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Modelling habitat preference of Caspian Kutum, *Rutilus kutum*, using non-linear habitat suitability indices and generalized additive models

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ABSTRACT

The distribution of Caspian Kutum, *Rutilus kutum*, an economically important fish species with a limited understanding of its ecology, was investigated along the southern Caspian Sea coast to identify the environmental drivers of its occurrence. The environmental predictors including sea surface temperature, chlorophyll-a concentration, particulate organic and inorganic carbon, aerosol optical thickness, depth, bottom slope, coastline aspect and distance to rivers, and long-term monthly commercial beach seine catch data, procured from 2002 to 2012, were analysed. Using two alternative approaches to describe catch per unit effort (CPUE), a multiplicative effect of predictors was found that is often being used in fishery studies (the so-called continued product model, HSI_{CPM}) to perform weaker than a Generalized Additive Model (GAM). The highly variable CPUE was strongly related to sea surface temperature, bottom slope, aerosol optical thickness and distance to rivers using HSI_{CPM}, but coastline aspect, particulate inorganic carbon and bottom slope in the GAM. The steps involved in computing the HSI_{CPM} led to a biased fit. This study provides a robust quantification of habitat characteristics of Caspian Kutum that can be used to inform management plans with both commercial and conservation goals.

1. Introduction

Conservation and management of a species depend on a sound spatio-temporal understanding of its presence and survival (Giannoulaki et al., 2013). Determining the environmental factors influencing the spatial distribution of fishes have become a mainstay of ecological investigations being studied through habitat evaluation models (Giannoulaki et al., 2013; Guisan and Zimmermann, 2000). These models indicate principally the relationship between environmental and occurrence data describing the appropriateness of a habitat for a given species (Su et al., 2020; Zwolinski et al., 2011). Such models have greatly been employed in aerial assessment and management of commercial fish species (Ramirez-Llodra et al., 2011; Tian et al., 2009). Finding reliable data may thus be challenging task in fisheries ecosystem management to identify optimum core habitats of target species (Chang et al., 2012; Liu et al., 2019; Vinagre et al., 2006).

Among the wide range of modelling techniques being used to quantify the relationship between fish occurrence and habitat quality, empirical habitat suitability index (HSI) models have been extensively used by ecologists (Ahmadi-Nedushan et al., 2006; Brown et al., 2000; Druon, 2010; Su et al., 2020; Vadas and Orth, 2001; Valavanis et al., 2004). HSI models are also applied in the studies on the distribution of commercial fish species (Druon, 2010; Yen et al., 2012). The information from those models has high importance in defining fish's key habitats and helps find optimum fishing locations (Chang et al., 2012). These non-statistical HSI models are based on observed preferences along univariate habitat factors (i.e. suitability indexes (SIs)), which are then mathematically combined to estimate and predict habitat quality (Chen et al., 2010; Tian et al., 2009), and may hence delimit the optimal fishing zones (Chang et al., 2012).

The Generalized Additive Models (GAM) are frequently used to assess non-linear relationships between occurrence and environmental variables (Knudby et al., 2010; Leathwick et al., 2006;

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Parra et al., 2017; Schismenou et al., 2017; Su et al., 2020). GAM models have been used to explain relationships between fish abundance and environmental factors (Murase et al., 2009; Rezaei and Sengül, 2018) and predict the relative fish abundance (Drexler and Ainsworth, 2013; Parra et al., 2017; Schismenou et al., 2017). These models have been utilized to define fish habitat preference functions in other habitat modelling frameworks (Grüss et al., 2018). A good performance and predictive ability of GAM in modelling the relationship between fish biomass and habitat parameters, compared to empirical HSI models and machine learning techniques, have been reported in several studies (Knudby et al., 2010; Parra et al., 2017; Schismenou et al., 2017; Su et al., 2020).

Caspian Kutum (*Rutilus kutum* Kamensky 1901) is an endemic species of the Caspian Sea belonged to the family Cyprinidae with high commercial importance (Abdolhay et al., 2012; Afraei Bandpei et al., 2011; Fazli et al., 2013). This species is mainly distributed over southern and south-western coastal waters of the Caspian Sea (Valipour et al., 2011). Kutum is an anadromous fish that migrates into the rivers of the northern regions of Iran for spawning between March and April, and after that, it returns to the sea (Afraei Bandpei et al., 2011). Although Kutum is an omnivorous fish, it mainly feeds on bivalves and benthic invertebrates (Valipour et al., 2011; Naderi Jolodar et al., 2013). This species accounts for more than 70% of the teleost fish total catch and fisheries income along the southern Iranian coast of the Caspian Sea (Esmaeili et al., 2014; Ghasemi et al., 2014). However, during the last decades, overfishing, excessive pollution and degradation of riverine nursery habitats have impacted the abundance and distribution of this species (Ghani Nejhad et al., 2000; Razavi Sayyad, 1999). Therefore, updated information on the spatial and temporal dynamics of catch distribution and analysing the habitat characteristics of Caspian Kutum is necessary for appropriate exploitation, conservation and recovery of its populations (Gheshlaghi et al., 2012; Vayghan et al., 2016).

Few studies investigated the habitat preferences of Caspian Kutum (Vayghan et al., 2013, 2016). In these studies, fish occurrence data obtained from research bottom trawl surveys conducted on short periods. However, this species is not restricted to benthic habitats and thus the bottom trawl is likely to miss a portion of its environmental niche. The present study, for the first time, used the commercial beach seine fishing data of Caspian Kutum for a period of 10 consecutive catch seasons (2002/3–2011/12) at almost 100 fixed fishing locations along the southern coast of the Caspian Sea to investigate habitat preferences of this species. The objectives of our study were to (1) find the most relevant habitat predictors driving the distribution of *R. kutum*, and their optimum ranges; (2) compare the performance and predictive ability of two practical modelling approaches, HSI and GAM, in assessing habitat quality of the fish.

2. Material and methods

2.1. Fishery data

Catch season of the Caspian Kutum along the southern coast of the Caspian Sea lasts from mid-September and to mid-April. Daily catch data of Caspian Kutum during catch season, from 2002/3 to 2011/12, were obtained from Iran Fisheries Organization (IFO). The catch data included beach seine fishing records at 125 fishing points comprising fish biomass (kg), number of dragged seine nets (each with a mean length of 1200 m), and the duration of fishing operation (hour). Among all fishing points, 90 stations had complete temporal coverage during the study period (2002/3–2011/12) and were thus selected for further analysis. Fig. 1 represents the spatial distribution of the selected fishing points along the Iranian Caspian Sea coast.

To standardize catch data, the mean monthly catch per unit of effort (CPUE) was calculated as below:

$$\mathrm{CPUE}(\mathrm{kg\ seine}^{-1}\ \mathrm{h}^{-1}) = \frac{catchbiomass\ (\mathrm{kg})}{number\ of\ seine\ nets \times duration\ of\ fishing\ period\ (\mathrm{h})} \quad (1)$$

Finally, averages of mean monthly CPUE values for all the catch season were calculated and used in subsequent data analyses and modelling.

2.2. Environmental habitat predictors

Environmental variables including day-time sea surface temperature (SST (°C)), aerosol optical thickness (ASL (unitless)), particulate organic carbon (POC (mg m^{-3})), particulate inorganic carbon (PIC (mol m^{-3})), near surface chlorophyll-*a* concentration (CHL (mg m^{-3})), distance to rivers (km), depth (m), bottom slope (°) and coastline aspect (°) at the fishing points were considered as potential environmental predictors. These variables can have direct or indirect effects on the water environment in relation to the presence of fish (SST Chen et al., 2012; Hua et al., 2020; PIC Hopkins et al., 2019; Mitchell et al., 2017; POC Zhang et al., 2019; ASL Mahowald et al., 2018; CHL Giannoulaki et al., 2013; Depth Vayghan et al., 2013, 2016; Slope Parin et al., 2010; Parra et al., 2017; Aspect Parra et al., 2017; Pirtle et al., 2019; Distance to rivers Froeschke et al., 2013). Data of SST, ASL, POC, PIC and CHL for the period of 2002 to 2011 were obtained from MODIS project database with 4 km resolution and processed using the "raster" package (version: 3.4–10) in R 3.6.1 (NASA Goddard Space Flight Center, Ocean Ecology Laboratory, 2021). The monthly mean values of these remotely-sensed parameters at fishing points were averaged over each catch season. The mean depth at fishing locations were extracted from the world bathymetry raster file obtained from the GEBCO database (GEBCO). The difference between the water level of the Caspian Sea and open oceanic waters is 27 m (Chen et al., 2017). Hence, 27 subtracted from the values of the bathymetry raster map to achieve the real depths at fishing points. The slope and aspect of the fishing locations were found from the slope and aspect maps made from the bathymetry map. Since aspect is a circular parameter, its obtained values at fishing locations ([0°–100°) and (220°–360°]) were transformed respectively as (aspect value – 220) and (aspect value + 140) to have a continuous range of this variable in modelling analysis. The distance between fishing points and the rivers was calculated as their nearest direct distance to the mouth of the main rivers along the coast.

To examine the relationships between predictors and assess the levels of multi-collinearity between them, the variance inflation factor (VIF) was calculated using the "usdm" package (version 1.1–18). All VIF values were <3 indicating no problematic collinearity among the predictors (Dormann et al., 2013).

2.3. HSI modelling

2.3.1. Fitting suitability index (SI) models

The data of each environmental variable was divided into equal intervals and the mean CPUE of each interval was found (Hua et al., 2020). A spline regression was then fitted between mean CPUEs (as the response) and average interval values of the variable (as the predictor) using the mgcv function of the mgcv package (Wood, 2017). Next, the fitted CPUEs were normalized to the interval [0,1] using the following equation:

$$\widehat{SI}_i = \frac{\widehat{CPUE}_i - \widehat{CPUE}_{min}}{\widehat{CPUE}_{max} - \widehat{CPUE}_{min}} \quad (2)$$

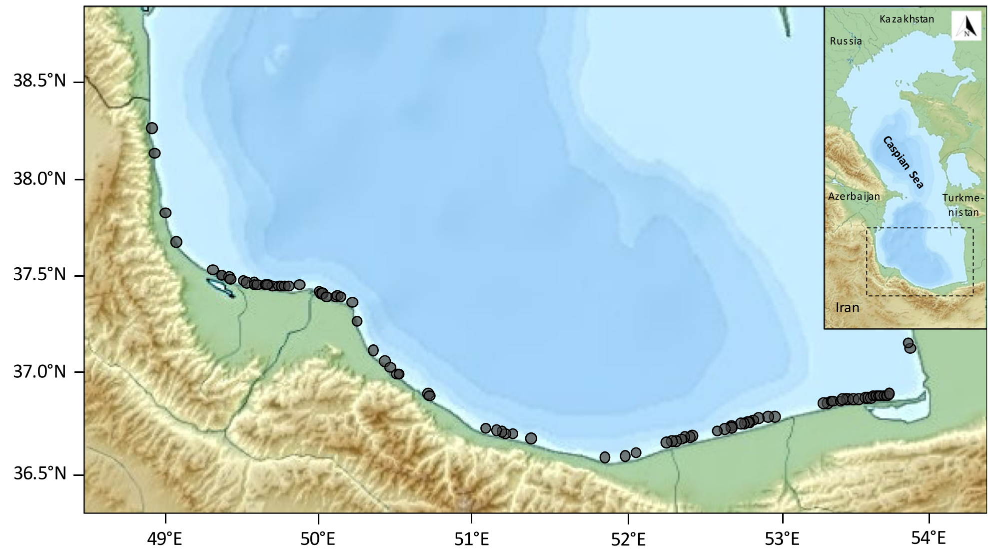

Fig. 1. The distribution of fishing points (•) along the southern coast of the Caspian Sea during 2002/3–2011/12 catch seasons.

where $\widehat{SI}_i$ is the estimated SI score for the ith value of the predictor variable; $\widehat{CPUE}_i$ is the fitted mean CPUE for the ith value of the predictor variable; and, $\widehat{CPUE}_{max}$ and $\widehat{CPUE}_{min}$ are the maximum and minimum fitted mean CPUE for the whole range of a given predictor. The optimum range of each variable was defined as $\widehat{SI}_i$ scores ≥ 0.6 (Hsu et al., 2021).

2.3.2. Habitat suitability index (HSI) model development

$\widehat{SI}_i$ of the n significant predictors (with P-value < 0.05) were used to calculate the HSI using five empirical methods: arithmetic mean model (AMM; Chen et al., 2010), geometric mean model (GMM; Tian et al., 2009), continued product model (CPM; Grebenkov et al., 2006), minimum model (MINM; Van der Lee et al., 2006), and maximum model (MAXM; Chen et al., 2012):

$$\widehat{HSI}_{AMM} = \frac{1}{n}\sum_{i=1}^{n}\widehat{SI}_i \tag{3}$$

$$\widehat{HSI}_{GMM} = \sqrt[n]{\prod_{i=1}^{n}\widehat{SI}_i} \tag{4}$$

$$\widehat{HSI}_{CPM} = \widehat{SI}_i \times \cdots \times \widehat{SI}_n \tag{5}$$

$$\widehat{HSI}_{MINM} = \min\left(\widehat{SI}_i \ldots \widehat{SI}_n\right) \tag{6}$$

$$\widehat{HSI}_{MAXM} = \max\left(\widehat{SI}_i \ldots \widehat{SI}_n\right) \tag{7}$$

2.4. Generalized additive model (GAM)

As alternative approach, a Gaussian generalized additive model was fitted between log-transformed CPUE and the environmental variables using mgcv function of the mgcv package with default settings (Wood, 2017):

$$\log10(\mathrm{CPUE}) \sim s(\mathrm{SST}) + s(\mathrm{CHL}) + s(\mathrm{ASL}) + s(\mathrm{PIC}) + s(\mathrm{POC}) + s(\mathrm{Aspect}) + s(\mathrm{Slope}) + s(\mathrm{Depth}) + s(\mathrm{Distance}),$$

where s() indicates the default penalized thin-plate regression spline function.

2.5. Model validation

To compare the HSI-scores with the predicted values of GAM, the observed CPUEs were also normalized, which is called the relative biomass index (RBI) hereafter:

$$RBI = \frac{CPUE_{ij} - CPUE_{min}}{CPUE_{max} - CPUE_{min}} \tag{8}$$

where $CPUE_{ij}$ is CPUE at the ith fishing point for the jth year; $CPUE_{min}$ and $CPUE_{max}$ are, respectively, the lowest and the highest CPUE among all fishing points and years. Therefore, a RBI with a value of 0 or 1 represent the fishing points with the lowest or highest probability of fish occurrence/biomass, respectively.

For both HSI and GAM, the data of the first eight years of the study were used for training and the rest for testing. The performance of HSI models was assessed by three statistical measures: Akaike's information criterion (AIC), root mean squared error (RMSE), and mean absolute error (MAE). AIC scores were calculated as below (Burnham and Anderson, 2002, 2004):

$$AIC = n \cdot ln\left(\frac{RSS}{n}\right) + 2 \cdot k \tag{9}$$

where: RSS is the residual sum of squares, n is the number of observations, and k is the number of predictors. Residuals of HSI models were calculated as the difference between RBI and HSI scores (Vayghan et al., 2013). If $\frac{n}{k} < 40$, AIC_c was calculated as a bias-adjusted version of AIC:

$$AIC_c = n \cdot ln\left(\frac{RSS}{n}\right) + 2 \cdot k + \left(\frac{2 \cdot k \cdot (k+1)}{n-k-1}\right) \tag{10}$$

RMSE and MAE values were obtained using the below formulae:

$$RMSE = \sqrt{\frac{\sum_{i=1}^{N}(x_i - \hat{x}_i)^2}{N}} \tag{11}$$

$$MAE = \frac{\sum_{i=1}^{N}\left|x_i - \hat{x}_i\right|}{N} \tag{12}$$

The predictive performance of the best HSI model and the GAM were evaluated using normalized RMSE (nRMSE) and normalized MAE (nMAE) scores of the testing data, obtained as below:

$$nRMSE = RMSE/\left(x_{max} - x_{min}\right) \tag{13}$$

$$nMAE = MAE/\left(x_{max} - x_{min}\right) \tag{14}$$

where: x_{max} and x_{min} are, respectively, the maximum and the minimum of the observed data. Also, the relationships between

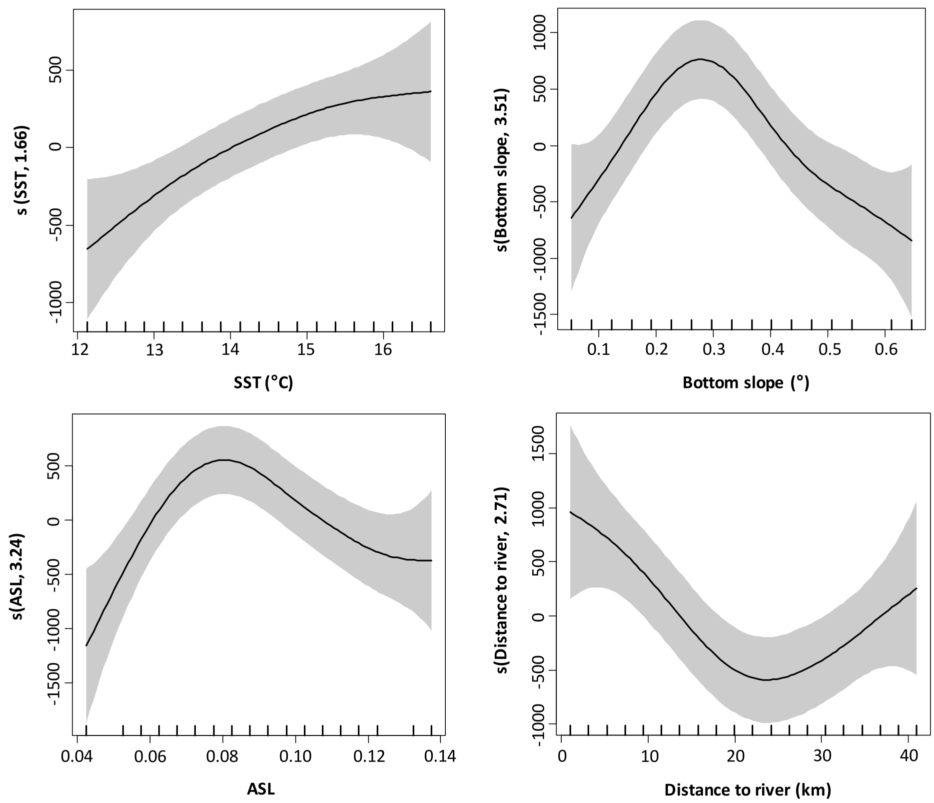

Fig. 2. Mean-centred effect plots of SI models for the significant habitat variables. Smoother fits: solid line; 95% confidence intervals: shaded area.

Table 1
A summary of fitted univariate suitability index (SI) models for habitat predictors using spline regression method.

Predictor	Deviance explained (%)	*P*
SST (°C)	78.4	<0.001
Bottom slope (°)	74.0	0.001
ASL (–)	60.6	0.003
Distance to river (km)	59.6	0.021
Coastline aspect (°)	24.9	0.134
POC (mg m^{-3})	20.2	0.183
Depth (m)	64.8	0.266
PIC (mol m^{-3})	54.7	0.359
CHL (mg m^{-3})	0.21	0.832

RBI scores and final HSI and normalized fitted values of GAM (calculated using the same equation of RBI) were assessed through fitting linear models and correlation test.

3. Results

3.1. HSI modelling

3.1.1. SI models

The SI regressions models for SST, bottom slope, ASL and distance to rivers were significant (Table 1). The highest percentage of deviance were belonged to SST (78.4%) and bottom slope (75.0%).

Habitat suitability increased linearly with increase of sea surface temperature while for bottom slope and aerosol density the relationship exhibited a clear peak (Fig. 2). Thus, *R. kutum* preferred the substrates with a slope of ∼0.25° and the aerosol densities of ∼0.08. In contrast, habitat suitability decreased in locations far from river inlets up to a distance of 20 km where it levelled off. However, there was an uptick at distances >30 km (Fig. 2, bottom right).

Table 2
HSI methods' performance indices. AIC (Akaike's Information Criterion); RMSE (Root mean squared error); MAE (mean absolute error).

Model	AIC	RMSE	MAE
CPM	−2200.3	0.236	0.193
MINM	−1714.4	0.312	0.239
GMM	−1054.4	0.493	0.443
AMM	−917.8	0.559	0.524
MAXM	−414.4	0.761	0.740

Table 3
A summary of GAMs (adjusted R^2 = 0.307; deviance explained = 33.8%).

Predictor	Deviance explained (%)	P value
Coastline aspect (°)	37.2	<0.001
PIC (mol m^{-3})	13.6	<0.001
Bottom slope (°)	12.7	<0.001
Distance to river (km)	9.13	<0.001
Depth (m)	8.72	<0.001
SST (°C)	8.69	<0.05
ASL	5.54	<0.001
CHL (mg m^{-3})	4.46	<0.01
POC (mg m^{-3})	–	0.950

3.1.2. HSI model

The continued product model (CPM) had the lowest scores of AIC, RMSE and MAE (Table 2) and thus was the best for predicting habitat suitability.

3.2. GAM

Coastline aspect and PIC were the most important factor in the GAM (Table 3).

The smoothers of the GAM components are depicted in Fig. 3. The fishing points with northern orientation (i.e. aspect: 0°–40° and 330°–360°) had the highest abundance/biomass of fish. The

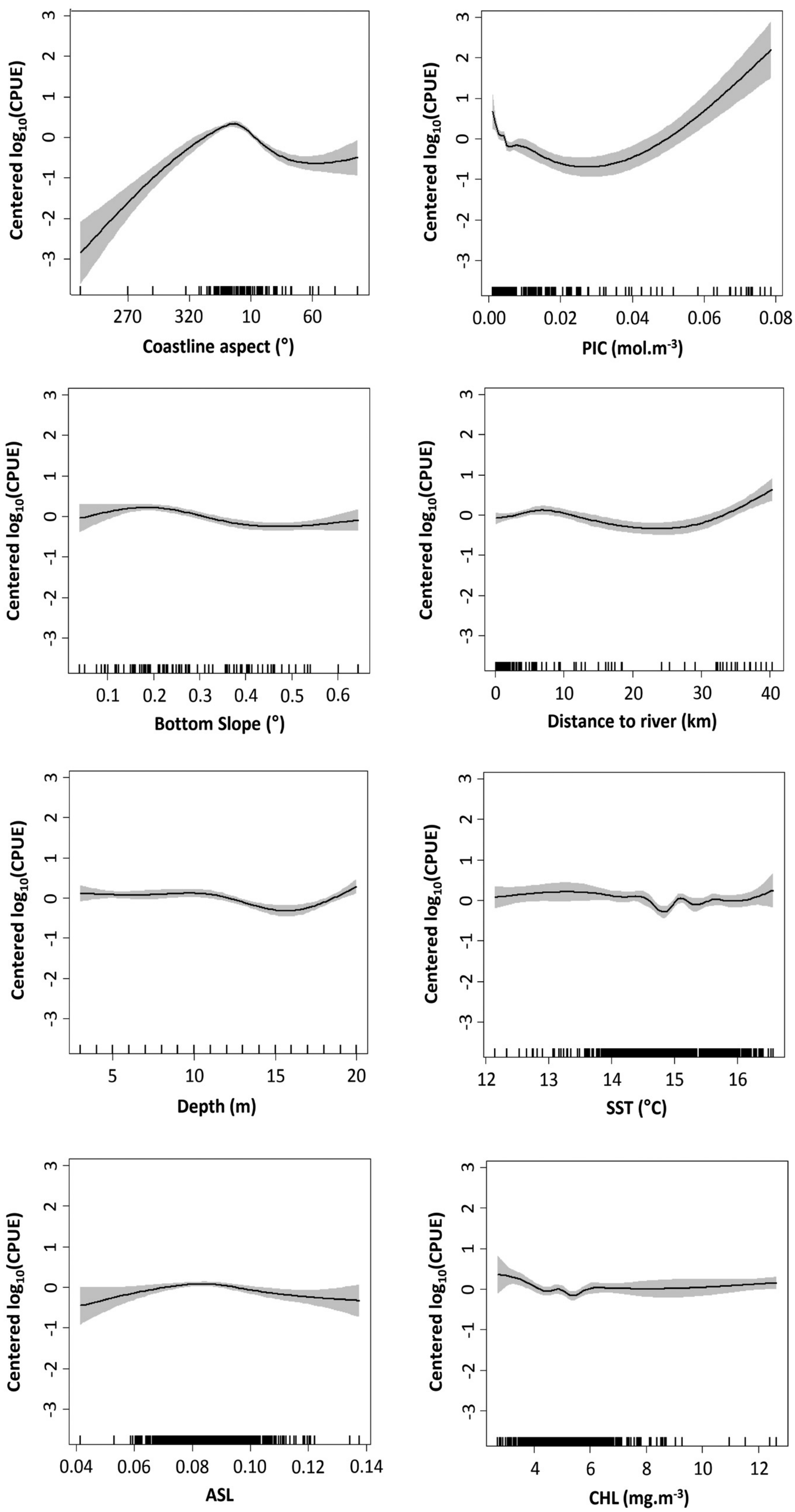

Fig. 3. Partial dependence plots for the additive effects of habitat predictors on $\log_{10}$(CPUE). Smoother fits: solid line; Approximate 95% confidence intervals: shaded area. Rug indicates values of data points.

highest presence of fish was found in areas with the lowest concentrations of PIC (0.00–0.01 mol m^{-3}) followed by a sharp decrease with increase of PIC. The substrates with a slope of 0.1–0.3° were the preferred slope for the fish.

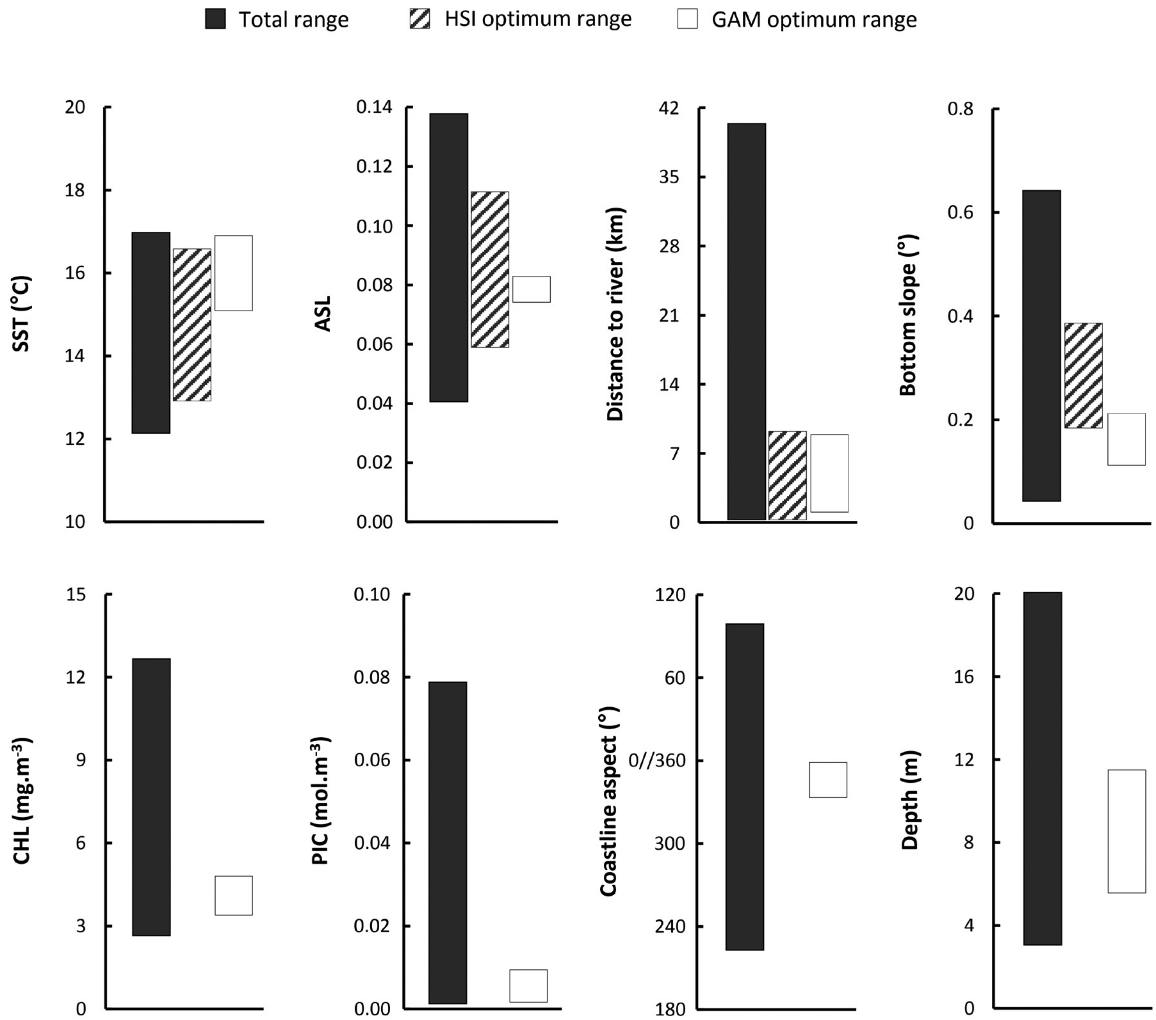

Fig. 4. The preferred ranges of significant environmental parameters based on the HSI and GAM models. SST, ASL, distance to rivers and bottom slope were significant for both models, but CHL, PIC, coastline aspect and depth were only significant in GAM.

3.3. Preferred ranges of environmental parameters

The preferred ranges of the environmental parameters were corresponded to the top 40% of HSI and GAM fitted values (Fig. 4). Apart from SST, models always estimated a smaller and non-random use of environmental conditions within the available (black in Fig. 4). For the common predictors (i.e. SST, ASL, distance to rivers, and bottom slope), much narrower optimum ranges were obtained for the GAM, were included in the preferred ranges of the HSI model.

3.4. Model performance and validation

The nRMSE and nMAE values of the GAM for testing data were lower than those of the HSI (nRMSE: 0.165 vs. 0.277; nMAE: 0.125 vs. 0.216). There was a greater correlation between RBI and GAM predicted values rather than RBI and HSI predicted values (0.57 vs. 0.37; Fig. 5). A linear regression between RBI and the predicted values of GAM or HSI indicated that GAM prediction was less-unbiased than that of HSI, with lower intercept value ($\alpha = 0.06$) and higher slope ($\beta = 0.57$), in contrast to those of the HSI ($\alpha = 0.12$; $\beta = 0.35$).

3.5. Spatiotemporal habitat quality distribution

Spatiotemporal distribution of habitat quality scores for both models, as well as RBI values, showed that eastern coastal fishing points offered the preferred habitat condition for the fish (RBI $\geq$ 0.6) over the catch seasons of 2005/6 to 2010/11 (Fig. 6). HSI output presented a wider extent as having optimum habitat quality, which indicates model over-estimation, compared to GAM which had more temporally accurate prediction and consistency with RBI.

4. Discussion

The present study used commercial beach seine catch data to find the environmental parameters influencing the distribution of Caspian Kutum along the northern Iranian coast of the Caspian Sea. Compared to prior studies on habitat preference of Caspian Kutum, which was based on research trawl surveys data (Vayghan et al., 2013, 2016), our dataset had wider temporal and geographical ranges being collected from fixed fishing locations, that can lead to better understanding of fish habitat preference and modelling performance. Also, most fisheries activities, such as trawl fishing, tend to concentrate on limited areas with high quantities of fish stocks (Yu et al., 2018) and the yielding data may hence bias fish distribution and habitat models.

Among the fitted HSI models, HSI_{CPM} had the best performance with the lowest predictive error despite its reported weaknesses in fish distribution prediction compared to other HSI calculating methods (Gong et al., 2011; Li et al., 2016; Xue et al., 2017; Yu et al., 2018). However, GAM predicted the testing data

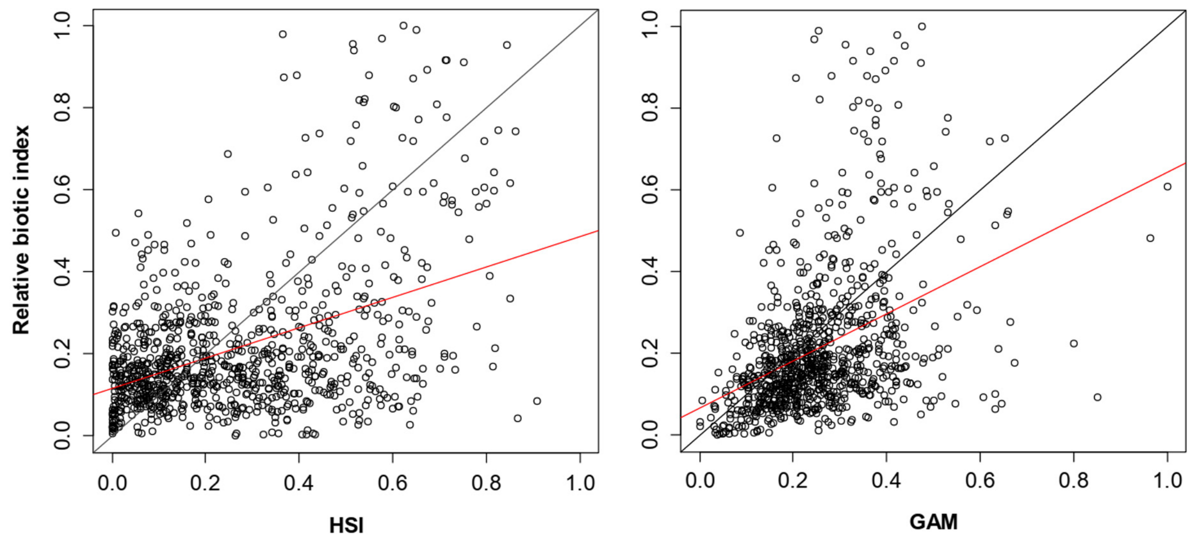

Fig. 5. Scatter plot of the relative biomass index (RBI) values (observed habitat quality index) and normalized GAM and HSI fitted values (predicted habitat quality index) for the period of 2002/3–2011/12. Red line: best linear model fit; Black line: perfect model. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

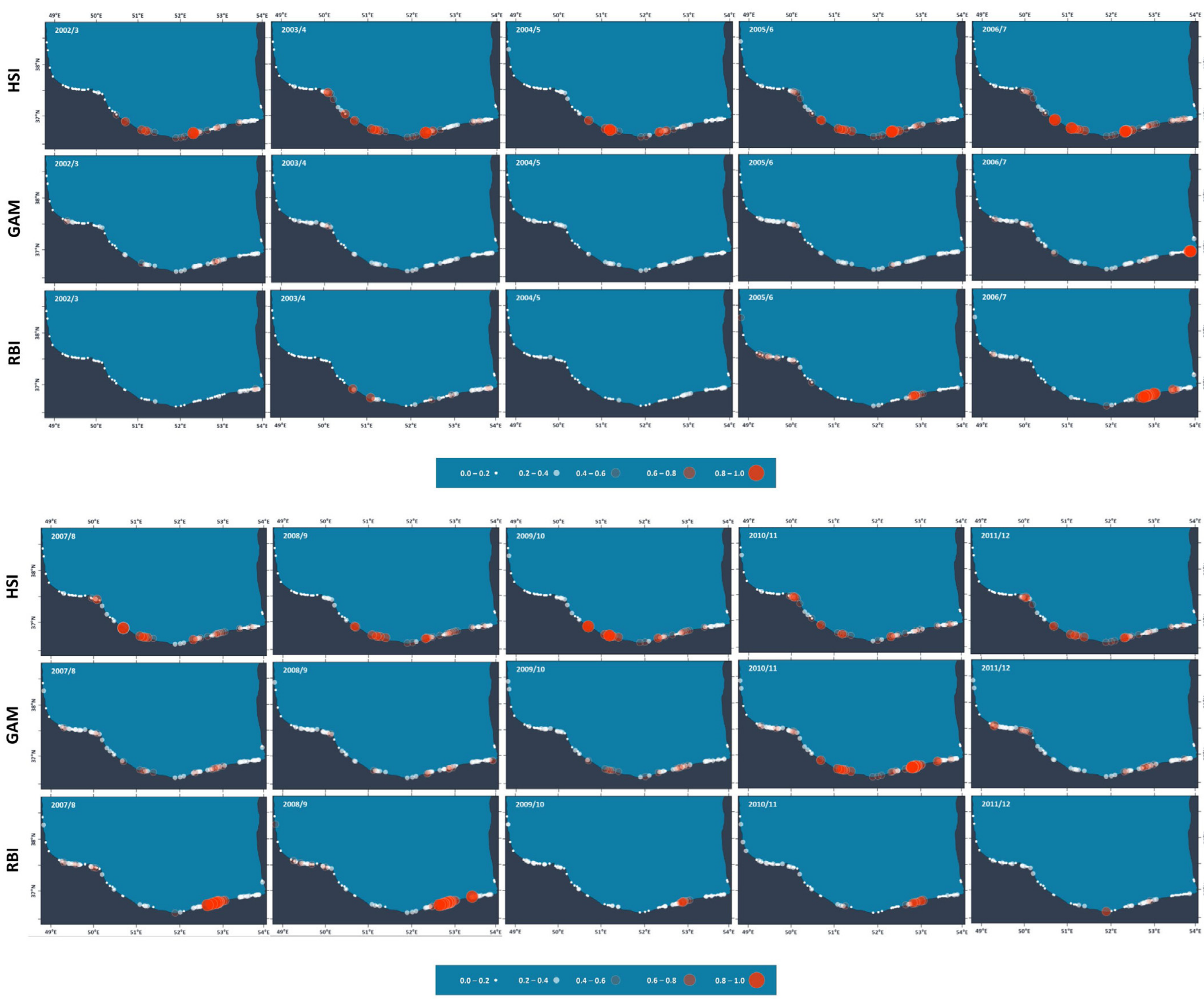

Fig. 6. Spatio-temporal distribution of HSI, normalized GAM fitted values, and RBI over fishing locations during the catch seasons 2002/3–2011/12.

more accurately than HSI. The GAM indicated a smaller range of the predictors as the optimum range than the HSI_{CPM} and had more accurate performance based on explained deviance with greater predictability. Furthermore, the predicted values from the HSI_{CPM} suggested that this model overestimated habitat suitability over most fishing points (Fig. 6) which has been reported in previous studies on HSI models (Gong et al., 2011; Yu et al., 2018). Basically, GAM uses non-parametric smoothing functions with non-normal error terms in explaining complex responses (Ahmadi-Nedushan et al., 2006; Swartzman et al., 1995; Leathwick et al., 2006; Knudby et al., 2010). This method is reported as a model with high flexibility in describing relationships between biomass and environmental variables (Ahmadi-Nedushan et al., 2006; Jowett and Davey, 2007; Murase et al., 2009).

In this study, the models highlighted different variables as the principal drivers of habitat suitability for Caspian Kutum, i.e. SST and bottom slope in HSI_{CPM}, and coastline aspect and PIC in the GAM. Selection of predictors and how to use them in explaining response variations has high importance in determining model performance and reliability (Dambach and Rödder, 2011; Su et al., 2020). In HSI modelling, all model predictors are independently incorporated into the model structure and have equal importance to the response variable (Beecher et al., 2002). Also, the SI models are highly dependent on class numbers and the midpoint of the response parameter in each class (Li et al., 2016). Stratifying predictors' ranges and summing up the response values (here CPUEs) over each predictor interval into only one score resulted in drastic losses of variance in response data. This simplifying process of data could lead to non-significant predictor–response relationships (as the case for coastline aspect, POC, depth, PIC and CHL in our analysis). Therefore, some predictors with real explanatory potential could be excluded from the final HSI model. Furthermore, the obtained significant fitted SIs would not be good representatives of the whole variation in the response parameter. In the GAM modelling, on the other hand, all of the predictors were used to describe the total variance of data, and consequently the additive effect of simultaneous use of their smoothed functions (even of predictors with the lowest explanatory potentials) led to a final GAM model with higher descriptive and predictive power. Such approaches to fitting HSI and GAM models resulted in different main predictors and changes in their importance levels in the GAM model (as also reported by Su et al. (2020)).

The SST has frequently been found as a factor having a substantial effect on fish occurrence (Chen et al., 2012; Froeschke and Froeschke, 2011; Hua et al., 2020; Maravelias et al., 2007; Menezes et al., 2006; Olsen, 2019; Perry et al., 2005); However, Vayghan et al. (2013, 2016) did not report it as an influencing predictor on the Kutum distribution. Such difference may be related to different modelling techniques in these studies because the GAM model also indicated that the SST had a low influence on fish abundance.

Among topographical predictors, bottom slope and aspect of coastline had high power in explaining Kutum distribution in HSI_{CPM} and GAM models, respectively. The influence of slope in shallow areas was in agreement with other studies on benthophagus fishes (Menezes et al., 2006; Parin et al., 2010; Parra et al., 2017). The slope may determine the hydrodynamics of the sea substrate and the current condition impacting fish distribution (Parra et al., 2017). This factor was also found to greatly affect the fish biomass in our GAM model. The GAM indicated that aspect had the greatest influence on fish abundance. Hence, Caspian Kutum preferred substrates with a northern orientation. Aspect is one of the main morphological features of aquatic systems that affects the distribution and diversity of aquatic fauna directly through light penetration and local hydrodynamic conditions (Bouchet et al., 2015; Parra et al., 2017; Pirtle et al., 2019; Stamoulis et al., 2018), and indirectly by influencing local productivity and food availability (Cameron et al., 2014; Moore et al., 2010; Pittman and Brown, 2011). In the GAM model, depth had low but significant importance on Kutum presence, while in prior studies by Vayghan et al. (2013, 2016), it was a predictor with the greatest influence on fish presence. This inconsistency is probably because of that the environmental extent of their studies included sampling places mainly with high depths despite that they finally reported a depth range lower than 22 (m) as the optimum range of this parameter for the fish, but most of our fishing points were located in areas with a mean depth of less than 20 (m). Therefore, depth was not an essential significant predictor in our analyses.

In the HSI_{CPM} model, ASL had an interesting relationship with Kutum presence. Deposition of atmospheric aerosols is one of the primary sources of nutrient elements that enter the aquatic ecosystems (Yang et al., 2019) that strongly impacts their nutrient limitation patterns and auto- and chemotrophic production (Jickells and Moore, 2015; Mahowald et al., 2018). It has been reported that atmospheric depositions of nutrients to coastal waters are large and equal to or exceed those of rivers (Duce et al., 1991; Rendell et al., 1993). Aerosol inputs occur all year round, while there are fluctuations in nutrients loads of riverine flows into the coastal regions (Spokes and Jickells, 2005). This feature has high importance in providing nutrients for autotrophic and heterotrophic production (Marañén et al., 2010; Romero et al., 2011), especially during stratification periods (Marín et al., 2017). Such an increase in water productivity can result in higher loads of organic matter in bottom water layers (Boyd et al., 2007) and enhance the secondary production of benthic fauna. This condition can affect the distribution of benthivorous fish species like Kutum. However, the aerosols simultaneously introduce toxicants to the water body (Gallisai et al., 2014; Kim et al., 2014), and their high inputs can negatively change water chemistry and limit aquatic organisms' distribution, especially in coastal waters, which was observed for Kutum over highest values of ASL.

The GAM model showed the highest abundance of Kutum in areas closest to the river mouth locations. Kutum has reproductive migrations towards river headwaters, and therefore, its aggregations near river inlets are not unexpected. Also, the river flows into marine regions can affect local water quality conditions (e.g. salinity), substrate gradients and food availability for fish (Froeschke et al., 2013; Froeschke and Froeschke, 2011).

The GAM model indicated that the areas with a low PIC concentration were the preferred habitat for Kutum. The relationship between this parameter and large-scale fish distribution has not been yet investigated. PIC, or $CaCO_3$, is an indirect index of autotrophic production in water bodies (Hopkins et al., 2019) used in the shells of marine organisms (Mitchell et al., 2017; Wilson et al., 2009). Elevated PIC concentrations in aquatic systems are related to the high export of organic carbon from dead bodies of organisms to the sea floor (Hopkins et al., 2019), leading to a higher biomass of benthic fauna. On the other hand, the PIC content of the water column has a critical role in light scattering, and its high levels can result in poor light penetration into deeper layers (Mitchell et al., 2017). In our study, the highest abundance of fish was related to the lowest PIC concentrations. Despite the nutritional effects of PIC, it can be said that its importance in the GAM model in explaining Kutum distribution in coastal waters could mainly belong to its impact on the physical environment of coastal waters by affecting light conditions.

CHL was the predictor with the lowest contribution in predicting Kutum abundance by the GAM model. The same situation for this variable has been reported by Vayghan et al. (2016). In some prior studies, chlorophyll-a concentration was an important factor in defining the habitat extent of juvenile fish and nursery grounds (Giannoulaki et al., 2013). Considering the selectivity of beach seine nets and the high contribution of larger fish in the catch composition of these nets, we can say that the low CHL importance in the GAM could be reasonably expected. However, prior studies have not considered this point (Johnson et al., 2013).

5. Conclusions

The present study was the first attempt to model the habitat quality of the *R. kutum* using commercial catch data collected over a long period. The modelling analyses showed the environmental habitat factors with strong connections with fish catch (i.e. SST, slope, PIC, and Aspect), the outperformance of GAM technique in habitat modelling with more accuracy and lower bias in predictions, and explicit dynamics in spatial and temporal habitat suitability conditions. These results provide the reliable information about the essential habitat requirements of the fish using remotely-sensed environmental data that can be used more effectively by Iranian fisheries managers to make appropriate policies and decisions to rehabilitate, conserve and/or exploit fish stocks.

CRediT authorship contribution statement

Fateh Moëzzi: Conceptualisation, Methodology, Formal analysis, Visualization, Writing – original draft. **Hadi Poorbagher:** Conceptualisation, Methodology, Formal analysis, Review and editing, Supervision. **Soheil Eagderi:** Conceptualisation, Review and editing. **Jahangir Feghhi:** Conceptualisation, Review and editing. **Carsten F. Dormann:** Conceptualisation, Methodology, Review and editing. **Sabah Khorshidi Nergi:** Data acquisition. **Kaveh Amiri:** Data acquisition.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Data availability

Data will be made available on request.

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