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ORIGINAL ARTICLE

Temporal habitat suitability modeling of Caspian shad (*Alosa* spp.) in the southern Caspian Sea

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ABSTRACT

*To comprehensively manage an ecosystem such as that of the Caspian Sea, the world's largest lake, detailed knowledge of the habitat traits of the living organisms in the ecosystem is essential. The present study examined environmental variables and used the Habitat Suitability Index (HSI) model to determine the most preferred seasonal habitat and optimal environmental range of Caspian shad (*Alosa *spp). The fish preferred deep waters with low levels of total organic matter and sea level anomaly in winter and productive areas with a high concentration of chlorophyll-a (Chl*a*) and relatively high benthos biomass in spring. The number per unit area (NPUA)-based HSI model determined that the geometric mean model (GMM) was the optimal model for defining a suitable habitat in winter. For spring, the arithmetic mean model (or GMM) in the NPUA-based HSI model most accurately predicted preferred habitat for Caspian shad. The average NPUA in both seasons increased with the HSI; areas with an HSI of between 0.4 and 0.6 in spring and between 0.6 and 0.8 in winter had a high percentage of total catch. Areas with an HSI of more than 0.5 had over 91% and 63% of the total catch in spring and winter, respectively, demonstrating the reliability of the NPUA-based HSI model in predicting Caspian shad habitat. The present study shows that remotely sensed data plus depth are the most critical environmental variables in Caspian shad habitats and that Chla and SLA are the most critical remotely sensed parameters for near real-time prediction of Caspian shad habitat.*

Key words: Caspian Sea; habitat suitability index (HSI) model; Caspian shad; ecosystem-based management; habitat modeling.

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INTRODUCTION

The Caspian Sea, bordered by five countries in West Asia, is the world's largest lake (Dumont, 1998) and provides both major economic resources, such as petroleum, gas, and caviar (Dumont, 1998), and ecological challenges (Nasrollahzadeh, 2010). The lake is generally divided into northern (25%), middle (36%), and southern (39%) areas (Nasrollahzadeh *et al.*, 2008). The southern area is the largest and deepest part of the lake (Tahami *et al.*, 2012). The ecosystem is unique because of the lake's many endemic and ancient fish species (*e.g.*, sturgeon), which are under increasing pressure as a result of inconsistent socioeconomic development across the five countries. An accurate overview of the lake's environmental traits and the habitat of its most economically valuable species is necessary for decision makers to initiate appropriate ecological policy for the Caspian Sea.

As part of efforts to conserve and restore declining fish stocks worldwide (Abell *et al.*, 2007; Thrush and Dayton, 2010), reducing allowable fishing catches (Worm *et al.*, 2009) and protecting essential habitat (Thrush and Dayton, 2010) have been proposed as the main mechanisms for maintaining a viable population of exploited species (Hermosilla *et al.*, 2011). The ecosystem-based fishery management (EBFM) framework has drawn attention to the effective management of marine environments (Brodziak and Link, 2002; Pikitch *et al.*, 2004). Implementing EBFM necessitates knowledge of essential habitats (Thrush and Dayton, 2010) for the conservation and restoration of fish stocks (Abell *et al.*, 2007; Thrush and Dayton, 2010). The effective management of living resources generally requires knowledge of the relevant ecosystem (Mangel *et al.*, 1996). A species' distribution and environmental affinities are essential to comprehending numerous aspects of its ecology, to its effective conservation and management (Hermosilla *et al.*, 2011), and to assessing how anthropogenic activity may affect it (Macleod *et al.*, 2008; Valavanis *et al.*, 2008). The geographical distribution of a species is critical to gaining a comprehensive knowledge of its populations, ecology, and management (Hermosilla *et al.*, 2011). Habitat Suitability Index (HSI) models are valuable ecological tools

(Schamberger *et al.*, 1982; Allen *et al.*, 1983; Vinagre *et al.*, 2006; Chen *et al.*, 2009) that can be used to rapidly assess the relative potential of a habitat and may be combined with geographical information system (GIS) data to evaluate the habitat of a species. HSI models use suitability indices (SIs) as a function of one or more individual habitat variables that are scored on a standard scale of 0-1 to indicate the quality and suitability of habitats (Brown *et al.*, 2000; Chen *et al.*, 2009; Tian *et al.*, 2009; Chen *et al.*, 2010). A composite HSI score is then computed with a range of 0-1, from unsuitable to optimal habitat (Brooks, 1997). The HSI models were developed to reflect the hypotheses of species-habitat relationships and facilitate environmental impact studies (Schamberger *et al.*, 1982). When combined with adequate data about key habitat variables, the models have successfully predicted changes in fish species' spatial patterns worldwide (Chen *et al.*, 2009; Tian *et al.*, 2009; Chen *et al.*, 2010; Chang *et al.*, 2013), including in the Caspian Sea (Haghi Vayghan *et al.*, 2013).

Alosa species are widely distributed in the Caspian Sea, Black Sea, Mediterranean Sea, and Atlantic Ocean. Caspian shad (*Alosa* spp) is a commercial fish species of the Clupeidae family and is widely distributed in the Caspian Sea, mostly in the western half and southern area of the Caspian Sea basin (Coad, 1995). Caspian shad, members of the valuable commercial herring family, are fed on by most predators in the Caspian Sea (*e.g.*, Caspian salmon and sturgeon) and compete for food with other herring species such as kilka (Abbasi and Sabkara, 2004; Abdollapour *et al.*, 2007). Caspian shad usually reach maturity at age 2-5 years and have a life span of up to 10 years, though these periods may differ between subspecies; the prevalent sizes and weights have been reported as 16-21 cm and 60-130 g, respectively, for males and 18-23 cm and 70-140 g, respectively, for females (Coad, 1995; Coad, 1997; Abdollapour *et al.*, 2007). *Alosa* spp naturally move to the northern waters of the Caspian Sea for spawning in spring, with migration peaks occurring in April and May. Some subspecies spawn in the open sea and some of them spawn in northern water (Whitehead *et al.*, 1985; Coad, 1995; Coad, 1997). Caspian shad have various seasonal habitat preferences, chiefly in the warmer and deeper waters of the south in winter, and move to the northern waters in spring to spawn and feed (Coad, 1995), which makes the species interesting for temporal habitat study. No previous studies have investigated the habitat preferences or optimal management strategies of the species to inform policy making for recovery programs, EBFM implementation, or marine spatial planning (MSP) (Foley *et al.*, 2010) in the Caspian Sea. However, the models applied in the present study enable the selection of the most critical explanatory variables, thus revealing the variables' optimal ranges and the species' temporal responses to variables changes and facilitating the creation of successful conservation and management programs in the Caspian Sea.

This study applied and compared four empirical HSI models to determine the most appropriate model and find out the SI's of selected remotely sensed and field variables in regard to winter and spring. The key variables in the spatial distribution of the Caspian shad in the southern Caspian Sea were also investigated, and the spatio-temporal habitat preferences of the target species were investigated to facilitate an effective conservation and management program in the Caspian Sea.

METHODS

Study area, fishery, and environmental data

The study area comprised the entire southern area of the Caspian Sea, which borders the Iranian provinces of Guilan, Mazandaran, and Golestan (Fig. 1). Daytime bottom trawl were performed in winter (152 trawls from 2009 to 2011) and spring (155 trawls from 2008 to 2010) by a Guilan research vessel. In total, 78 sites were considered for data collection. The total weight and number of specimens were recorded at each sampling station. In the present study, *Alosa* was recorded with average weights of 55.9±4.54 (means ±SE) and 155.7±14.49 (means ±SE) in spring and winter seasons, respectively. To determine stock abundance index, representing the habitat preference (Maunder and Punt, 2004; Tian *et al.*, 2009; Haghi Vayghan *et al.*, 2013), the catch per unit area (CPUA) and number per unit area (NPUA) of each site were calculated using an equation designed by Sparre and Venema (1998).

A set of environmental variables derived from remotely sensed and field sampling data was selected based on survey time (Tab. 1). The variables were assumed to be linked directly or indirectly to the biology and ecology of the Caspian shad.

Developing suitability index curves and Habitat Suitability Index models

Initially, the SI for every environmental variable was fixed to clarify the relationships between the environmental variables and abundance index (NPUA or CPUA) of the Caspian shad in spring and winter. The SI is continuous and ranges from 0 to 1. For the SI model, each abundance index was used as the response variable, and the environmental variable was used as the explanatory variable. One HSI model for both abundance indices (SI-CPUA and SI-NPUA) was examined for each season. Both scatter plot analysis and preliminary linear regression failed to detect a linear relationship between the environmental variables and CPUA (or NPUA) as response

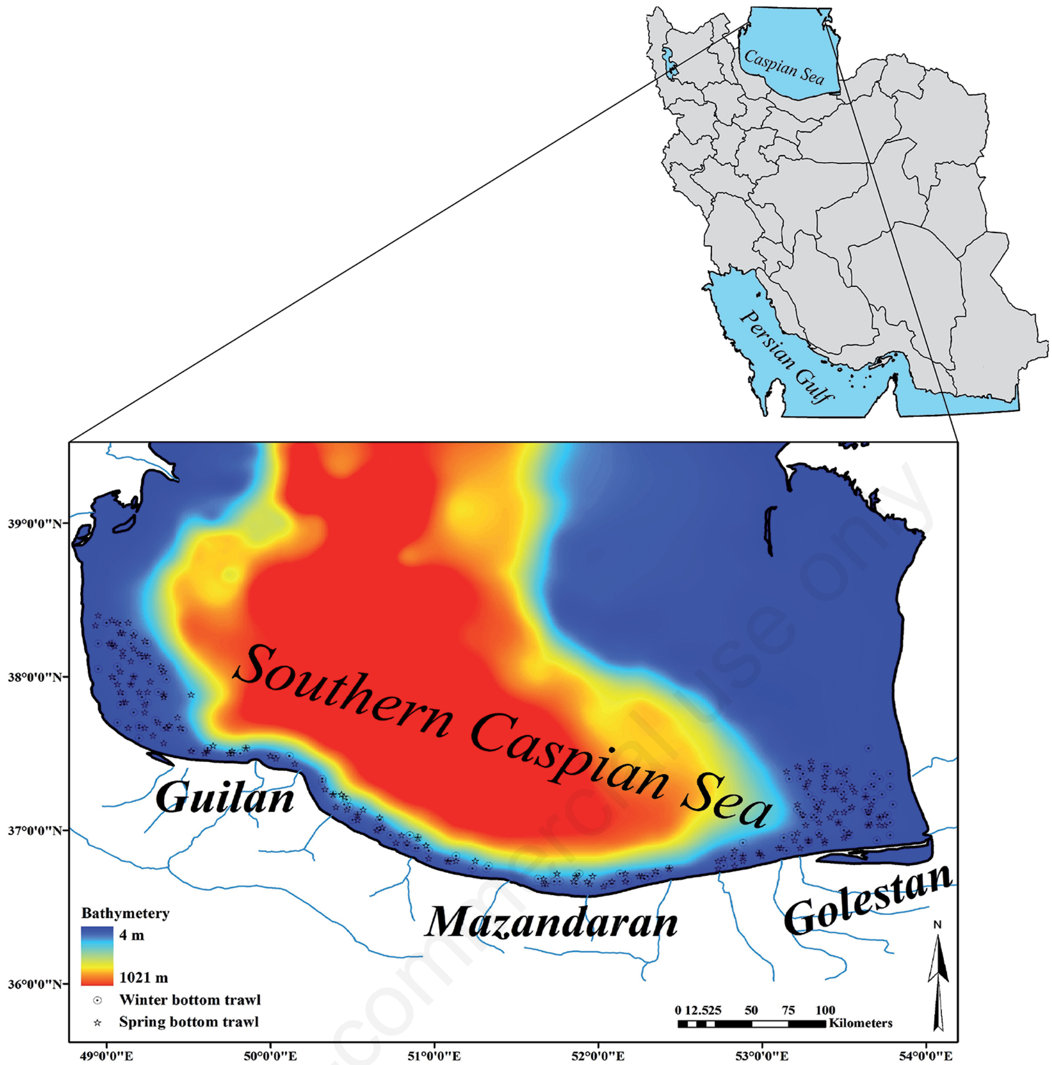

Fig. 1. Map showing the study areas of the southern part of the Caspian Sea and bottom trawl survey points of winter and spring.

Tab. 1. Data sources and description of environmental variables used as model inputs.

Parameter	Sensor/Model	Units	Resolution	Source/map
Remotely sensed data				
Sea surface temperature (SST)	MODISA	°C	0.0416667°	http://oceancolor.gsfc.nasa.gov
Photosynthetically active radiation (PAR)	MODISA	E/m²/d	0.0416667°	http://oceancolor.gsfc.nasa.gov
Sea level anomaly (SLA)	Merged Jason-1, Envisat, 2, GFO, T/P	cm	0.2942888°	www.jason.oceanobs.com
Sea surface Chlorophyll-a (Chl*a*)	MODISA	mg/m³	0.0416667°	http://oceancolor.gsfc.nasa.gov
Field sampling data				
Sediment total organic matter (TOM)	-	%	0.01°	Produced by author
Sand percent	-	%	0.01°	Produced by author
Depth	-	m	0.01°	Bathymetry map produced by author using CEP data (http://www.caspianenvironment.org)
Benthos biomass	-	g/m²	0.01°	Produced by author

variable; therefore, we examined nonlinear relationships (Hastie and Tibshirani, 1990; Guisan *et al.*, 2002; Zuur *et al.*, 2007). The spline smooth regression method was applied in the SI models by using S-PLUS ver. 8.0.4 to fit environmental variables and the CPUA (or NPUA) as smoother and response variables, respectively (Chen *et al.*, 2009; Tian *et al.*, 2009). The SI of each environmental variable was calculated using the following equation (Zuur *et al.*, 2007; Tian *et al.*, 2009):

$$SI = \frac{Y^{\wedge} - min\, Y^{\wedge}}{maxY^{\wedge} - minY^{\wedge}} \quad \text{(eq. 1)}$$

where $Y^{\wedge}$ is the predicted value of CPUA or NPUA, and $minY^{\wedge}$ and $maxY^{\wedge}$ are the minimum and maximum CPUAs or NPUAs of all predicted CPUAs or NPUAs, respectively.

The range of each environmental variable corresponding to SI values larger than 0.6 was considered optimal for the fish (Tian *et al.*, 2009). The SI values derived from each environmental variable were then integrated into the empirical HSI models.

The four most common empirical HSI models, namely the continued product model (CPM) (Grebenkov *et al.*, 2006; Chen *et al.*, 2009), arithmetic mean model (AMM) (Chen *et al.*, 2009; Tian *et al.*, 2009; Chen *et al.*, 2010), geometric mean model (GMM)(Lauver *et al.*, 2002; Tian *et al.*, 2009), and minimum model (MINM) (Van Der Lee *et al.*, 2006), were used to construct an optimal HSI model as follows.

The CPM:

$$\mathrm{HSI_{CPM}} = \prod_{i=1}^{n} \mathrm{SI_i} \quad \text{(eq. 2)}$$

The AMM:

$$\mathrm{HSI_{AMM}} = \frac{1}{n}\sum_{i=1}^{n} \mathrm{SI}_i \quad \text{(eq. 3)}$$

The GMM:

$$\mathrm{HSI_{GMM}} = \sqrt[n]{\prod_{i=1}^{n} \mathrm{SI}_i} \quad \text{(eq. 4)}$$

The MINM:

$$\mathrm{HSI_{MINM}} = \mathrm{Min}\ (\mathrm{SI_1}, \mathrm{SI_2}, \ldots, \mathrm{SI_n}) \quad \text{(eq. 5)}$$

where n is the number of environmental variables and SI_i is the suitability value associated with the i^{th} environmental variable. We weighted the environmental variables equally because we had no prior information on their relative importance in defining the habitat of Caspian shad. A forward selection (based on P-values) of different SI values was used to estimate the habitat availability for each HSI model.

Data recorded over 2 years were used to construct the models, and data from the following year were used to validate the models. The 4 HSI models were examined using the Akaike information criterion (AIC) (Akaike, 1974, 1981):

$$\mathrm{AIC} = n \times \ln\ (\mathrm{RSS}/n) + 2 \times K \quad \text{(eq. 6)}$$

When $n/k < 40$, a supplementary AIC ($\mathrm{AIC_c}$) was used to adjust for bias (Burnham and Anderson, 2004):

$$\mathrm{AIC_c} = n \times \ln(\mathrm{RSS}/n) + 2 \times K + (2 \times K \times (K+1))/(n-K-1) \quad \text{(eq. 7)}$$

where n, k, and RSS are the number of sampling points, number of variables, and residual sum of squares (RSS), respectively. The RSS was set as the discrepancy between the NPUA (or CPUA) and the NPUA (or CPUA) predicted by each HSI model. The predicted NPUA or CPUA was determined using a linear regression equation fitted between the HSI model and NPUA (or CPUA) as the independent and dependent factors. The model with the lowest AIC was considered the optimal model and selected for model testing and validation. When the difference in AIC between the two top-ranked models was negligible (Fotheringham *et al.*, 2003), the alternative model is introduced in parentheses.

The map predictions of the HSI models were then compared with the bottom trawl data recorded in spring 2010 and winter 2011 to evaluate the models' accuracy. Root mean square error (RMSE) was used to compare the forecasting errors of different HSI models (measure of accuracy) (Hyndman and Koehler, 2006), and residual sum of squarer (RSS) and mean square error (MSE) were used to determine the extent to which the models fit the data (Draper and Smith, 1998).

Data analysis and mapping

All remote-sensing satellite data and field data were prepared and calculated using ArcGIS Version 9.3 (ESRI) and ILWIS Academic ver. 3.1 were then used for spatial analysis and mapping the distribution of HSI values. Prior to the model development, all data were resembled to the same geographic datum (WGS 1984) and spatial extent. The final HSI map was calculated by performing the SI equation of selected explanatory variables and most appropriate modeling by using the spatial analyst extension in ArcGIS. The variance inflation factor (VIF) was used to examine multicollinearity to prevent model over fitting (Montgomery and Peck, 1982; Catterjee and Hadi, 2006; Montgomery *et al.*, 2007). Variables with a VIF of more than10 and highly correlated variables were excluded from the models.

RESULTS

Multicollinearity, optimal range, and suitability index of environmental variables

No strong correlations except for photosynthetically active radiation (PAR; in winter) and sea level anomaly (SLA; in spring) were detected in multicollinearity diagnostic analysis (Chatterjee *et al.*, 2000; Catterjee and Hadi, 2006), which supports the use of the rest of the environmental variables in the model (Tab. 2). The PAR variable was correlated to sea surface temperature (SST) (r=0.86) and SLA had a VIF of more than 10 in winter and spring; therefore, PAR and SLA were excluded from the modeling process in winter and spring, respectively. The depth, benthos biomass, and sand percentage SIs exhibited similar patterns in both types of modeling; by contrast, the other variables demonstrated anomalous trends in winter (Fig. 2). In spring, the SI curve had relatively similar trends in regard to both applied abundance index (Fig. 3). In both seasons, the SI values predicted that the preferred optimal ranges of the Caspian shad would differ according to environmental variables and season. Caspian shad preferred shallow waters with high Chl*a*, PAR, SST, and sand percentages in spring, in contrast to its winter preferences (Figs. 2 and 3).

Model selection

We used forward stepwise variable selection (based on P-values) to identify the most parsimonious model through the four empirical HSI models in each season (Tabs. 3 and 4). Goodness of fit was evaluated according to AIC and AIC_c (eqs. 6 and 7). In the top-ranked model, AIC showed very close together but benthos biomass, Chl*a*, and total organic matter (TOM) as explanatory variables in NPUA-based modeling gained low AIC value among the 4models, indicating that those explanatory variables by applying AMM (or GMM) represents the most accurate estimate of habitat suitability of the Caspian shad in spring (Tab. 4). In winter, NPUA-based modeling (AIC=25.56) with SLA, depth, and TOM using the GMM (or MIN) estimated habitat suitability most accurately (Tab. 3). The AMM (or GMM) in CPUA-based modeling (AIC=28.42) was also demonstrated as being suitable for estimating Caspian shad habitat suitability according to benthos biomass, depth, sand percentage, and Chl*a* in winter (Tab. 3).

Model validation

Based on compared errors (Tab. 5) and the AIC, the HSIs of spring and winter were estimated using an NPUA-based AMM and GMM, respectively. We produced GIS maps for both seasons according to the spatial analysis results of corresponding HSI values, which was performed by integrating SI equations (Fig. 4). The Pearson correlation showed relatively high correlations (r=0.64 and r=0.67 in spring and winter, respectively) between the map derived from the model and the validated points recorded the next year. A positive relationship among the average NPUA, percentage of the total catch, and HSI value was found. Scatter Plot with 95% confidence interval of percentage of catch (%) against the HSI values were shown that the correlation coefficient between two variables (percentage of catch (%) against the

Tab. 2. Multicollinearity diagnostic analysis (VIF) of environmental variables; range and optimal range of explanatory variables defined by the spline smooth regression method for the Caspian shad in the southern Caspian Sea in winter and spring.

Environmental variables	VIF	Range	Optimal	
		SI-NPUA or SI-CPUA	SI-NPUA	SI-CPUA
Winter				
Chl*a*	1.40	1.49 to 7.77	1.49 to 2.58	1.49 to 2.58 and 7.04 to 7.77
PAR	5.17	12.7 to 30.84	27.01 to 30.84	12.7 to 14.63
SST	4.86	5.50 to 13.74	12.23 to 13.74	5.50 to 7.96
SLA	1.30	-51 to -28	-36.4 to -28	-51 to -48.56
Depth	1.40	3.45 to 189.8	98.42 to 189.8	93.04 to 189.8
TOM (%)	1.46	1.79 to 4.46	1.79 to 2.48	1.79 to 2.43 and 3.64 to 4.46
Benthos biomass	1.31	4.63 to 151.78	4.63 to 44.25	4.63 to 66.88
Sand (%)	1.79	2.35 to 44.85	36.26 to 44.85	28.91 to 44.85
Spring				
Chl*a*	1.25	0.90 to 6.32	5.38 to 6.32	2.26 to 6.32
PAR	4.48	4.73 to 57.28	55.40 to 57.28	53.668 to 57.28
SST	3.23	17.5 to 23.67	19.62 to 22.8	20.49 to 23.67
SLA	11.28	-21 to -9	-14 to -9	-15.66 to -9.48
Depth	1.41	5 to 281.25	5 to 175.21	5 to 130.57
TOM (%)	2.43	1.87 to 4.63	1.88 to 3.57	1.87 to 2.9
Benthos biomass	1.69	7.92 to 174.94	19.73 to 105.77	34.91 to 97.33
Sand (%)	3.71	7.07 to 42.51	31.77 to 42.51	38.21 to 42.51

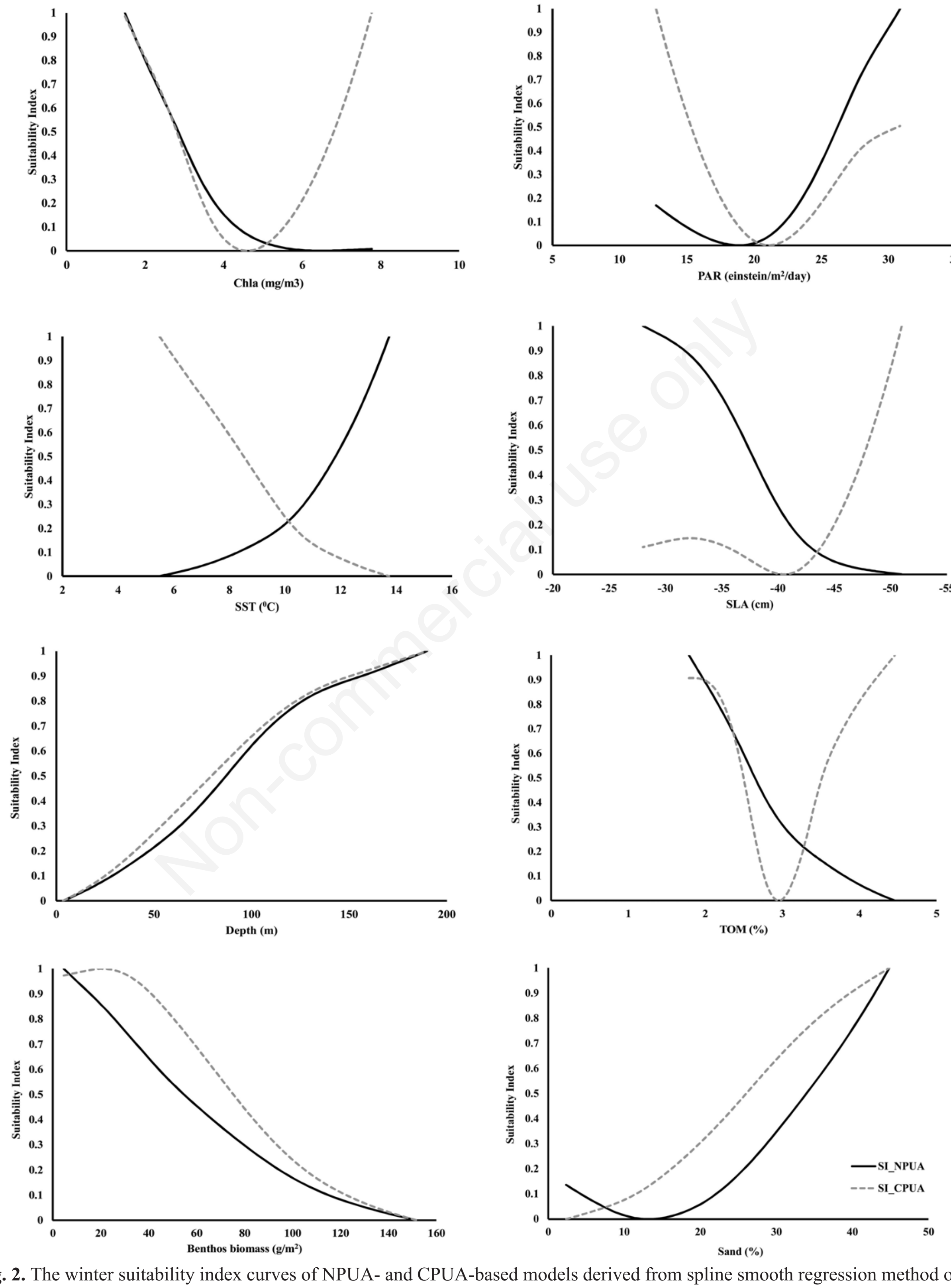

Fig. 2. The winter suitability index curves of NPUA- and CPUA-based models derived from spline smooth regression method of each environmental variable.

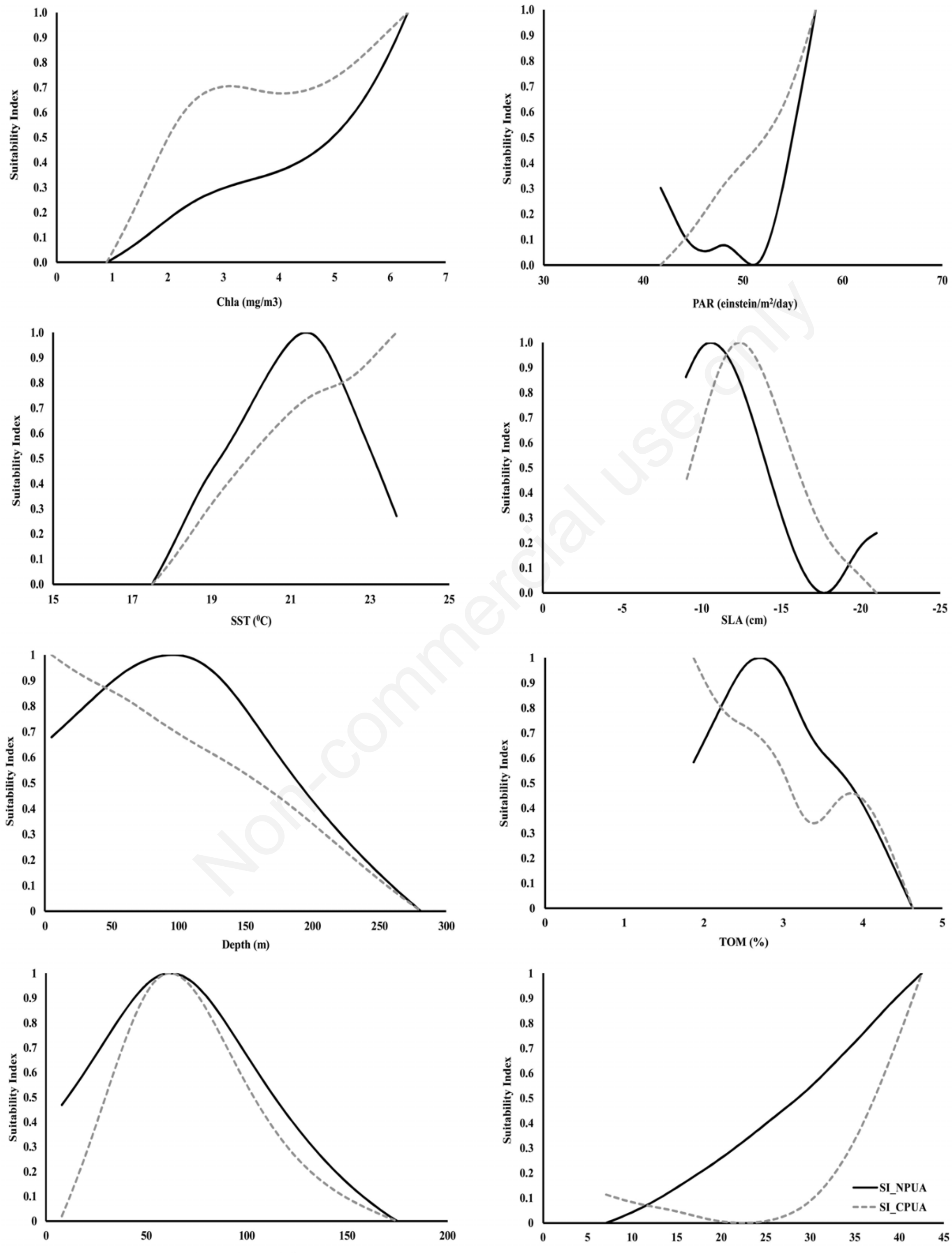

Fig. 3. The spring suitability index curves of NPUA- and CPUA-based models derived from spline smooth regression method of each environmental variable.

HSI values) were calculated to be 0.37 and 0.55 during spring and winter, respectively (P<0.05). In addition, the correlation coefficient between two variables (average NPUA against the HSI values) were registered to be 1.00 and 0.57 during spring and winter, respectively (P<0.05). The average NPUA of both seasons increased with the HSI; areas with an HSI of between 0.4 and 0.6 in spring and between 0.6 and 0.8 in winter had a high percentage of total catch.

Although a high percentage of total catch was caught in areas with an HSI of between 0.4 and 0.6, the NPUA exhibited higher values in areas with an HSI of more than 0.6, indicating that these areas are suitable habitats for Caspian shad in spring (Fig. 5). According to NPUA-based HSI modeling, Caspian shad have a seasonal preference of suitable areas regarding key explanatory variables in the southern Caspian Sea. Unfortunately, no sampling was conducted in areas with an HSI of more than 0.8 in both seasons and less than 0.2 in spring. Our results suggested that the AMM in spring and the GMM (or MIN) in winter based on NPUA data would reasonably predict suitable habitats for Caspian shad in the southern Caspian Sea.

DISCUSSION

The present study described the most preferred seasonal habitat and optimal environmental range of the Caspian shad by using HSI models. There were lack of available data on the biology, ecology, and habitat of the Caspian shad in the southern of Caspian Sea. Our results showed that the Caspian shad preferred different environments depending on the season. The fish preferred deep waters with low TOM and SLA levels in winter and productive areas with high Chl*a* and benthos biomass in spring. In winter, for the NPUA-based analysis, although the GMM had the lowest AIC, the AIC for the MINM was within 2 value, which is a negligible difference (Fotheringham *et al.*, 2003); thus the data provides approximately equal support for these two models. For spring, the AMM

Tab. 3. Forward stepwise selection of variables and the goodness of fit (AIC) test for selecting the most accurate model (top-ranked models) in winter.

NPUA-based				CPUA-based			
Variable(s) in model	Model	AIC	ΔAIC	Variable(s) in model	Model	AIC	ΔAIC
SLA, depth, TOM	GMM	25.56	0.00	Ben, depth, sand, Chl*a*	AMM	28.42	0.00
SLA, depth, TOM	MIN	26.63	1.08	Ben, depth, sand, Chl*a*	GMM	28.52	0.09
SLA, depth, sand	AMM	32.63	7.07	Ben, depth, sand	AMM	30.87	2.45
SLA, depth	GMM	32.91	7.36	Ben, depth	AMM	31.84	3.42
SLA, depth, sand	MIN	33.48	7.92	Ben, depth, Sand, Chl*a*	MIN	32.61	4.19
SLA, depth, TOM, sand	MIN	33.89	8.33	Ben, sand	AMM	34.26	5.84
SLA, depth, TOM	AMM	34.12	8.56	Ben, depth, sand	GMM	34.37	5.95
SLA, depth	AMM	34.34	8.79	Ben, depth	GMM	35.99	7.57
SLA, depth, TOM, sand	AMM	34.78	9.22	Ben, sand	GMM	37.94	9.52
SLA, depth, TOM	CPM	35.04	9.49	Ben		40.14	11.72

Tab. 4. Forward stepwise selection of variables and the goodness of fit (AIC) test for selecting the most accurate model (top-ranked models) in spring.

NPUA-based				CPUA-based			
Variable(s) in model	Model	AIC	ΔAIC	Variable(s) in model	Model	AIC	ΔAIC
Ben, Chl*a*	AMM	-22.97	0.00	Ben, sand	AMM	-19.36	0.00
Ben, Chl*a*	GMM	-22.53	0.44	Ben, Chl*a*	AMM	-19.19	0.16
Ben, Chl*a*, TOM	GMM	-20.92	2.05	Ben, Chl*a*, TOM	CPM	-18.88	0.48
Ben, Chl*a*, TOM	AMM	-19.94	3.03	Ben, sand, Chl*a*	AMM	-18.87	0.48
Ben, Chl*a*	CPM	-17.68	5.29	Ben, Chl*a*	GMM	-18.78	0.58
Ben, Chl*a*, TOM	CPM	-17.65	5.31	Ben		-18.61	0.75
Ben, Chl*a*, Sand	AMM	-17.04	5.92	Ben, TOM	AMM	-18.49	0.86
Ben		-16.28	6.68	Ben, Chl*a*, TOM	AMM	-18.46	0.89
Ben, Chl*a*, Sand	GMM	-15.87	7.10	Ben, Chl*a*	CPM	-18.29	1.07
Ben, depth	CPM	-15.68	7.29	Ben, Chl*a*, TOM	GMM	-17.57	1.79

Tab. 5. Compared errors of selected NPUA-based models derived from goodness of fit (AIC) selection in winter and spring.

Model (parameters)	RSS	MSE	RMSE	R
Winter				
NPUA-based GMM HSI (SLA, depth, TOM)	85.93	0.82	0.91	0.74
Spring				
NPUA-based AMM HSI (Ben, Chl*a*)	17.41	0.36	0.60	0.77

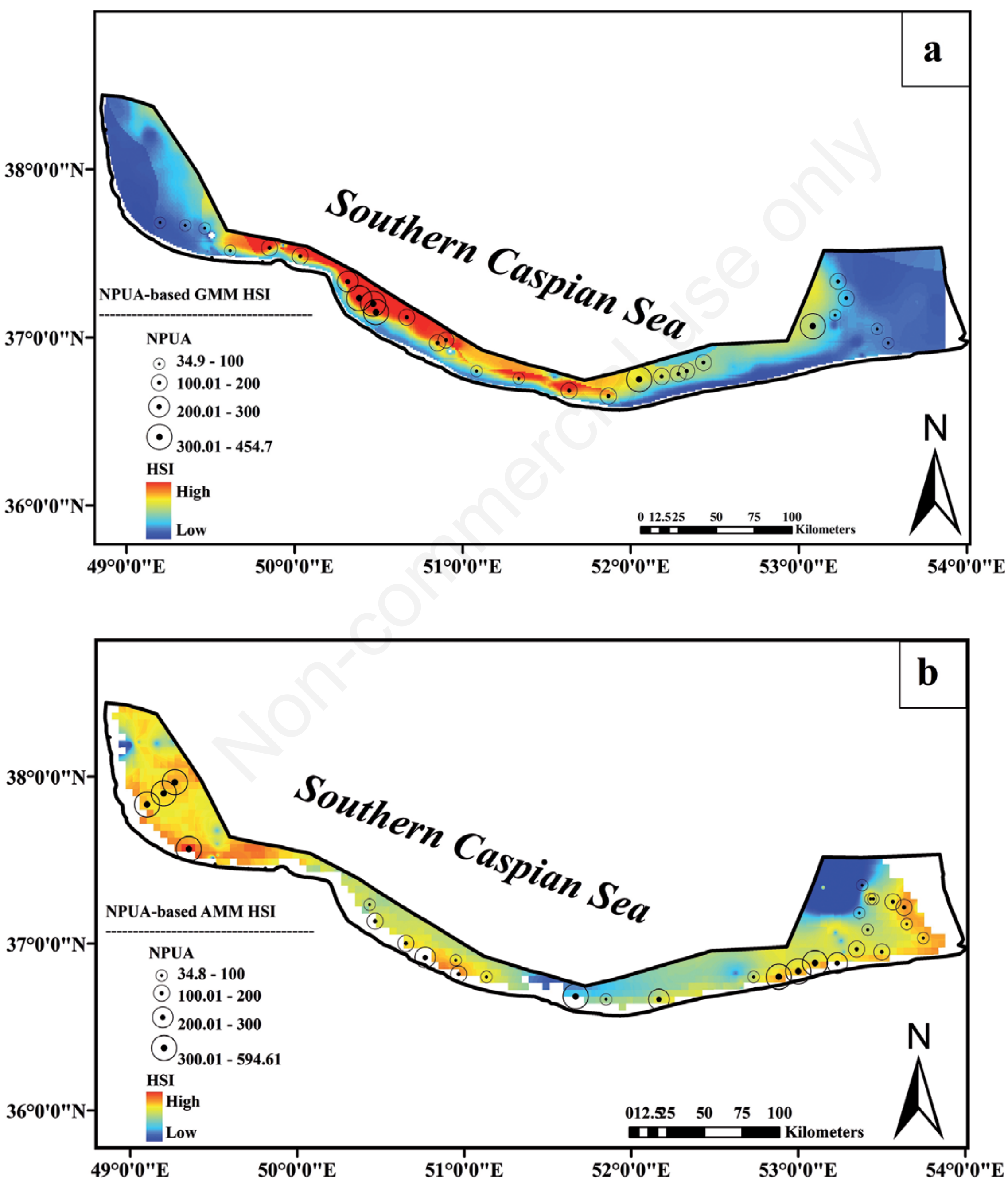

Fig. 4. The spatial distribution of (a) the NPUA-based GMM HSI and the measured NPUA in winter 2011and (b) the NPUA-based AMM HSI and the measured NPUA in spring 2010.

(or GMM) in NPUA-based HSI modeling was the most accurate model in predicting Caspian shad habitat by using benthos biomass and Chl*a*. In contrast to winter, the fish preferred areas with high Chl*a* and benthos biomass in spring. *Alosa* species in the Caspian Sea migrate seasonally to warmer and deeper water in winter and shallow water in spring for feeding and reproduction (Coad, 1995, 1997). Afraei Bandpei *et al*. (2006) reported that substrate type and temperature mainly affect the distribution of *Alosa* spp., with sandy substrates preferred by these fish. No studies have clearly determined how environmental effects influence fish distribution; however, our work demonstrates how fish might respond to environmental variables seasonally.

Chlorophyll is a proxy of biological productivity index in that it reflects the standing stock of phytoplankton in surface waters (Bellido *et al.*, 2008), which indicates marine productivity hotspots (Valavanis *et al.*, 2004) and can describe the habitat productivity of fish species (Chassot *et al.*, 2011). Furthermore, the Chl*a* index enables the characterizing of animal habitats (Polovina *et al.*, 2000; Kobayashi *et al.*, 2008) and is widely used in fish habitat modeling (Crec'hriou *et al.*, 2008; Valavanis *et al.*, 2008; Haghi Vayghan *et al.*, 2015). The Caspian shad in the southern Caspian Sea typically feed on zooplankton, phytoplankton, and benthic communities (*e.g.*, small fish, crab, shrimp, and benthic invertebrate); their intensive feeding period begins after reproduction ends in June (study time) (Abbasi and Sabkara, 2004; Abdollapour *et al.*, 2007; Coad, 2014). However, examining environmental varia-

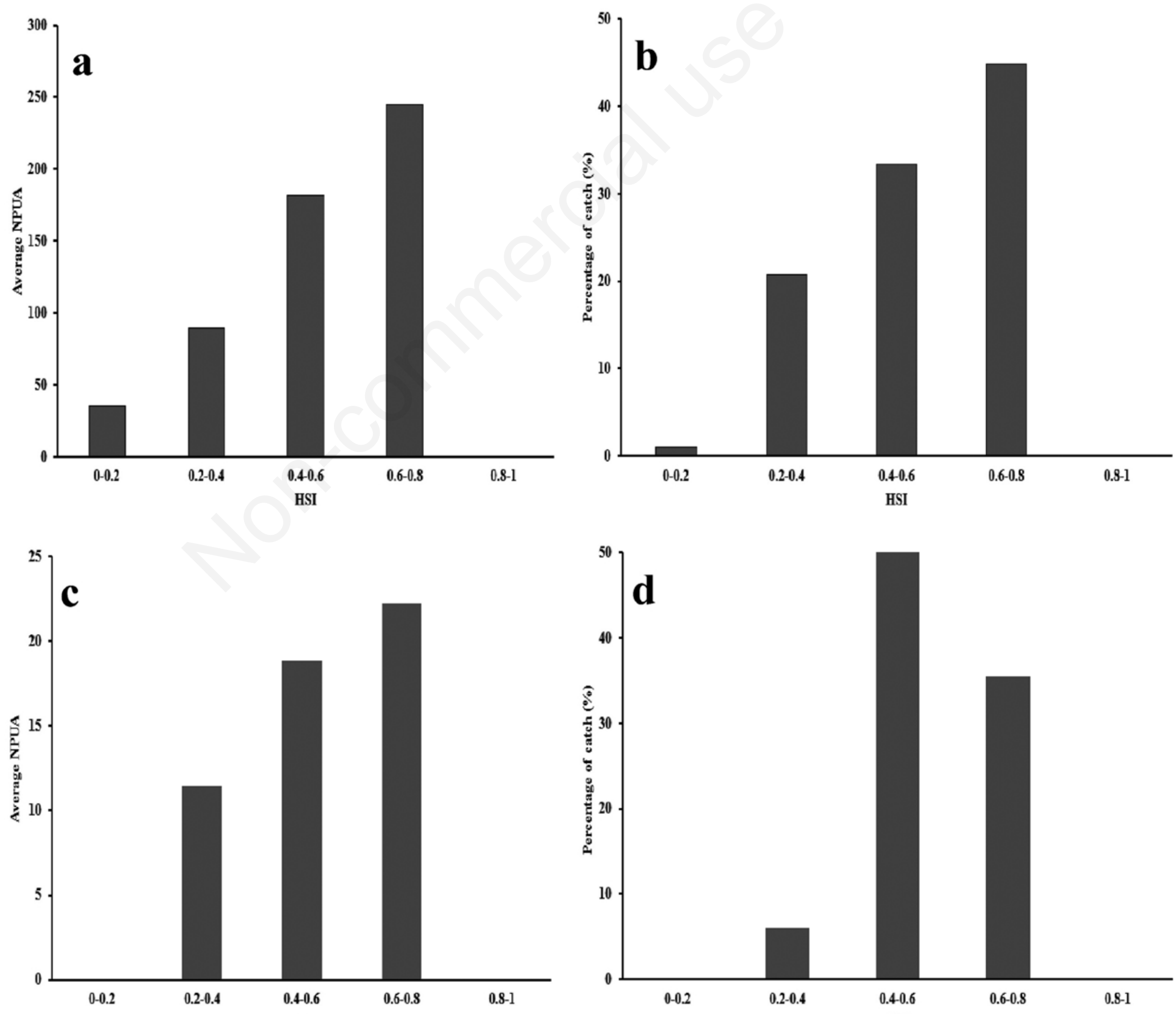

Fig. 5. The fluctuation of HSI values derived from the selected model, and the average NPUA (a, c) and percentage of total catch (b, d) in winter and spring, respectively.

bles by using the AMM (or GMM) with NPUA-based HSI models and the pattern of environmental variables in the SI curves contributed to the literature by determining Caspian shad spring habitat preferences in the southern Caspian Sea.

According to the NPUA-based GMM, Caspian shad preferred deeper, offshore waters and areas with less TOM and negative SLA (anticyclonic current). The SIs revealed that the fish selected deeper areas in offshore waters with lower TOM, benthos biomass, and Chl*a* levels. As a wintering location of numerous fish species, deep water naturally has a low concentration of nutrients and organic matter (Damalas *et al.*, 2010) and have been influenced suitable habitat of some fish such as Caspian kutum in the Caspian Sea (Haghi Vayghan *et al.*, 2013, 2015). Caspian shad prefer wintering in deeper waters in the southern Caspian Sea (Coad, 1995; Coad, 1997; Afraei Bandpei *et al.*, 2006), where temperature at deep water was at least two degree more than other season in the southern of Caspian Sea at winter time (Nasrollahzadeh *et al.*, 2013). The role of SLA has been demonstrated in fish habitat modeling (Valavanis *et al.*, 2008) as describes ocean processes (Larnicol *et al.*, 2002; Pujol and Larnicol, 2005), being useful in measuring productivity, and often influencing the distribution of species throughout their life stages (Giannoulaki *et al.*, 2008). Furthermore, SLA was found to be a predictor in fish habitat studies in the southern Caspian Sea (Haghi Vayghan *et al.*, 2013) and Mediterranean Sea (Crechriou *et al.*, 2008; Tserpes *et al.*, 2008).

However, discrepancies in the SI of SLA and some variables (*e.g.*, SST) in the NPUA- and CPUA-based HSI models in winter may be closely related to differences between NPUA and CPUA at the same sampling point (Fig. 2). A specific point (trawling station) with a low CPUA value may have a high NPUA value simultaneously as a result of a high abundance of small fish. Hence, areas with similar NPUAs and a high SI value in an NPUA-based model may exhibit a high abundance of small fish simply because they are preferred areas with low current speeds, low SLA, or even high SST; the inverse may be true for CPUA-based SI. Furthermore, the dominant current direction in the southern Caspian Sea is anticyclonic (negative SLA) (Gunduz, 2014) and Caspian shad may prefers low currents to save energy in winter, when food is scarce (Coad, 1995, 2014).

Interest is growing in species distribution modeling (Hirzel *et al.*, 2006) and many methods have been used to study the distribution of fish relative to explanatory variables (Guisan and Zimmermann, 2000; Brotons *et al.*, 2004; Guisan and Thuiller, 2005; Elith *et al.*, 2006; Austin, 2007; Valavanis *et al.*, 2008). HSI models summarize the relationship between species and their habitat, and analyze essential characteristics of suitable habitats that are correlated linearly with carrying capacities (Zohmann *et al.*, 2013). Equal influence, the independent inclusion of variables in model when defining habitat quality (Song and Zhou, 2010), and rapid habitat assessment tools enable HSI models to yield more accurate and realistic results compared with those obtained using statistical methods (Li *et al.*, 2014). Several methods have been applied to determine SI curves illustrating the relationships between SIs and environmental variables. The SI curves could be defined according to expert knowledge (Brown *et al.*, 2000) or a piecewise linear function (Vincenzi *et al.*, 2007), quantile regression (Feng *et al.*, 2007), spline smooth regression and nonlinear regression (Chen *et al.*, 2009; Tian *et al.*, 2009), cubic spline smoothing function (Chang *et al.*, 2012), or fuzzy chart analysis (Zohmann *et al.*, 2013). Nonlinear spline smooth regression method has been the most widely used method of quantifying SI curves worldwide (Chen *et al.*, 2009; Tian *et al.*, 2009; Chang *et al.*, 2013; Li *et al.*, 2014), including for Caspian Sea studies (Haghi Vayghan *et al.*, 2013).

The selection of the four empirical HSI models and cautious combining of the various SIs was conducted according to their compensatory nature of the model function (Van Horne and Wiens, 1991) and even species ability to respond to habitat changes. For example, an arithmetic mean of SI scores is used in scenarios involving habitat variables with highly compensatory effects. By contrast, limiting or critical factors are represented using the geometric mean model (Brown *et al.*, 2000; Zohmann *et al.*, 2013). Therefore, generally, defining a HSI model could almost clear the target species reaction (it meant if the model results uncover that geometric mean model is the best selection, thus decision makers ought to consider that those selected variables playing as limiting or critical factor in fish habitat selection) or strategies to selected environmental variation in its habitat to finally apply appropriate policies for current or future management. Modeling suitable habitats by using remote sensing and field data may be problematic because the delineation of modeling results depends heavily on the accuracy of the data, and the scale on which a study is conducted can influence the results (Zohmann *et al.*, 2013). The HSI approach has been criticized in the ecological field because it considers only environmental characteristics and a multitude of factors that influence the distribution and abundance of a species (Angelstam *et al.*, 2004) or factors corresponding to specific habitat features [*e.g.*, predation avoidance [(Říha *et al.*, 2014), competition, and climatic stochasticity] that are partly beyond human control (Zohmann *et al.*, 2013); however, the HSI is still useful for simplifying operational planning purposes. Although the HSI models used in this study had several advantages, some limitations were also present, namely that the relationship between carrying capacities and HSI was linear, the geographic scope of study was small, neither age nor size was assessed in SI development, and the variables included in the models were independent and exerted equal influence (weight) in defining the habitat quality of Caspian shad. Overall, by using habitat-monitoring tools and defining the spatio-temporal extent of suitable habitat of fish species, effective fisheries management policies can be easily devised for not only the Caspian Sea but other ecosystem worldwide. Defining the habitat needs of the target fish would enhance local fisheries performances and the long-term conservation planning of the fish to implement the EBFM in the world's largest lake, the Caspian Sea. As an example, improvement of the state of *Alosa* species in the Caspian Sea will require coordinated activities between the counties that are sharing fish stocks. Their local fisheries activities would have to become harmonized to achieve optimal fish stock management and sustainable exploitation that the coordinated management and protection of nursery grounds, seasonal habitat preferences and prevent further damages to essential habitats in near to countries shallow waters is needed. Furthermore, the long-term monitoring and management of human driven impact (*e.g.*, climate change and pollutions) may aid in slowing the change and destruction of ecosystems. However, the model we applied can be implemented easily for spatially explicit habitat suitability assessment and is an effective tool for planning and monitoring Caspian Sea ecosystem.

CONCLUSIONS

In this study, we used NPUA and CPUA data as abundance index and remote sensing and field data to quantify four empirical HSI models for the Caspian shad in the southern Caspian Sea. The NPUA was determined to be more reliable than the CPUA for use as the abundance index in Caspian shad HSI modeling. The average NPUA in both winter and spring increased with the HSI; areas with an HIS of between 0.4 and 0.6 in spring and between 0.6 and 0.8 in winter gained high percentage of total catch. Although a high percentage of total catch was caught in areas with an HSI of between 0.4 and 0.6, the NPUA was higher in areas with an HSI of more than 0.6, indicating that these areas are suitable habitats for Caspian shad in spring. Areas with an HSI of more than 0.5 had over 91% and 63% of the total catch in spring and winter, respectively; supporting the reliability of the NPUA-based HSI model's prediction of Caspian shad habitat. Moreover, the AMM (or GMM) in spring and the GMM (or MIN) in winter yielded reliable predictions of suitable habitats, indicating that the predictors used in the models could be considered critical factors for the fish in different seasons. The present study also showed that field data (bathymetry and substrate structure) plus SLA and Chl*a* are the most important environmental variables in the HSI modeling of the Caspian shad in the southern Caspian Sea. In remotely sensed data, SLA and Chl*a* had critical role in mapping suitable habitats. Nevertheless, knowing the seasonal habitat suitability and SI of each environmental variable of the fish in relation to the season and predictors could be useful in implementing ecosystem-based management (EBM) in the Caspian Sea, balancing local fishery management, and preventing further damage to essential habitats (*e.g.*, nursery and feeding grounds), particularly in spring when fish reside in shallow waters.

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