sup>, Mingshuai Sun<sup>1,2</sup>,  
Xingxing Zhou<sup>1,2</sup>, Peiwen Jiang<sup>1,2</sup>, Zuozhi Chen<sup>1,2\*</sup>  
and Jiangtao Fan<sup>1,2\*</sup>

<sup>1</sup>South China Sea Fisheries Research Institute, Chinese Academy of Fishery Sciences, Guangzhou, China, <sup>2</sup>Key Laboratory of Open-Sea Fishery Development, Ministry of Agriculture and Rural Affairs, Guangzhou, China

Largehead hairtail *Trichiurus japonicus* is a major commercial fish species in the Beibu Gulf of the northwestern South China Sea. Despite much effort to protect the fishery resource, the current stock of *T. japonicus* is overexploited. As the impacts of climate change unfold globally, seasonal changes in the distribution of largehead hairtail in the Beibu Gulf have not yet been clarified. Maximum entropy model based on mixed layer depth and salinity were projected onto seasonal habitat changes of *T. japonicus* in the Beibu Gulf under a current scenario and three different Representative Concentration Pathways (126, 370, 585) to evaluate geographic distribution changes under the different climate-change scenarios. The current geographic distribution results showed variation with seasonality, as the wintering population shifts toward the northeast. Under each of three SSP scenarios, there is higher risk to habitat suitability in the 2090s as compared with that in the 2050s. The disadvantage to *T. japonicus* distribution is greatest in winter under each of the three climate change scenarios, both in the short- and long-term. Potential suitable habitat distributions have a minor range extension in Representative Concentration Pathway 370–2050 winter, but in the rest of the scenes and years they contract to south of the Beibu Gulf. The overall results indicate that seasonal differences in suitable habitat should be considered to ensure effective planning of future management strategies for *T. japonicus*.

## KEYWORDS

habitat suitability, maximum entropy model, potential distribution, seasonal change, climate-change biology

# 1 Introduction

Climate change is affecting the distributions of marine organisms on regional and global scales. It is expected that climate-driven changes in various environmental factors will alter the composition and distribution of marine biota to various extents (Davis et al., 2020; Hu et al., 2022). The Intergovernmental Panel on Climate Change predicts that by the end of the 21st century the average global temperature would increase by 1°C to 4°C (IPCC, 2007). Sea surface temperatures in China's coastal waters rose at a rate of 0.27°C per decade from 1980 to 2020 (MNR, 2021). Changes in the distributions of marine species as a consequence of global warming are now documented in Chinese waters. For instance, a tropical threadfin bream, *Nemipterus mesoprion*, was newly found in the Beibu Gulf (Cai et al., 2020), and the flatfish *Tosarhombus octoculatus*, is previously recorded in the waters off Kochi Prefecture, Japan, has moved southward into the South China Sea (SCS) (Jiang et al., 2015). And some studies related to the impact of climatic change on species' distribution reach similar conclusions. By the 2050s, some suitable fish habitats, such as for Japanese scad *Decapterus maruadsi* and Japanese jack mackerel *Trachurus japonicus*, are expected to shift northward under anticipated climate-change conditions (Hu et al., 2022). The warming ocean will drive a substantial shift in Japanese anchovy habitat in the China seas (Liu et al., 2020). Such changes are expected to lead to decreases in species richness in southern areas of China's seas and increases in the northern areas. Thus, with climate change already affecting all oceans, it is necessary to consider how fish distributions might change in Chinese waters to promote adaptive conservation and management strategies (Zhang et al., 2020b).

The largehead hairtail *Trichiurus japonicus* is an economically important fishery species with a wide distribution along Chinese coast (Chen et al., 2019). The Chinese domestic annual marine catch of hairtails (*Trichiurus* spp.) in 2020 was 903,345 tons, which accounted for ~14% of the total fish production in China, and the species ranked top in fish catches of both the northern SCS and nationwide (MARA, 2021). The importance of the hairtail fishery has resulted in considerable conservation measures. For example, to protect fish spawning stocks and juveniles, the SCS fishery was closed for 2 months yearly (in June and July) from 1999 to 2008, and the closure has been prolonged to 3.5 months yearly (May to August) since 2017 (Zhang et al., 2022a). Despite these efforts, the current stock of *T. japonicus* in the Beibu Gulf is overexploited, and its length frequency now tends to simplification and miniaturization (Shi et al., 2020; Zhang et al., 2022b). Fully understanding the habitat environments of *T. japonicus* in the Beibu Gulf and its likely responses to climate-induced environmental changes is critical for sustainable exploitation and management of the fishery.

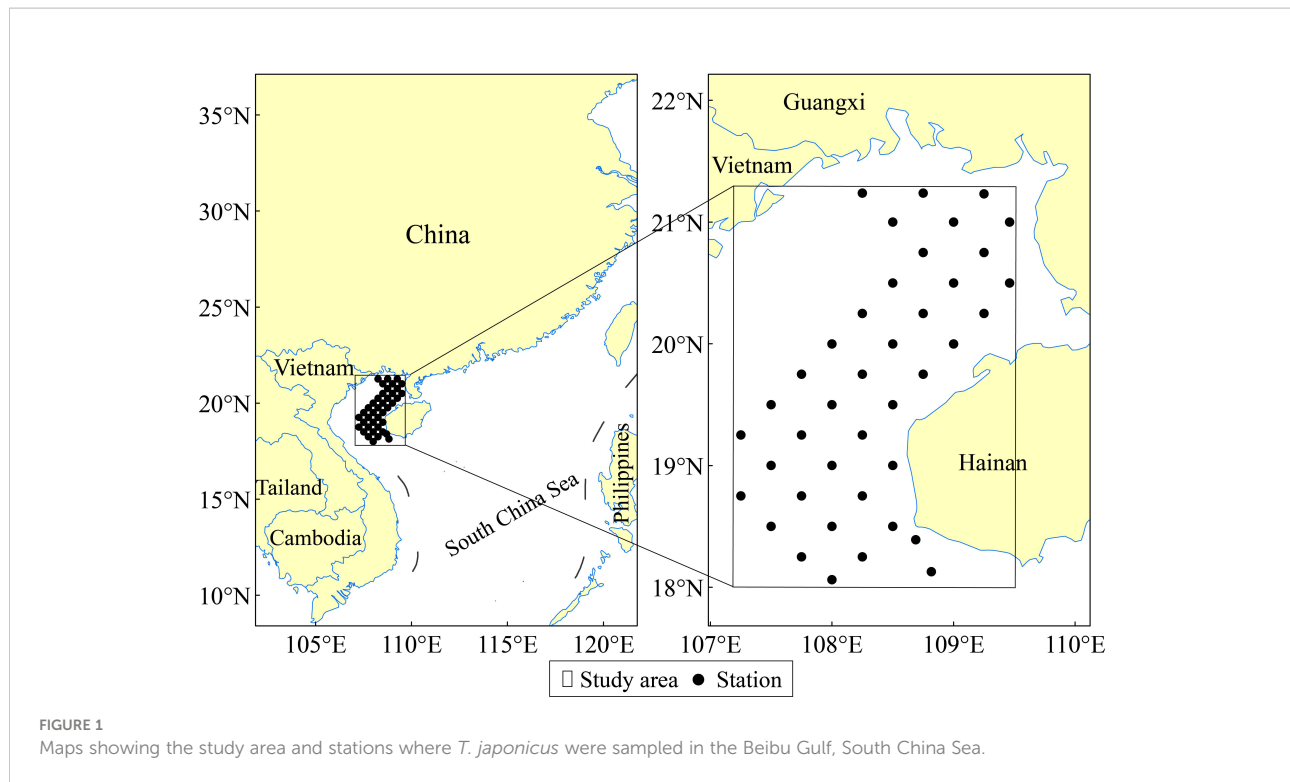
The Maximum Entropy model (MaxEnt) is the most important statistical method for ecological modelling that is widely used to predict the geographic distribution of a species based on areas of suitable habitat (Harte and Newman, 2014). Based on machine learning and maximum entropy theory, MaxEnt model use occurrence records and associated environmental data to infer the ecological needs of a species and then predict its potential distribution in the area studied (Phillips et al., 2006; Phillips and Dudík, 2008; Zhao et al., 2021). Compared with other models, MaxEnt shows accurate prediction capabilities in simulations and evaluations with presence-only data (Mamun et al., 2018), and is relatively robust even with small sample sizes (Zhao et al., 2022).

This study used a MaxEnt model that had been optimized by the 'kuenm' package to forecast the potential geographic distribution of *T. japonicus* in the Beibu Gulf under the current scenario and three future climate scenarios (SSP126, SSP370 and SSP585), in the 2050s (short-term) and 2090s (long-term). 2050s was defined as short-term change and 2090s was defined as long-term change in the present study. The aim was to project the potential suitable habitat of *T. japonicus* in the Beibu Gulf under current climatic conditions in different seasons, and to explore the important climatic factors limiting this species' distribution. On the basis of the changes of mixed layer depth and salinity, we predict the potential suitable habitat for *T. japonicus* according to future global climate-change scenarios, and we discuss the changes in the habitat suitability distributions during three periods (current, 2050s, and 2090s). The present results may provide implications for investigations of variations in fishery resources in the context of climate change. And the study could provide important information for planning future preventive measures of *T. japonicus* fishery to cope with the impact of global warming.

## 2 Materials and methods

### 2.1 Fishery data

Catch data were collected through four independent surveys from 2014–2015 and used to identify fishing locations for *T. japonicus* in the Beibu Gulf, and the occurrence records were then used as presence points in MaxEnt models. The surveys were conducted between 18°00'–21°15' N and 107°15'–109°30' E (Figure 1). The fishery data were provided by the South China Sea Fisheries Research Institute, Chinese Academy of Fisheries Science and were split into four quarters: summer (July–August), autumn (October–November), winter (January–February), and spring (April–May). The survey vessel, with weight 242 tons and length 36.8 m, was equipped with a bottom trawl; the main dimensions of the net were 80.4 × 60.54 m, total length 60.58 m, and net cage mesh size 40 mm. Fishing locations with a 0.25°



spatial resolution were divided into four grids of 0.05°, because a larger dataset for presence data allows for a greater range of features in MaxEnt. We removed presence points that were outside the study area and those in fishing locations without *T. japonicus*.

## 2.2 Collection and screening of environmental data

Environmental variables employed in prediction models for marine fishes include chlorophyll *a*, mixed layer depth, salinity, water temperature and depth (Montiel et al., 2019; Zhang et al., 2020a). Distance from land and sea surface temperature are known to influence marine fish in different ways, among which sea temperature is usually the dominant driver (Ma et al., 2019; Tian, 2020). The feeding activity of *Trichiurus* spp. in the Beibu Gulf was distributed from the middle part of the upper water layer to the bottom (Yan et al., 2012). Adults and juveniles of *T. japonicus* have opposing, complementary vertical diurnal feeding migration: large adults usually feed near the surface during the daytime and migrate to the bottom at night, while juveniles and small adults form schools near the bottom during the daytime and then loose feeding aggregations near the surface at night (Fishbase). In addition, the temperature difference between the surface and bottom water was identified as an important environmental factor in the reproductive process and early growth of *T. japonicus* (Yan et al., 2012). Therefore,

we also selected the temperature in the 10-m and 20-m water layers, the bottom temperature, and the temperature difference between the surface and bottom water as model predictors. These satellite-derived oceanographic variables were obtained from official platforms (Table 1).

To keep the same resolution and achieve better accuracy, all environmental data were resampled using bilinear interpolation to 0.5° resolution. It is well documented that high collinearity of predictor variables can negatively affect a model's prediction accuracy and the estimate of a variable's effect (Xiao et al., 2019). Multicollinearity of variables were assessed with Pearson's correlation analysis to confirm independence of variables in the study. Combined the results of the contribution rate of pre-experimental and Pearson's results, compare with any two highly correlated environmental variables ( $r > 0.85$ ), the variable that had a more vital contribution to the model was retained (Appendix A). variables were retained for prediction of suitable habitat of *T. japonicus* in four seasons: spring (S, DFL, CHL, MLD, SSH, TD, Temp\_20m), summer (S, DFL, CHL, SSH, MLD, SST, BT, Temp\_10m), autumn (S, DFL, MLD, TD), and winter (S, DFL, CHL, MLD, TD, Temp\_20m).

## 2.3 Species distribution modeling

In this study, MaxEnt 3.4.4 was used to predict *T. japonicus* geographic distribution (Phillips et al., 2017). The feature class (FC) and regularization multiplier (RM) greatly influence the

TABLE 1 Candidate factors for construction of the MaxEnt model for prediction of *Trichiurus japonicus* geographic distribution.

Variable	Description	Source	Product	Unit	Spatial resolution
S	Seawater salinity	Copernicus Marine Service	Global Ocean Physics Reanalysis	‰	0.083°
DFL	Distance from land	Global Fishing Watch	the Pacific Islands Ocean Observing System	m	1 km
CHL	Chlorophyll <i>a</i>	Coastwatch	Aqua MODIS	mg m <sup>-3</sup>	4 km
SSH	Sea surface height	Copernicus Marine Service	Global Ocean Physics Reanalysis	m	0.083°
MLD	Mixed layer depth	Copernicus Marine Service	Global Ocean Physics Reanalysis	m	0.083°
SST	Sea surface temperature	Copernicus Marine Service	Global Ocean Physics Reanalysis	°C	0.083°
BT	Bottom temperature	Copernicus Marine Service	Global Ocean Physics Reanalysis	°C	0.083°
TD	Temperature difference (SST–BT)	Copernicus Marine Service	Global Ocean Physics Reanalysis	°C	0.083°
Temp_10m	Temperature of 10-m water layer	Copernicus Marine Service	Global Ocean Physics Reanalysis	°C	0.083°
Temp_20m	Temperature of 20-m water layer	Copernicus Marine Service	Global Ocean Physics Reanalysis	°C	0.083°

accuracy of the MaxEnt model (Phillips and Dudík, 2008). For both parameters, default settings based on MaxEnt outputs are sometimes unreliable, making the results difficult to interpret (Zhu and Qiao, 2016; Sill and Dawson, 2021). To arrive at an appropriate model, the FC and RM settings were adjusted using the kuenm R package (Cobos et al., 2019). For each seasonal model, we created 1,160 candidate models by combining 40 values of RM (0.1–4.0, at intervals of 0.1) and all 29 possible combinations of the five FCs (linear = l, quadratic = q, product = p, threshold = t, and hinge = h).

The selection of the final model was based on three main criteria: the partial ROC, omission rate, and delta Akaike Information Criterion (delta AICc). Evaluation of the models in terms of statistical significance rely on the partial ROC ( $p < 0.05$ ) (Cobos et al., 2019). For each model in this study, the omission rate was >10%, suggesting overfitting of the model (Angeles-Gonzalez et al., 2021). The values of AICc and Delta\_AICc were used to search for the most parsimonious model with fewer fit parameters (Angeles-Gonzalez et al., 2021; Rodriguez-Burgos et al., 2022). Model with the lowest AICc value (i.e.  $\Delta AICc = 0$ ) is considered the best model out of the current suite of models (Muscarella et al., 2014).

To reduce the uncertainty of a MaxEnt model, 75% of the occurrence data are selected for training, and the remaining 25% are selected for testing. We selected the bootstrap method, with the average of 10 replicates used to determine the probable distribution of *T. japonicus*. Maximization of the sum of specificity and sensitivity was used to create habitat suitability maps using the binary choice of suitable or unsuitable (Lin et al., 2022). In MaxEnt models, the receiver operating characteristic (ROC) curve and the area under the ROC curve (AUC) are used to evaluate the precision of the model. Values of AUC range from 0 to 1, wherein 1 equals optimal performance and 0.5 denotes low predictive performance.

The value of the map of the MaxEnt model output was used to define habitat appropriateness. *T. japonicus* habitat

appropriateness was categorized as follows: Unsuitable = a value of 0–0.25, indicating that the environment is not suitable for *T. japonicus* in theory; Marginally suitable = a value of 0.25–0.50, indicating that habitat elements are insufficient to allow persistent *T. japonicus* presence; Moderately suitable = a value of 0.50–0.70, indicating that the habitat characteristics support *T. japonicus* occurrence on a broad scale; or Highly suitable = a value of 0.70–1.0, indicating that the habitat characteristics enable *T. japonicus* presence at an ideal level.

## 2.4 Future projection of suitable habitat distribution

For future scenarios, three SSP scenarios from CMIP6 were selected for projecting changes in the potential distribution of *T. japonicus* in the Beibu Gulf under predicted future climate change. These scenarios are described as follows: (1) the SSP126 scenario is the low-end of the future scenario range, with radiative forcing stabilizing at 2.6 W/m<sup>2</sup> in 2100; (2) the SSP370 scenario is a moderately stable scenario in which radiative forcing stabilizes at 7.0 W/m<sup>2</sup> by 2100; and (3) the SSP585 scenario is considered a high radiative forcing scenario, whereby radiative forcing stabilizes at 8.5 W/m<sup>2</sup> in 2100. The environmental variables in CMIP6 were extracted from the BCC-CSM2-MR climate model (Beijing Climate Center). To reduce bias yielded in the global climate model (GCM) projections, the delta method, a widely used bias-correction technique, was applied. Because we could not obtain all the future environmental factors selected in this study, the future modeling was carried out with only the MLD and salinity changes. The parameters of the future models remain the same as for the present models. The distribution models were projected onto climate conditions for comparison of potential suitable habitats under the present climate and three climatic scenarios in the future.

## 2.5 Changes in suitable habitat distribution and core distributional shifts

To examine the change trend in suitable habitat for *T. japonicus* in the Beibu Gulf, habitat loss or gain was calculated by combining the future binary maps and the current binary map using the Python-based ArcGIS toolkit SDM toolbox (Brown, 2014; Cong et al., 2020). A shifting map of distribution under each climate-change scenario was generated with the habitat range expansion, stable habitat, and habitat range contraction, respectively. Furthermore, for the sake of further exploring the dynamic migration paths, the centroids of future and current suitable areas were calculated and compared using the centroid changes tool in the SDM toolbox (Brown, 2014).

## 3 Results

### 3.1 Model parameter optimization

For each season, we selected the best-performing MaxEnt model based on the evaluation metrics. The best combination of parameters of RM and FC in the four seasons-spring, summer, autumn, winter-were 1.5\*1, 2\*t, 0.1\*q, and 1.4\*pt, respectively (Table 2).

### 3.2 Current geographic distribution

MaxEnt performed well in generating the potential distribution of *T. japonicus*, with a mean AUC of 0.767 across the four seasons; logic thresholds of 0.463, 0.558, 0.430, and 0.437 were achieved for spring, summer, autumn, and winter, respectively. The current habitat suitability map for *T. japonicus* in the Beibu Gulf is shown in Figure 2. The results reveal significant seasonal variation in habitat selection by *T. japonicus*, manifested as relatively high suitable habitat area in spring and winter, and low suitable habitat area in summer and autumn.

### 3.3 Jackknife test and response curves of the environmental variables

The jackknife test illustrated the contribution percentage of environmental variables of the predictive geographic distribution model (Figure 3). The importance of each variable and its relative contribution to the MaxEnt models differed between seasons. The results of the jackknife test in the models of the current scenario indicate the temperature difference between surface and bottom water contributed most in the spring model; the bottom temperature contributed most in the summer and autumn models; and mixed layer depth contributed most in the winter model.

The MaxEnt model provided a response curve to show the relationship between the presence probability of *T. japonicus* and the environmental variables (Figure 4). Generally, when the presence probability is >0.50, the corresponding environmental factor is suitable for the species' growth (Zhao et al., 2021). The probability of occurrence increased with the increase in TD in spring, and the optimum range was above 5.8 (with a probability occurrence value of >0.50). In relation to bottom water temperature, the largest probability of occurrence in summer was between 16.2 m and 20 m. In autumn, the BT was negatively correlated with habitat suitability, such that suitability was <50% when BT exceeded 23.8°C. The highest probability of *T. japonicus* occurrence was in areas experiencing a winter MLD of 28–35 m, and the optimum range was above 25.1 m. As the result in Table 3, Contribution (%) of S and MLD to the building of the Maxent models in winter greater than in the other seasons.

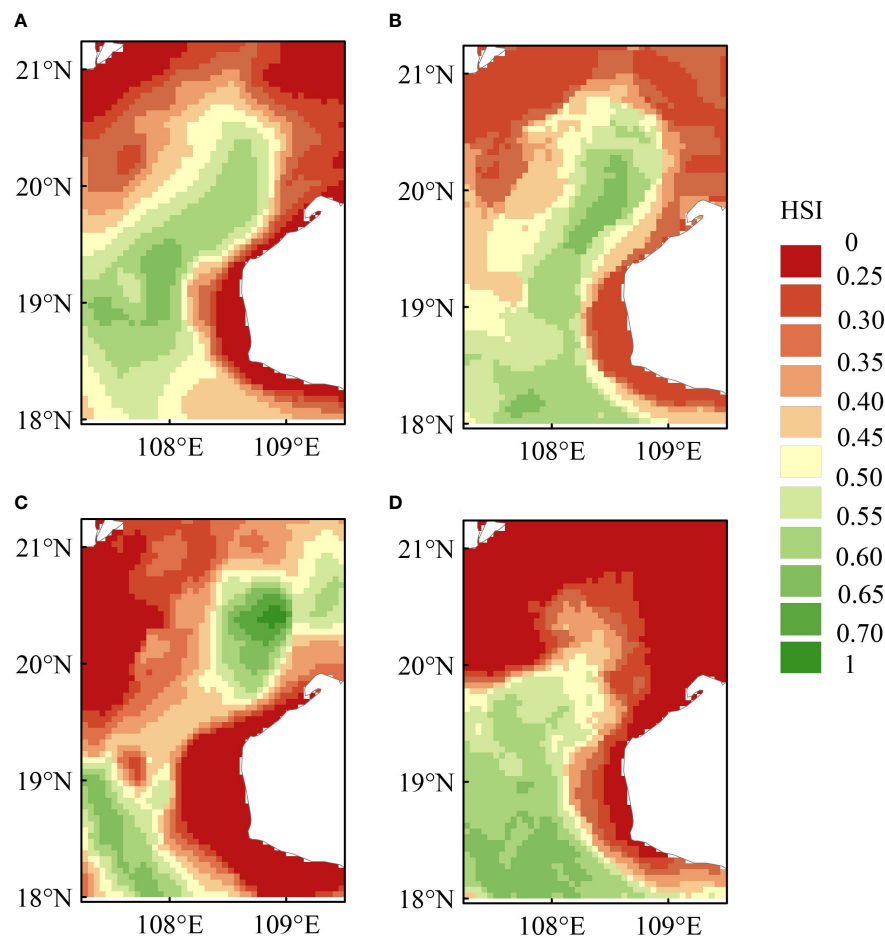
### 3.4 Changes in future potential suitable habitat

Based on MaxEnt modeling, *T. japonicus* in the Beibu Gulf shows both range expansion and contraction under the future climate scenarios; in Figures 5-7, blue and red represent estimated range reduction and expansion, respectively.

TABLE 2 MaxEnt model performance under default and optimized settings.

Season	Scenario	RM	FC	Partial ROC	OmissionRate 10%	AICc	Delta AICc
Spring	default	1.0	lqhpt	0	0.50	518.63	27.51
	optimization	1.5	l	0	0	496.68	0
summer	default	1.0	lqhpt	0	0	457.92	49.74
	optimization	2.0	t	0	0	409.93	0
Autumn	default	1.0	lqhpt	0	0.42	911.19	466.43
	optimization	0.1	q	0	0	447.98	0
Winter	default	1.0	lqhpt	0	0.33	506.01	116.70
	optimization	1.4	pt	0	0	390.38	0

AICc, Akaike information criterion corrected for small sample sizes; FC, feature class; RM, regularization multiplier; ROC, receiver operating characteristic curve.

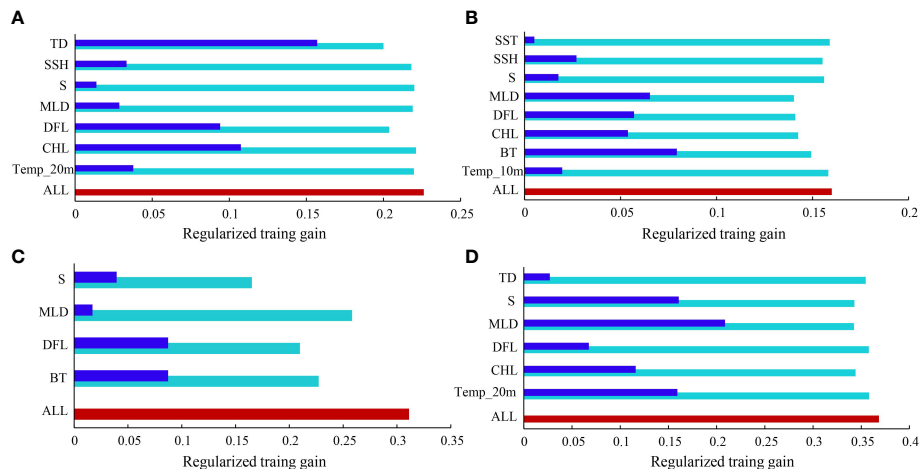


**FIGURE 2**  
The probability of occurrence of *Trichiurus japonicus* in the Beibu Gulf, South China Sea, in different seasons: (A) spring; (B) summer; (C) autumn; (D) winter.

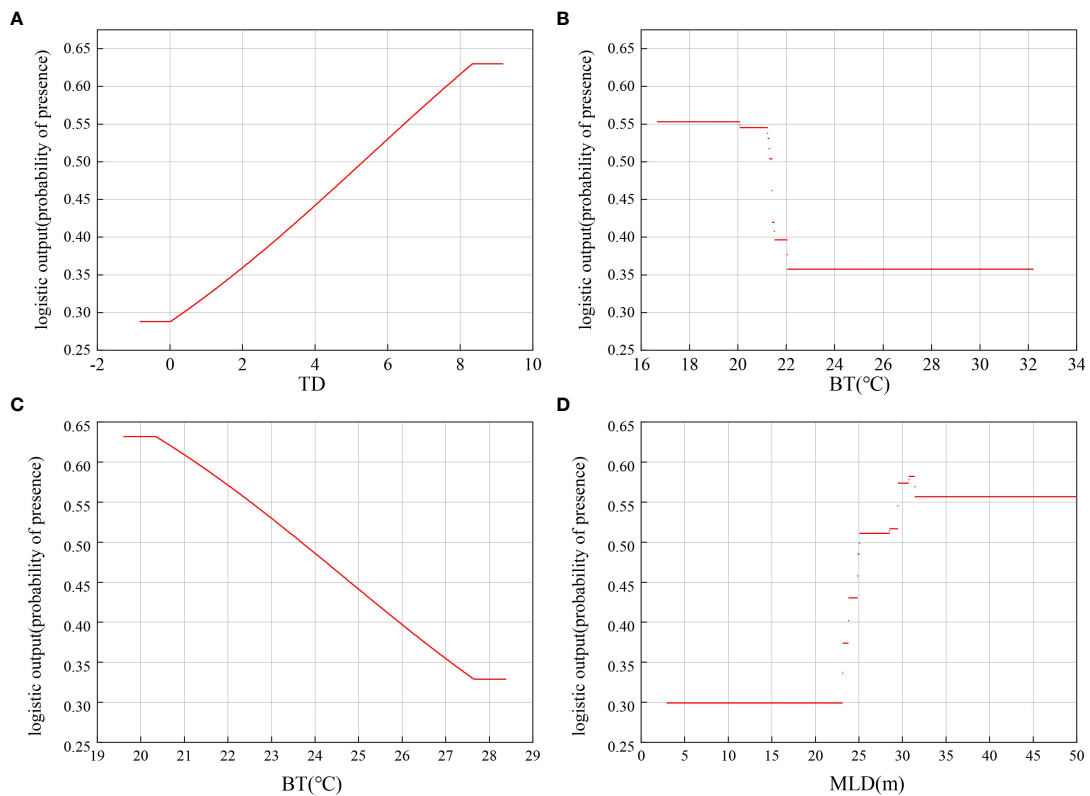
Under RCP126, the area of total potential distribution increased in all seasons except in winter, with the range-expansion predictions exceeding the range-contraction predictions (Figure 5). The short-term (2050s) scene shows changes of future potential suitable habitat in all seasons, wherein the potentially suitable habitats in spring show slight expansion in the margins of the northern parts of the current suitable habitat area. Range-expansion areas in summer could be divided as follows: a general trend of northward expansion of suitable habitat in the area near Guangxi, with suitable habitat mostly around 19°N, but expanding to the northwest. In autumn, northwestern areas of Hainan are characterized by a loss of suitable habitat areas, while gains in suitable area are observed in central parts of the study area. Areas that recognized as potentially suitable habitats in winter are located in southwestern parts of the study area, and the predicted

decrease in suitable areas were located mainly in the northern parts of the current suitable areas. Compared with the findings in the 2050s, the proportion of range-expansion area decreases and the range-contraction area increases in the 2090s.

Under RCP370, especially in the 2090s, the projected risk increases for the distribution range of *T. japonicus* in the Beibu Gulf (Figure 6). In the 2050s, the overall suitable distribution area increases across seasons except for in autumn. However, the suitable habitat areas reflecting total range expansion are smaller in spring and winter, comprising 3.005% range-expansion area and 6.454% range-contraction area when compared with the total study area. In the 2090s, the potential distribution area based on all suitable habitat areas decreases in all seasons except winter. Moreover, among seasons, the suitable habitat area suffers the largest and most dramatic decline in summer, and the new expansion areas that were seen in the 2050s disappear.



**FIGURE 3** Jackknife test of environmental variable importance for training data in the current scenario model of *Trichiurus japonicus* distribution in the Beibu Gulf in different seasons: (A) spring; (B) summer; (C) autumn; (D) winter. Colors of the bars represent the contribution when the model is executed only with the variable, without the variable, or with all variables.



**FIGURE 4** Relationship between the top environmental predictors and the probability of presence of *Trichiurus japonicus* in the Beibu Gulf under MaxEnt modeling of the current scenario: (A) spring temperature difference between surface and bottom water (TD); (B) summer bottom water temperature (BT); (C) autumn BT; (D) winter mixed layer depth (MLD).

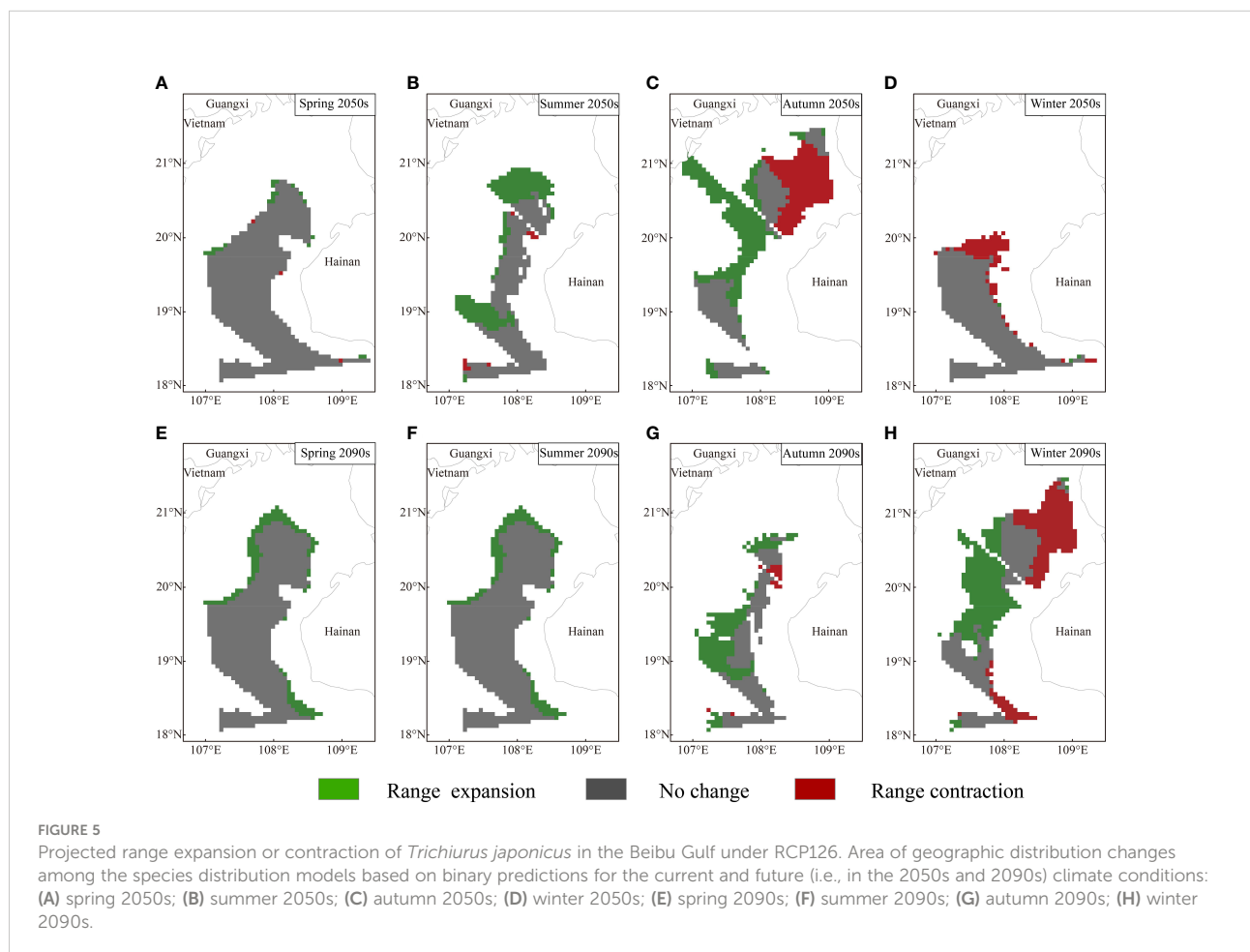
TABLE 3 Estimates of relative contributions of the S and MLD to the Maxent model for each season, the best run of *T. japonicus*.

Season	Percent contribution	
	S	MLD
Spring	4.5	4.7
Summer	2.2	17.6
Autumn	27.4	10.1
Winter	26.0	36.3

The expansion area of suitable distribution in the 2090s accounts for only 1.682% of the total study area.

Under RCP585, the trend in suitable habitat for *T. japonicus* varied among seasons. The area of suitable habitat shows an increasing trend but is smaller than the area of decrease in winter in the 2050s (Figure 7); the area of suitable habitat shows the opposite trend in other seasons, although with less variation in spring. The areas of suitable habitat near Vietnam increase substantially in summer, with the model-predicted area of

suitable habitat expansion at 8,900.18 km<sup>2</sup>. Trends in potentially suitable habitat in autumn and winter were similar under the three scenarios. Compared with that in the 2050s, the suitability of the future potential suitable habitat of *T. japonicus* in the 2090s decreases in autumn and winter, but increases in spring and summer. Also in the 2090s, the range-expansion area increases and the range-contraction area decreases in summer and both areas increase in spring, but the area of range expansion is larger.





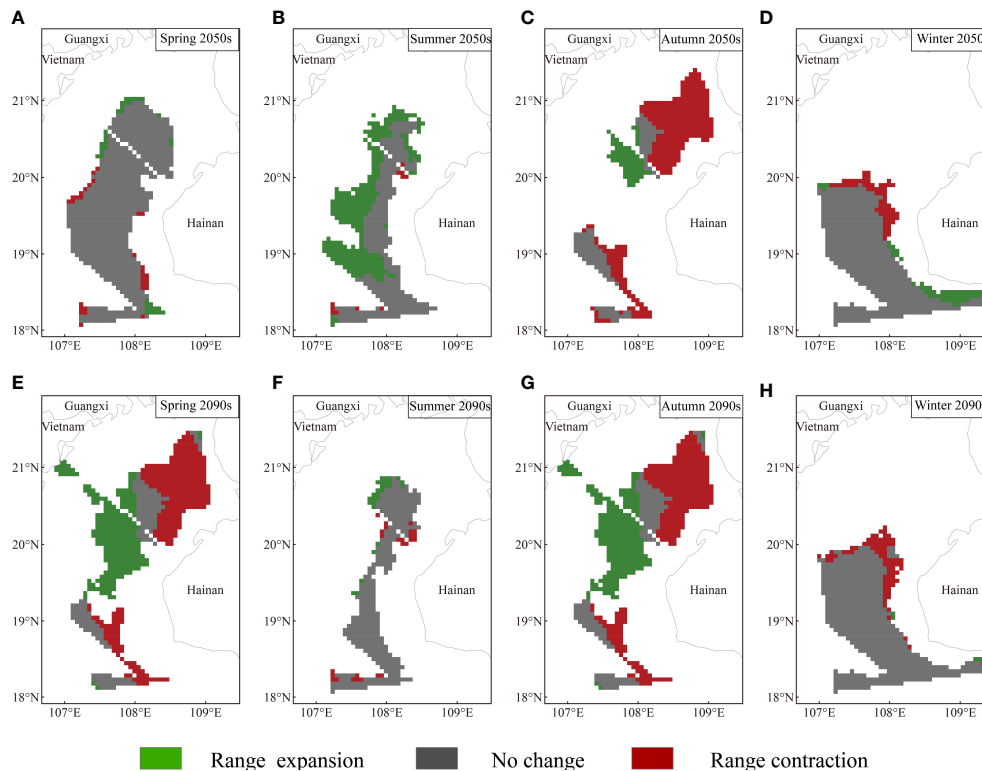


FIGURE 6

Projected range expansion or contraction for *Trichiurus japonicus* in the Beibu Gulf under RCP370. Area of geographic distribution changes among the species distribution models based on binary predictions for current and future (i.e., in the 2050s and 2090s) climate conditions: (A) spring 2050s; (B) summer 2050s; (C) autumn 2050s; (D) winter 2050s; (E) spring 2090s; (F) summer 2090s; (G) autumn 2090s; (H) winter 2090s.

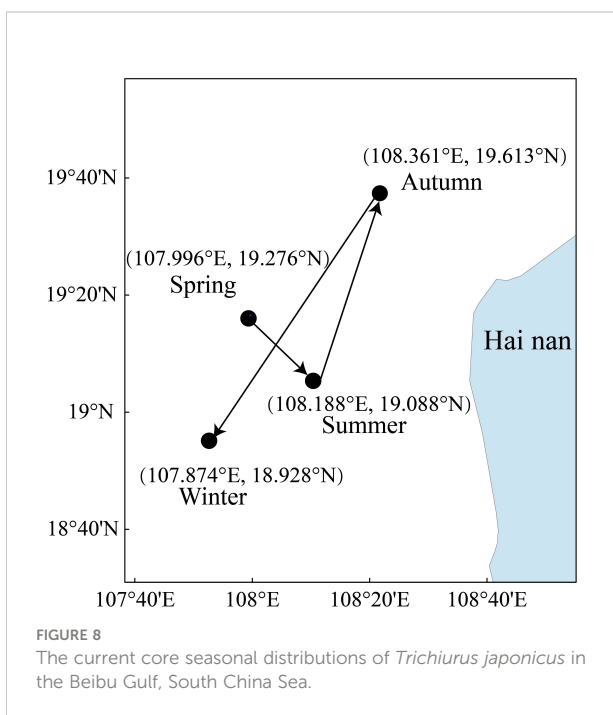
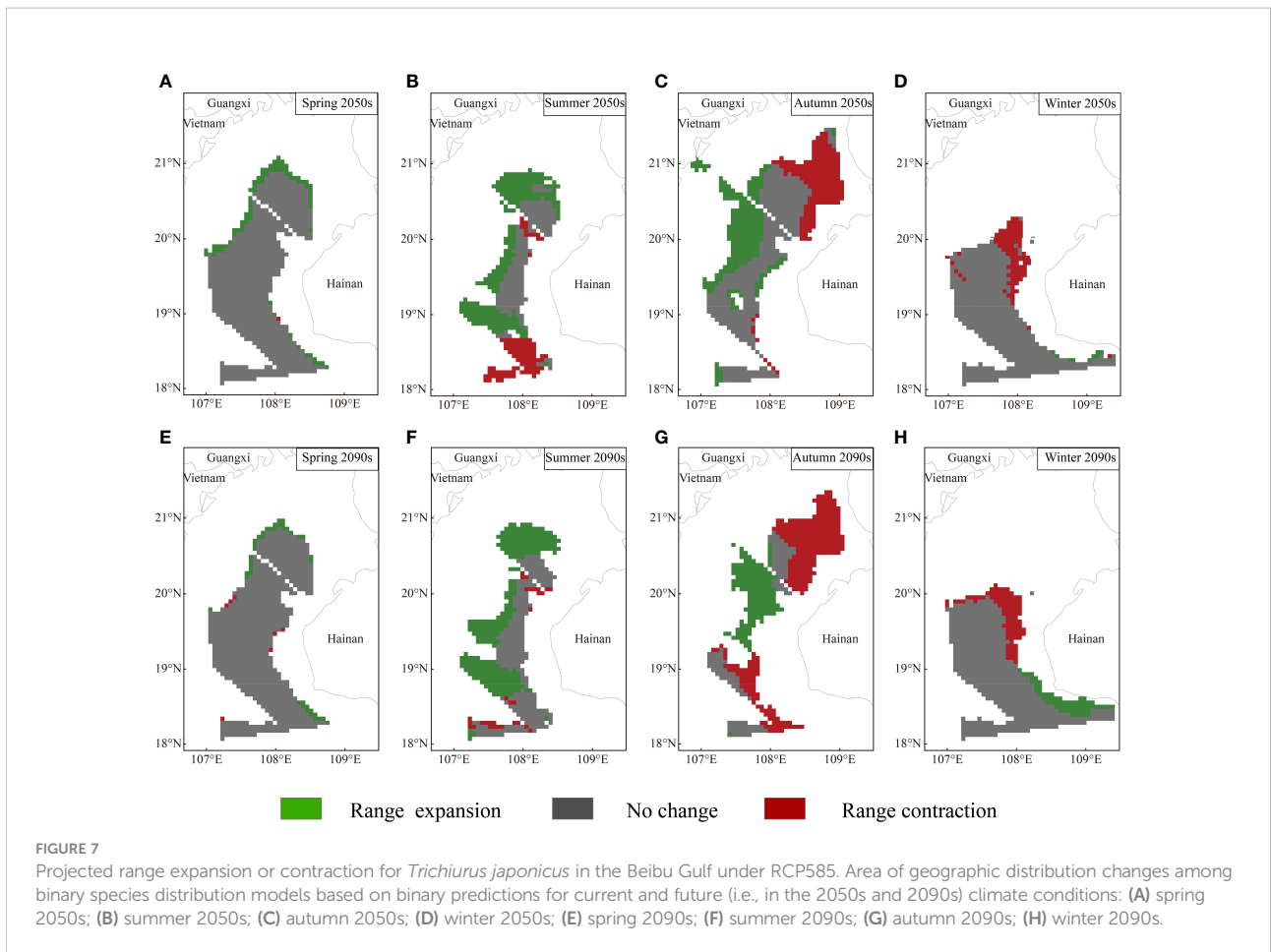
### 3.5 Core distributional shifts

The core distribution of *T. japonicus* in the Beibu Gulf showed pronounced seasonal variation, and the wintering population shifts toward the northeast (Figure 8). Under three climate-change scenarios, the core displacement was generated more toward central parts of the Beibu Gulf in spring, summer and autumn, but toward southern parts in winter (Figure 9D). The species' core distribution in spring in both the 2050s and 2090s under the three climate-change scenarios, except for RCP126–2050 spring, shifts northeastward (Figure 9A). In spring in the 2050s under RCP126, the centroids of the areas shifted as far as 11.060 km away from the current distribution core, as the distribution cores in summer, autumn, and winter moved toward the northwest, north, and south, respectively. By contrast, we examined the centroid distances in different seasons, and found the migration distances of the centroids were shortest in summer and longest in summer (Figure 9B). The maximum migration distance of the centroids of areas was 40.152 km, under RCP126\_2050 autumn (Figure 9C).

## 4 Discussion

### 4.1 Seasonal variation in the current potential distribution of *T. japonicus* and associated environmental drivers

*T. japonicus* was distributed chiefly in central and southern parts of the Beibu Gulf, which agrees with the findings of Hou et al. (2021). The Beibu Gulf is characterized by complex oceanographic processes, including seasonal mixing, upwelling, and circulation. We analyzed the environmental variables in the gulf to forecast the habitat characteristics available to *T. japonicus*. In spring, the variation between SST and SBT was significant, which reflects the phenomenon of water-column stratification, such that SST or SBT is the most-important environmental factor (Sun et al., 2020). The most-significant contributor was bottom water temperature, which was the top predictor explaining *T. japonicus* distribution in summer and autumn. The southwest monsoon prevails in the gulf in summer, when high temperatures induced by solar heat flux and this



monsoon limit the spawning activity of *T. japonicus* (Hou et al., 2021). Thus, we propose that the significant reduction in the suitable habitat area of the species is associated with the main season that *T. japonicus* feeds in the gulf (summer). The highest contribution to the model in summer was bottom water temperature, which in the Beibu Gulf is primarily associated with a middle-to-bottom cold water mass. This cold water mass reaches maximum intensity in summer, when the region surrounding it becomes rich in nutrients, and the bottom temperature significantly decreases (Gao et al., 2014). *Decapterus maruadsi* is the predominant bait of *Trichiurus* spp. And in autumn, the spatial distribution of suitable habitat largely matched the areas with the distribution of *D. maruadsi* (Chen et al., 2019). Maximum mixed layer depths occur in winter, which strengthens vertical convection mixing and provides nutrients needed to sustain plankton growth. This is beneficial for the feeding and overwintering of *T. japonicus*. Water temperature also had a high contribution to the models of *T. japonicus* geographic distribution in winter. The higher the temperature, the higher the probability of its distribution. In winter, the gulf temperatures are lower in the north and higher in the south, with a tongue-shape mass of warm water entering

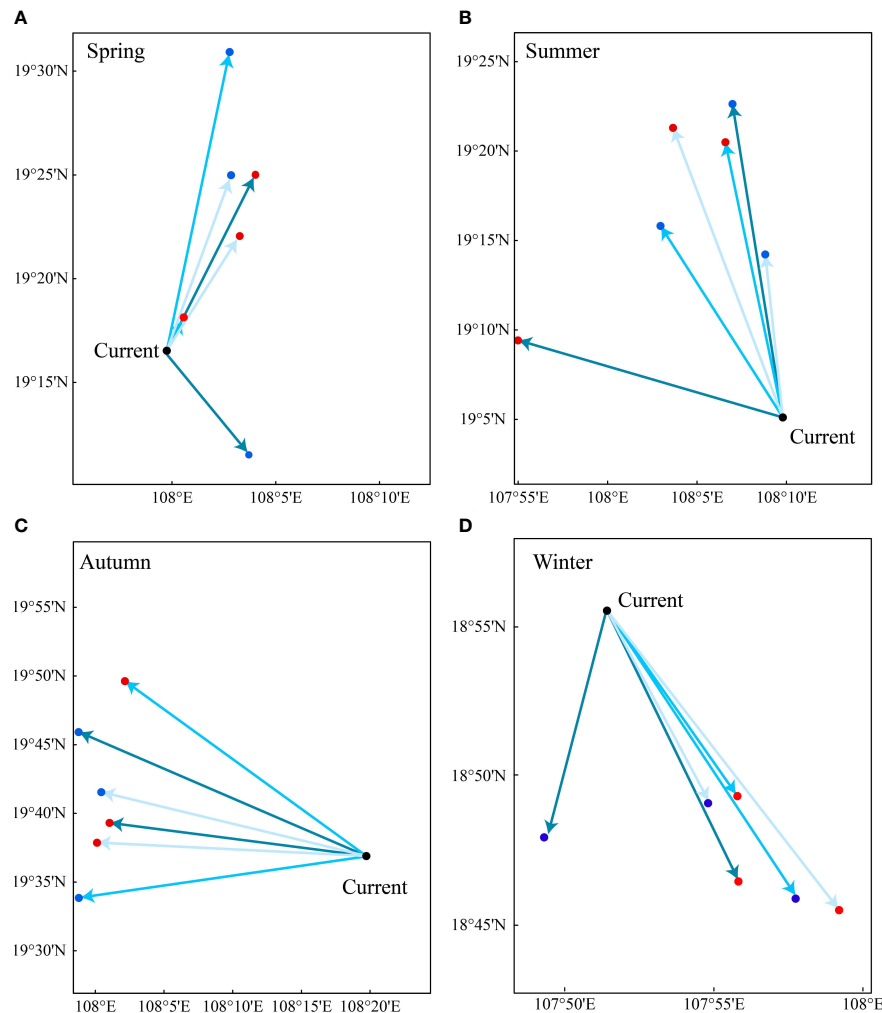


FIGURE 9

Current potential distribution pattern of *Trichiurus japonicus* in the Beibu Gulf, by season, and core distributional shifts of suitable habitat under future climate scenarios in the 2050s and the 2090s. Different colors represent different climate-change models: dark blue denotes SSP126, mid-blue SSP370, and light blue SSP585. The black dot represents the suitable habitat distribution center under the current climate scenario, blue dots represent that in the 2050s, and red dots that in the 2090s; red arrows indicate shifting routes of the suitable habitat distribution core. (A) spring; (B) summer; (C) autumn; (D) winter.

the gulf from the southwest; therefore, the temperature distribution in the southwestern areas is better suited as *T. japonicus* habitat (Huang et al., 2008; Ya et al., 2015).

## 4.2 Potential distributional shifts under future climate change in relation to environmental drivers

This study used *T. japonicus* as a case species and roughly estimated its distribution trends under possible pathways concerning future conditions of the mixed layer depth and salinity, based on MaxEnt niche modelling. Regarding climate-induced changes in the distribution of marine species, the FAO

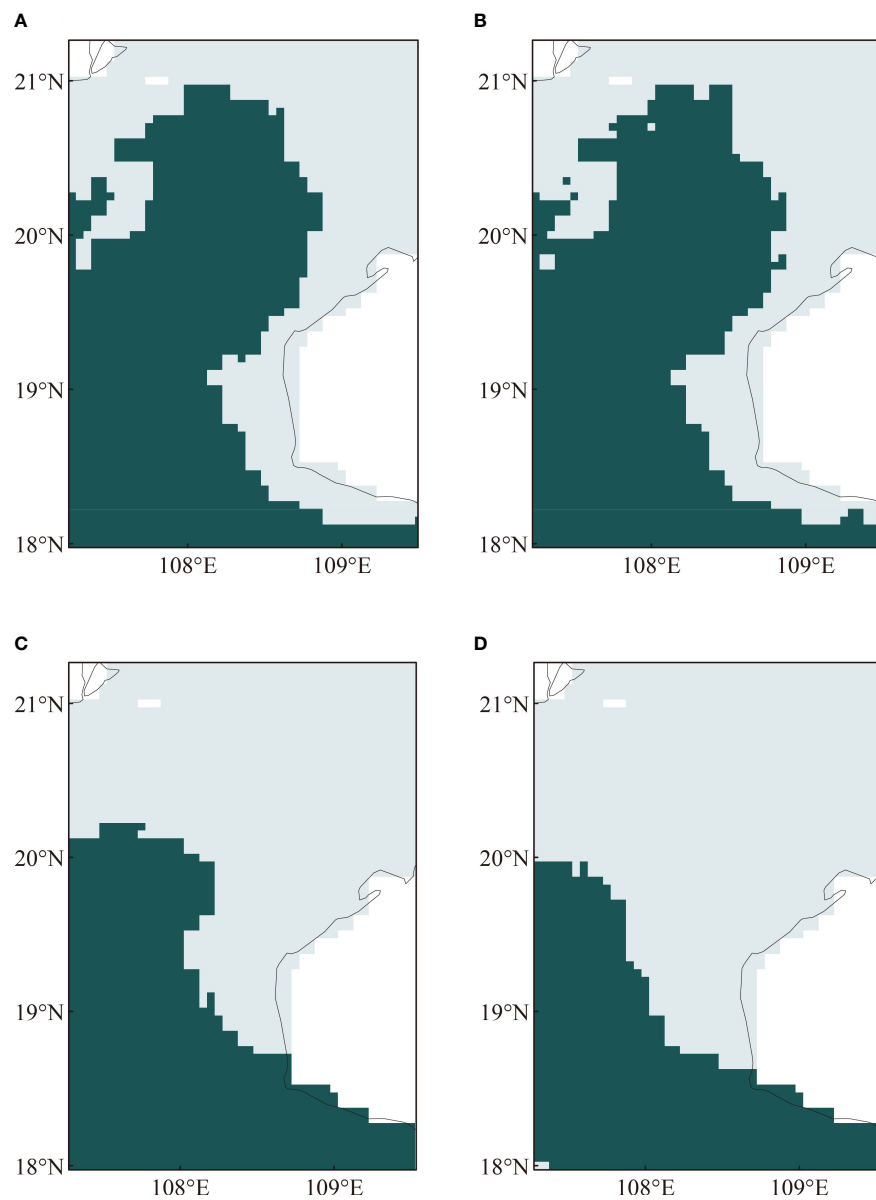
(2012) states that tropical zones are vulnerable to reduction in suitable habitat areas. Compared with that in the 2050s, under all three SSP scenarios, there is a higher risk of suitable habitats for *T. japonicus* in the Beibu Gulf in the 2090s. Under the three climate-change scenarios, the disadvantage to the distribution of *T. japonicus* is greatest in winter, both in the short-term and long-term. Potential suitable distributions for this species show a minor range extension in RCP 370\_2050 winter, but in the rest of the scenes and years its distribution contracts toward the southern part of the gulf.

Mixed layer depth and salinity were shown to be major environmental stress factors affecting the distribution of *T. japonicus*. Thus, with changes in only these two factors, the maximum impact of suitable habitat distribution was observed

during winter when compared with the findings for the other three seasons. Under RCP370\_2090, areas having a suitable mixed layer depth range for *T. japonicus* showed no obvious change, while areas with a suitable salinity range showed contraction in winter in the northern part of the Beibu Gulf. Under the RC370 climate-change scenario, the projected salinity range in the study area was 31.437–33.721‰ in the 2050s and 31.100–33.518‰ in the 2090s. Hence, the salinity threshold may remain relatively constant in the Beibu Gulf but with a gradual decline in the optimum salinity range for *T. japonicus* over time.

Cheng et al. (2020) studied the average salinity at a series of Argo floats in four ocean regions during 1960–2017; the results revealed a long-term trend of decreasing absolute salinity in the Pacific Ocean. The physiological responses of fish to environmental factors will prompt their movement to more suitable areas (Rodriguez-Burgos et al., 2022). Thus, we advise that salinity is the major environmental factor that will affect contraction of suitable habitat for *T. japonicus* in the long term.

In our results, the mixed layer depth is deeper in the 2050s and 2090s than in the current scenario. Under the same change



**FIGURE 10**  
Distribution of the most suitable salinity and mixed layer depth combination (darker color) for *Trichiurus japonicus* in the Beibu Gulf, as projected for the future (in the 2050s and 2090s), under SSP370: (A) mixed layer depth, 2050s; (B) mixed layer depth, 2090s; (C) salinity, 2050s; (D) salinity, 2090s.

trend, there is a higher risk to suitable habitat for *T. japonicus* in the 2090s. One explanation for this phenomenon could be that the contribution rates of the different environmental factors to the model will be affected by time. The present results align with previous studies (Mamun et al., 2018). For example, under RCP370, the gap between the relative contribution rate of the mixed layer depth (21.8%) and the salinity (17.4%) in the 2090s is smaller than the relative contribution rate of the mixed layer depth (31.7%) and the salinity (23.0%) in the 2050s (Figure 10).

Different seasons of *T. japonicus* change in the status of winners and losers in the face of future climate change. Such seasonal changes may be particularly relevant for understanding how future climate will impact marine life as many key biological processes. According to the results of this study, it might result in reducing population repopulation efforts for the following spring if the species in winter encounters conditions predicted in RCP126 or RCP585 for 2050s and especially 2100s. It will also have negative effects on the functioning of such tropical ecosystems and the livelihoods of local fisherfolk. So we suggest that protection measures should be adopted as early as possible for the conservation of the fishing grounds of *T. japonicus* in the Beibu gulf in order to mitigate the effects of climate change on the fisheries and the ecosystem.

## Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

## Ethics statement

The animal study was reviewed and approved by the South China Sea Fisheries Research Institute, Chinese Academy of Fishery Science.

## Author contributions

PX: conceptualization, Methodology, Formal analysis, Visualization, Writing - original draft. YX and MS: Investigation, Writing-review and editing. XZ and PJ: Formal analysis, Visualization. ZC: Methodology, Funding acquisition, Supervision, Validation, Writing-review and editing. JF: Conceptualization, Methodology, Supervision, Writing-review and editing. All authors contributed to the article and approved the submitted version.

## Funding

This research was funded by Key research and development project of Guangdong Province(2020B1111030001), Major Projects of Basic and Applied Basic Research Programs in Guangdong Province(2019B030302004), Central Public-Interest Scientific Institution Basal Research Fund, CAFS (2020TD05). Central Public-Interest Scientific Institution Basal Research Fund, South China Sea Fisheries Research Institute, CAFS (2021SD01), Financial Fund of the Ministry of Agriculture and Rural Affairs, P. R. of China (NFZX2021), National Key Research and Development Program of China (2018YFD0900906).

## Acknowledgments

We thank Cynthia Kulongowski with Liwen Bianji (Edanz) ([www.liwenbianji.cn](http://www.liwenbianji.cn)) edited the language of a draft of this manuscript. We are grateful to the crew members of Zhongyuke 301 and Beiyu 60011 for their help with the data collection. In addition, we sincerely thank the reviewers for their valuable comments on an early draft of this manuscript.

## Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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## Supplementary material

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fmars.2022.1079590/full#supplementary-material>

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