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RESEARCH PAPER

Hotspot Habitat Modeling of Skipjack Tuna (*Katsuwonus pelamis*) in the Indian Ocean by Using Multisatellite Remote Sensing

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Abstract

Skipjack tuna (SKJ) is one of the most targeted fish species globally, especially in the Indian Ocean. SKJ fishery data from Iranian purse seiners and multisatellite remote sensing data were used for hotspot habitat modeling from 2010 to 2018. Spatial and temporal variables were the most important predictors in the generalized additive model (GAM), and 58.6% of the variance was explained. In the MaxEnt model, sea surface temperature (SST), eddy kinetic energy (EKE), and sea surface height (SSH) were the most important predictors of SKJ hotspot habitat suitability in the tropical Indian Ocean between 2°S and 2°N. Furthermore, of the total studied area in the Indian Ocean defined as optimal habitat (habitat suitability index>0.6), 6.8% and 5.3% exhibited ordinary habitat suitability (AUC=0.934, P<0.01) and hotspot habitat suitability (AUC=0.952, P<0.01), respectively. Iranian purse seiners are distributed mainly in tropical areas, and in the present study, SKJ habitat was affected by environmental variables, as determined using multisatellite remote sensing data. In general, for effective regional monitoring and management strategies to ensure sustainable fisheries, diverse datasets compiled using satellite datasets and habitat modeling can help identify potential hotspot habitats, thereby enabling more accurate suitable habitat zone predictions and more efficient stock management.

Introduction

Fisheries managers aim to access adequate and safe food from nature by exploiting marine stocks in authorized areas with high concentrations of their target fish species. Tuna is a major commercially important group of fish in the world's oceans (Maguire *et al.,* 2006; McCluney *et al.,* 2019). The Indian Ocean, which is the origin of 19% of total tuna catches worldwide (International Seafood Sustainability Foundation, 2020), has three main targeted tuna species: yellowfin (YFT, *Thunnus albacares*), skipjack (SKJ, *Katsuwonus pelamis*), and bigeye (BET,*Thunnus obesus*). SKJ inhabits the upper ocean (shallower than 100 m) above the oceanic mixed layer and is distributed in warm waters (>28°C) in the temperate and tropical ocean between 45°N and 40°S (Kim *et al.,* 2020; Lehodey *et al.,* 1997). The spawning season of SKJ occurs mainly during the monsoon and intermonsoon periods (Grande *et al.,* 2014). SKJ are opportunistic predators (Nakamura 1965) and patrol considerable areas in search of forage (Sund *et al.,* 1981). They are most often captured by fishermen using purse seines in the Indian Ocean (Fonteneau *et al.,* 2000; Druon *et al.,* 2017). Despite high landings worldwide (3.16 million tons in 2019; FAO 2020); SKJ stocks remain at biologically sustainable levels (IOTC 2017). SKJ is frequently targeted by purse seine (associated school) fisheries, and the reported catch of this species in the Indian Ocean has increased steadily from the 1980s, peaking at over 600 000 tons in 2018 before decreasing slightly to approximately 550 000 tons in 2019. In 2018, purse seines accounted for approximately 49% of total SKJ catches, whereas gillnet, pole-and-line, and line fisheries accounted for 20%, 20%, and 5%, respectively (FU 2020; International Seafood Sustainability Foundation 2020; Muhsin *et al.,* 2020). Iran is a major exploiter of tuna in the Indian Ocean; its SKJ catch in 2006 was 102 668 Mt; however, this number dropped to approximately 50,000 t (44.4% of tropical tuna catches) in 2018 (Akhondi 2019).

Habitat modeling is a crucial element of ecosystem-based fisheries management (EBFM), especially for regional tuna fisheries (Juan-Jordá *et al.,* 2018). Predictive distribution modeling using habitat data is commonly used to investigate the spatiotemporal dynamics of the tuna population and has been applied to many fish species worldwide (Vayghan *et al.,* 2020a and b; Vayghan *et al.,* 2016a and b; Lan *et al.,* 2018; Lee *et al.,* 2020; Teng *et al.,* 2021). Environmental conditions significantly influence tuna distribution (Lee *et al.,* 2020; Vayghan *et al.,* 2020b), feeding habitats (Vayghan *et al.,* 2020a; Mondal *et al.,* 2021), annual recruitment levels (McKechnie *et al.,* 2016), and reproductive traits (Ashida 2020). SKJ movement varies widely and is reportedly affected by large-scale oceanographic variabilities such as ocean currents, sea surface temperature (SST), sea surface chlorophyll-a (SSC), and sea surface height (SSH; McKechnie *et al.,* 2016; Mugo *et al.,* 2010; Mugo and Saitoh 2020). Although habitat suitability modeling has its own limitations (Vayghan *et al.,* 2016a), different models including the habitat suitability index (HSI) model (Chen *et al.,* 2010; Vayghan *et al.,* 2016a; Vayghan *et al.,* 2013), optimized genetic algorithm (Vayghan *et al.,* 2016b; Sadeghi *et al.,* 2013), and generalized additive model (GAM; Vayghan *et al.,* 2017; Lan *et al.,* 2018)—can be used to assess the suitability of potential habitats and the factors influencing the movement of marine organisms. Multisatellite remote sensing is a powerful tool for determining ocean sea surface characteristics. Its fast and large-scale data preparation enables scientists to support the productivity of fisheries and the management of pelagic species (Khan *et al.,* 2020; Lan *et al.,* 2018) and to gain insight into the tuna living ecosystem and the factors affecting it (Lee *et al.,* 2020; Nieto *et al.,* 2017; Vayghan *et al.,* 2020b). Pelagic potential habitat hotspots are a topic of interest in fishery prediction (e.g., as fishing grounds) and in the development of policies related to marine resource management and conservation (Mugo *et al.,* 2020a). Hence, multisatellite remote sensing data are valuable for fisheries exploitation and management and can assist scientists in expanding sustainable strategies for fisheries management and modeling tuna habitats across the world's oceans. The present study developed an empirical habitat suitability model for SKJ by using Iranian purse seiner fishing data and multisatellite remote sensing data. The proposed model can be used to determine optimal combinations of environmental variables and to detect potential hotspot habitats in the Indian Ocean.

Material and Methods

SKJ Fishing Data

SKJ fishery data from Iranian purse seine fishing fleets in the Indian Ocean were collected for the period from 2010 to 2018 for application in various habitat models. The fishery data consisted of days employed, SKJ weight, year, month, latitude, and longitude. The effort and fishing data were pooled by year and month by using a 1° × 1° spatial grid. The catch per unit effort (CPUE) of the tuna purse seine fishery fleets was used as a reliable index of stock abundance in the fishing zones (Vayghan *et al.,* 2017; Vayghan *et al.,* 2018). Accordingly, CPUE served as the response variable and multisatellite environmental data, temporal (month and year), and spatial (latitude and longitude) data served as explanatory variables in the modeling process.

Multisatellite Remote Sensing Data

Based on relevant literature, a set of remotely sensed environmental variables were hypothesized to be associated with the potential SKJ catch from 2010 to 2018 (Table 1) and were applied in this study. The monthly satellite data from 2010 to 2018 presented in Table 1 were downloaded from various online databases to be fed into the model as follows: (i) SSC monthly

Table 1. Multisatellite remote sensing variables and satellite altimetry data applied in the model

Habitat Variables	Units	Data Source	Resolution
Sea Surface Temperature (SST)	°C	MODIS	4 km × 4 km
Sea surface chlorophyll-a (SSC)	mg m^{-3}	MODIS	4 km × 4 km
Sea Surface Salinity (SSS)	psu	MOVE-MRI	10 km × 10 km
Sea Surface Height (SSH)	cm	AVISO	25 km × 25 km
Mixed Layer Depth (MLD)	m	HYCOM	1/12° × 1/12°
Depth of 20 °C Isobath (D20)	m	ORAS5	0.25° × 0.25°
Eddy Kinetic Energy (EKE)	m^2s^{-2}	AVISO	25 km × 25 km

composite fields were prepared by data from the National Oceanographic Data Center at Oregon State University (http://www.science.oregonstate.edu); (ii) SST, SSH, MLD, and sea surface salinity (SSS, depth of 20°C isobath (D20), and eddy kinetic energy (EKE) data were collected from the Asia-Pacific Data-Research Center at the University of Hawaii (http://www.apdrc.soest.hawaii.edu). All the remote sensing variables were then resampled and computed as monthly means on a lower spatial grid of 1° × 1° resolution to meet the spatial resolution of the fishery data using the MATLAB (version R2015a) and Interactive Data Language (IDL, version 7.0) software packages. Multicollinearity was tested using a variance inflation factor (VIF) to avoid model overfitting (Catterjee and Hadi 2006; Montgomery *et al.,* 2007).

Model Developing

To predict potential SKJ spatial habitat patterns, a GAM (Guisan *et al.,* 2002; Hastie and Tibshirani 1990) was developed using the GAM function and mgcv package to identify nonlinear relationships among the covariates and the response variable in a semiparametric manner and to effectively and flexibly explain the variance in the response variable (Maunder and Punt 2004). The model can be written as follows:

$$g(\mu_i) = \mu + \sum_{j=1}^{p} f_j(X_i)$$

where μ_i is the response variable (CPUE), μ represents the intercept term in the fitted model, f_j is a smooth function (such as a spline or loess smoother), and x_i represents the independent variables. The effective degrees of freedom were estimated, and all the covariates were assumed to be continuous. To avoid log-transformation problems arising from the inability of the log-link function to handle zeroes, 10% of the mean CPUE was added to zero values of SKJ CPUE ((Lan *et al.,* 2018; Su *et al.,* 2008). In the first constructed model, the effects of all of the spatial (latitude and longitude), temporal (year and month), and environmental (SST, SSC, SSS, SSH, MLD, D20, and EKE) variables were considered. To identify redundant variables in the first run, the fits of the models were evaluated using standard diagnostics: changes in the residual variance, the Akaike Information Criterion (AIC; Akaike 1998), variance explained, R^2 values, and *P* values calculated using a chi-square test. The model selection was conducted using a stepwise procedure based on the lowest AIC value. The GAMs were constructed in R (version 4.0.0) software (R Development Core Team 2020).

MaxEnt Model

The maximum entropy (MaxEnt) species distribution model (SDM) identifies the probability of appropriate habitat for a species existing at each pixel within a geographic region by combining environmental layers with species presence data (Phillips and Dudik 2008). Because the primary SKJ fishing season (accounting for 76% of catches) occurs during the cold months (January, February, March, April, October, November, and December), we used cold-season data in this study. Possible SKJ habitats in the Indian Ocean were identified using a combination of SKJ presence data with positive catches and sparse sets of environmental data. To identify SKJ habitat hotspots, we used the 75th percentile of CPUE data as indicating the highest probability of a fish catch or relevant presence records. The habitat suitability analysis of SKJ was

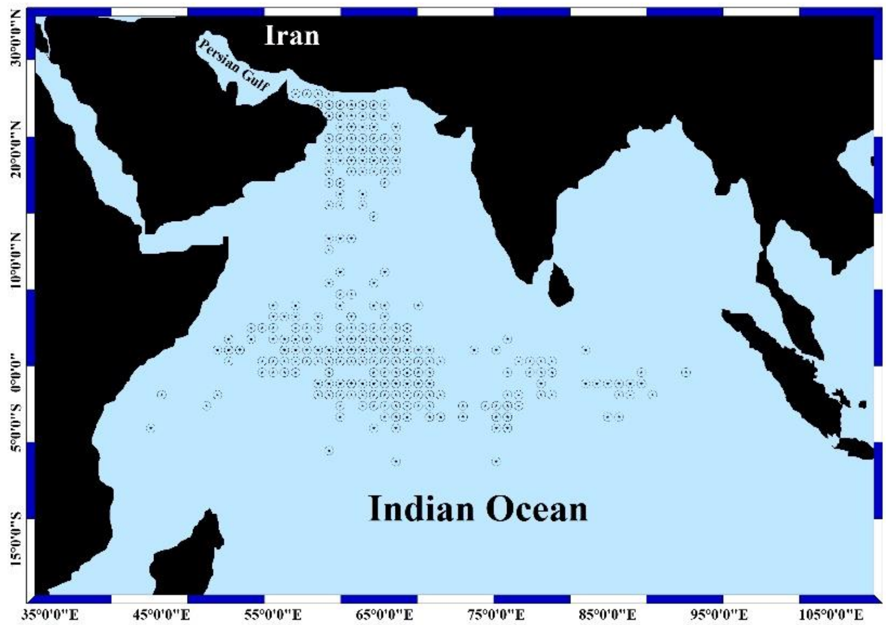

Figure 1. Study area and geographical distribution of Iranian purse seiner fishing in the Indian Ocean.

conducted using MaxEnt software (version 3.4.4). The cold-season SKJ presence data were split into training (70%) and testing (30%) sets. We evaluated the models' predictive performance (sensitivity and specificity) and identified the most important environmental variables to SKJ habitat suitability by using the area under the curve (AUC) of the receiver operating characteristic (ROC) curve and the percent variable contributions, respectively.

Results

The spatial distribution of SKJ catch was predominantly located within the tropical Indian Ocean and the Oman Sea (Figure 1). Multicollinearity diagnostic analysis of environmental variables revealed no correlations among any of the environmental variables except SSH (VIF>10). The GAM results clarified the effects of the temporal, spatial, and environmental variables on SKJ CPUE (Table 2). The overall variance explained by the model was 58.6%; temporal, spatial, and environmental factors accounted for 34.3%, 14.4%, and 9.8%, respectively, of the variance explained (Table 2). According to the GAM, the most crucial environmental variables were SSS, MLD, SSH, and SSC, in that order. The SKJ had a specific preference for the level of environmental variables during the cold season; the GAM plots indicated that oceanographic variables affected SKJ CPUE (Figure 2).

The ordinary habitat suitability and hotspot habitat suitability associated with environmental variables in the MaxEnt model were different (Figure 3). Of the optimal habitat (HSI>0.6) identified within the study area, 6.8% and 5.3% exhibited ordinary habitat suitability and hotspot habitat suitability, respectively. The hotspot habitat area was drooped nearly 1.5% (approximately 45000 km^2) smaller than the ordinary habitat area (Figure 3b). We calculated the percent contributions and permutation importance values for each factor in the MaxEnt model for two SKJ habitat suitability scenarios (i.e., ordinary habitat suitability and hotspot habitat suitability; Table 3). In both scenarios, SST, EKE, and SSH strongly contributed to the model and affected SKJ habitat suitability (Table 3). The model provided high-confidence predictions of ordinary habitat suitability (AUC=0.934, P<0.01) and hotspot habitat suitability (AUC=0.952, P<0.01; Figure 4).

Discussion

Effective regional monitoring and management strategies are key to ensuring sustainable management of tuna resources, especially in areas with high habitat variation (Hsu *et al.,* 2021). In this study, we applied multisatellite remote sensing environmental data and spatial and temporal data to identify associations with the CPUE of SKJ caught by Iranian purse seiners in the Indian Ocean. SKJ is mainly caught in the cold season in

Table 2. Statistical results of generalized additive modeling after skipjack tuna data input

Model	Residual Degree Freedom	Residual Deviance	Deviance	% Of Deviance Explained	AIC	% of AIC explained	Pr(>Chi)
Null	1149.00	9588.60	-	-	16.82	16.82	
Year	1141.00	8482.90	1105.70	11,50	5581.59	43.19	<2.2e-16
Month	1130.00	6297.30	2185.57	22,79	5260.97	14.90	<2.2e-16
LAT	1100.00	5428.90	868.42	9,06	5150.33	4,39	<2.2e-16
LON	1059.00	4914.00	514.92	5,37	5117.73	0,59	1.67E-11
SST	1058.00	4886.80	27.20	0,28	5113.35	4,97	0.00826
SSS	1049.10	4663.50	223.28	2,33	5076.41	6,92	4.14E-09
MLD	1033.30	4351.90	311.57	3,25	5025.05	4,91	1.46E-10
SSH	1032.30	4208.90	143.03	1,49	4988.59	1,56	1.16E-09
Chla	1018.80	4084.50	124.46	1,30	4977.03	1,59	0.003301
EKE	1015.90	4027.40	57.02	0,59	4965.26	0,16	0.001938
D20	1012.50	3970.60	56.80	0,59	4953.86	16,82	0.003361

R-sq.(adj)=0.533 Deviance explained=58.6%
Deviance explained by Spatial Variable 24.62%, Temporal Variable 58.58%, Environmental Variable 16.79%

Table 3. Percent contributions and permutation importance values of environmental variables for ordinary and hotspot habitat suitability in MaxEnt model.

Environmental	Ordinary habitat suitability		Hotspot habitat suitability	
variable	Percent contribution	Permutation importance	Percent contribution	Permutation importance
SST	42.1	19.5	34.8	7.8
EKE	39.5	30.1	55.5	51.6
SSH	8.6	36.9	6.5	31.9
SSS	3.4	4.8	0.4	0
Chla	3.3	0.2	0.7	1.2
D20	3	6.1	1.2	4.4
MLD	0.1	2.4	1	3.1

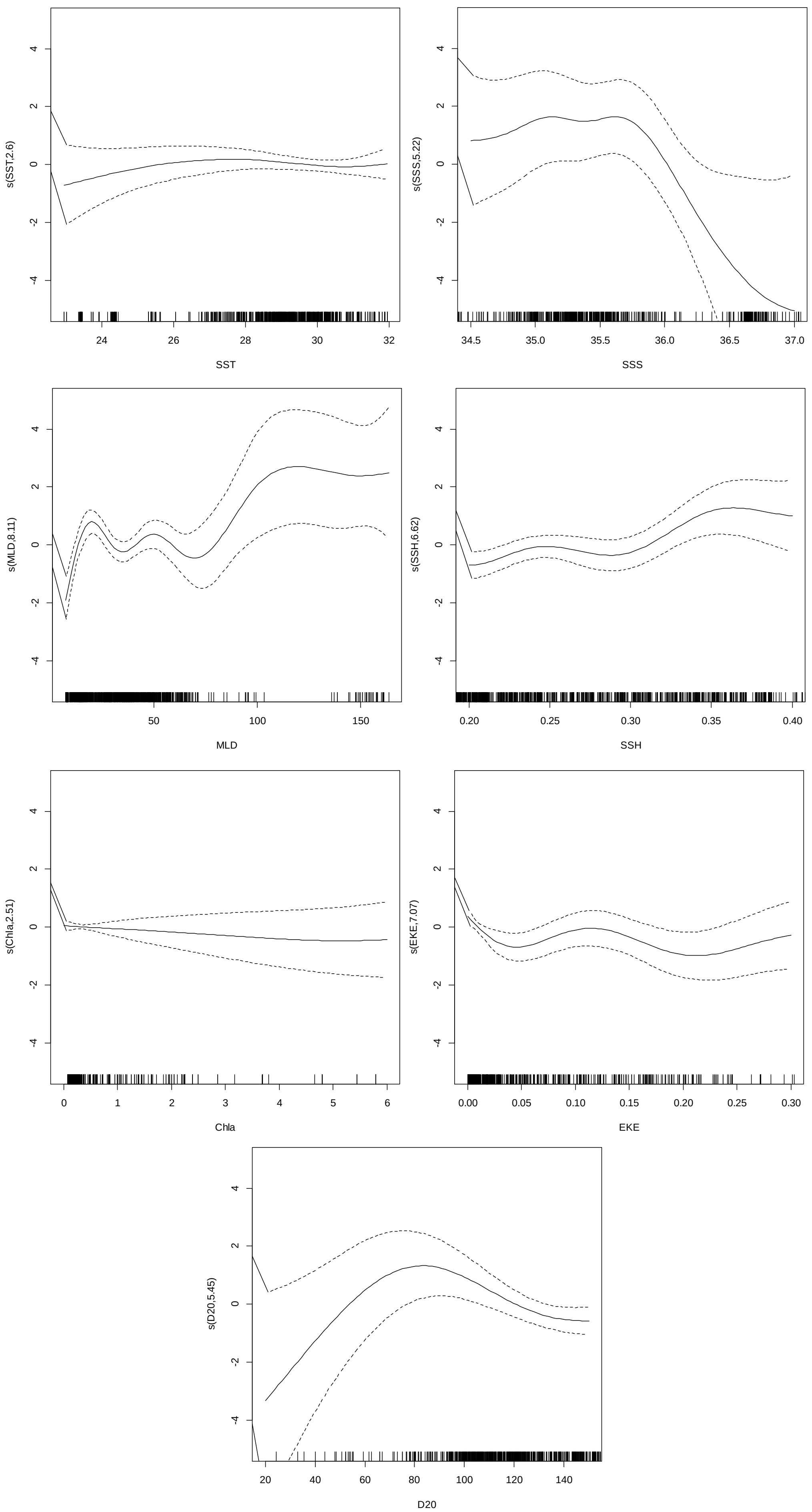

Figure 2. Generalized additive model (GAM) plots of the effects of oceanographic characteristics associated with skipjack tuna (SKJ) catch per unit effort (CPUE). Black and dashed lines represent fitted GAM function and 95% confidence interval, respectively.

the Oman Sea and tropical areas between 5°S and 5°N in the Indian Ocean. Our GAM determined that temporal (month) and spatial (latitude) variables were responsible for most of the variance in SKJ CPUE; SSS, MLD, SSH, and SSC were the most important multisatellite-measured environmental variables in the model (Table 2). The MaxEnt model revealed high habitat suitability in tropical areas between 5°S and 5°N and hotspot habitat suitability in a tight zone between 2°S and 2°N. Spatial and temporal variables strongly affect fishing location, habitat suitability (Vayghan *et al.,* 2020b; Vayghan *et al.,* 2018), and CPUE standardization (Maunder and Punt 2004; Su *et al.,* 2008). In this study, SST, EKE, and SSH strongly contributed to SKJ habitat suitability. SST is widely considered a key predictor of CPUE fluctuations for tuna catches *(Dunn 2006; Khan et al., 2020; Lan et al.,* 2018; Lee *et al.,* 2019; Nieto *et al.,* 2017; Vayghan *et al.,* 2020a) because of its limiting effect on distribution; moreover; migration is motivated by food richness, which is mainly promoted by SSC and optimal SST (Vayghan *et al.,* 2018; Mugo *et al.,* 2010, 2020b; Mugo and Saitoh 2020a; Mondal *et al.,* 2021). SST also affects spatial and temporal differences in the reproductive traits of SKJ by influencing physiological processes and food availability (Ashida 2020). In addition, the distribution, migration, and catchability of tuna may be closely associated with different oceanic fronts and eddies *(Hsu et al., 2021; Lee et al., 2019; Mugo et al.,* 2020b; Zainuddin *et al.,* 2008). SKJ habitat suitability might be amplified by mixture of the SST and SSC, initiating convergent oceanic fronts, where vertically well-mixed, cool, and highly productive surface waters settle beneath warm, stratified, and less productive waters, resulting in highly productive and suitable habitats for tuna schools (Lee *et al.,* 2019; Polovina *et al.,* 2001; Vayghan *et al.,* 2020a). Polovina et al. (2001) reported that a contour level of 20°C isotherm and 0.2 mg m^{-3} isopleth plus vertical mixing of water stimulated higher primary production in surface waters, thereby resulting in higher tuna CPUE. Indeed, SSC and SST fronts are used to track hotspots of pelagic productivity to detect areas that could serve as tuna feeding habitats (Cai *et al.,* 2020; Druon *et al.,* 2017; Lee *et al.,* 2020). Overall, SKJ prefer warm water, and the mechanisms by which they forage within warm waters along productive thermal and chlorophyll-a fronts have been verified in previous studies (Hsu *et al.,* 2021; Kiyofuji *et al.,* 2019; Saitoh *et al.,* 1986). High SSS induces oligotrophic conditions and results in less favorable primary conditions, which are associated with unsuitable feeding grounds for SKJ in tropical waters (Coletto *et al.,* 2019). In the present study, the suitable

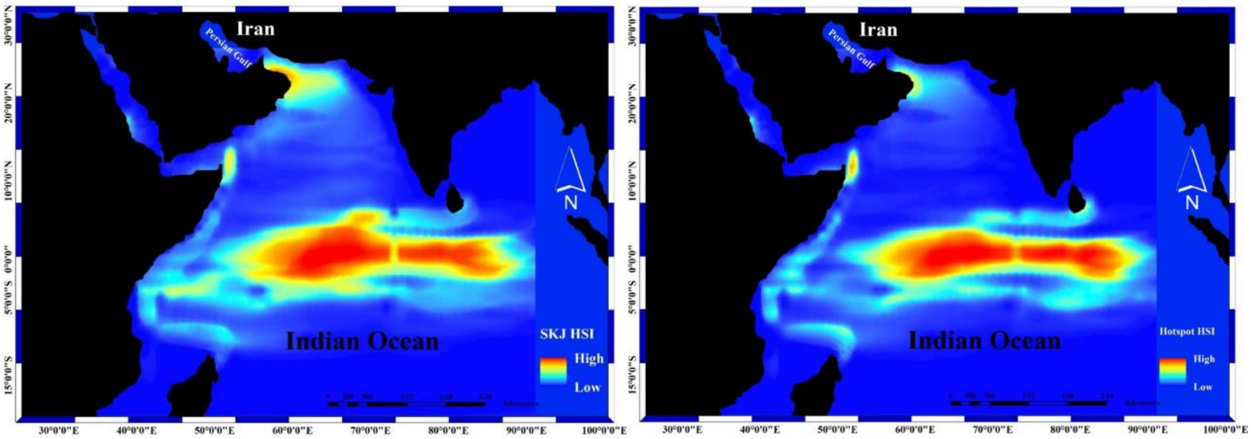

Figure 3. Skipjack tuna (a) ordinary habitat suitability and (b) hotspot habitat suitability associated with environmental variables in the MaxEnt model.

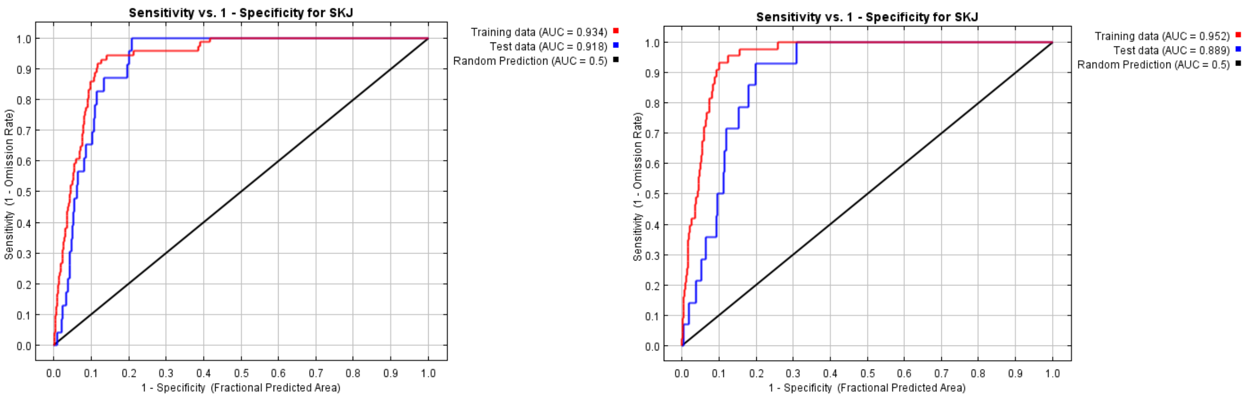

Figure 4. Receiver operating characteristic (ROC) curve for SKJ (a) ordinary habitat suitability and (b) hotspot habitat suitability associated with environmental variables in the MaxEnt model.

and unsuitable ranges of SSS were 34.5 to 35.5 PSU and 35.5 PSU, respectively (Figure 2), which is in line with previous research (Coletto *et al.,* 2019; Hsu *et al.,* 2021).

Water mixing occurs in several oceans and affects water oxygen concentration and productivity by bringing minerals from the depths to surface water, thereby increasing prey availability. The mixed layer above the thermocline is a favorable habitat for SKJ (Druon *et al.,* 2017; Mugo *et al.,* 2010); however, this does not directly affect SKJ fishing activities (Hsu *et al.,* 2021). MLD is formed by the action of water mass mixing induced by the potential energy of wind stress and heat exchange at the air–sea interface (Kara *et al.,* 2003). Furthermore, MLD is correlated with the SSH variation because SST cooling may cause convection, which enlarges MLD and reduces SSH (de Boyer Montégut *et al.,* 2004). In this study, the MaxEnt habitat suitability model revealed the role of ocean currents (EKE and SSH) in SKJ distribution in the Indian Ocean. In the Pacific Ocean, SKJ distribution and movement is influenced by dominant currents, as indicated by SSH and EKE (Mugo *et al*., 2020b; Zainuddin *et al*., 2006). It's also confirmed that higher SSH values influence the suitability of habitats for SKJ in the western Pacific Ocean (Hsu *et al.,* 2021). Through the interpretation of SSH data, the edges of large warm core eddies, which are suitable fishing grounds for SKJ, are easily detectible (Nihira, 1996). The role of currents in producing favorable habitats for tuna species (Dunn & Curnick, 2019) and other fish (Vayghan, *et al*., 2016a; Vayghan *et al*., 2013) has also been explored. Meanwhile, the CPUE and tuna catches may be affected by climate variability in the dynamic ocean, which must be considered to improve the precision of tuna distribution modeling (Yen *et al*., 2012; Kumar *et al*., 2014; Lan *et al*., 2018; Sculley & Brodziak, 2020; Yen and Lu, 2016). Overall, SST, SSH, EKE, and SSC values determined through multisatellite remote sensing are essential to predicting distribution patterns and variation in the abundance of tuna and tuna-like species in the Indian Ocean. Indeed, spatial and temporal variables strongly affect the volume of tuna caught by Iranian purse seiners. To further elucidate SKJ distribution, ensemble modeling conducted in addition to inter- and intra-annual studies of habitat changes may be appropriate as a next step, and GAMs have exhibited consistently high performance in ensemble modeling (Alabia *et al*., 2016; Mugo & Saitoh, 2020). In addition, we need to keep in the mind that, fishery-derived data are subject to various biases associated with fisherfolk behavior, fishery instruments, and sampling effort distribution (Hsu *et al.,* 2021), which may be influenced by weather considerations.

In conclusion, this study employed multisatellite remote sensing data and spatial and temporal data as predictor variables in SKJ distribution modeling by Iranian purse seiner in the Indian Ocean. Temporal and spatial variables had a strong effect, and SST, EKE, and SSH were key predictors in hotspot habitat suitability modeling of SKJ in the Indian Ocean. However, other potential effects of climate change, inter- and intra-annual fluctuations in catch, and effort-based biases must be considered to further elucidate SKJ distribution. Overall, the use of diverse datasets combination and tools such as satellite datasets and habitat modeling in fisheries oceanography can advance our knowledge of pelagic hotspots, thereby enabling more accurate suitable habitat zone predictions and more effective stock management.

Ethical Statement

Not applicable

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Author Contribution

Conceptualization, data curation, calculation and analysis, writing, review and editing made by Haghi Vayghan, A. Conceptualization, review and editing made by Lee, M. A. All authors have read and agreed to the published version of the manuscript.

Conflict of Interest

The authors declare no conflict of interest.

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