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Evaluating climate impact and anthropogenic activity on the pelagic species, *Clupeonella caspia* population parameters in the Caspian Sea

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ABSTRACT

This study aimed to assess the effects of various environmental factors, including sea surface level (SSL), seawater surface temperature (SST), the East Atlantic-West Russian pattern (EA_WR), river discharges (RD), and one human activity, fishing effort (E) on the variability of *Clupeonella caspia* bio-indicators over the last 27 years, using 118604 specimens. To analyze the data, dynamic factor analysis (DFA) was applied to parameters such as catch, abundance, spawning stock biomass (SSB), the percentage of immature individuals (Immature), the percentage of mega spawners (Mega), and the relative condition factor (Kn) derived from *C. caspia* datasets. Throughout the study period, catch, abundance, SSB, Mega, and Kn exhibited increasing trends, whereas the Immature displayed a decreasing one. Among the 324 models examined, the best-fit model featured a "diagonal and unequal" matrix and utilized SSL as an exploratory covariate, revealing two common trends. The first trend demonstrated a positive correlation with catch, abundance, SSB, and Mega, while negatively correlating with the percentage of immature individuals. The second trend showed a positive relationship solely with Kn. Additionally, catch, abundance, SSB, Mega, and Kn were positively correlated with SST but negatively with SSL. In contrast to two other kilka species, *C. engraliformis* and *C. grimmi*, *C. caspia* exhibits a distinct pattern; despite a decline in SSL and an increase in SST, its catch, abundance, and SSB all demonstrate an upward trajectory. Based on the indicators of Mega and Immature, the population structure of *C. caspia* appears to be relatively healthy.

Keywords: Abundance, Condition factor, Immature and mega spawner, Climate-driven, *Clupenella caspia*, Dynamic factor analysis, Caspian Sea.
Article type: Research Article.

INTRODUCTION

In recent decades, the Caspian Sea (CS) has experienced significant changes due to both climate change and human activities (Karpinsky *et al*. 2005; Beyraghdar Kashkooli *et al*. 2017; Fazli *et al*. 2021a). These influences manifest across various spatial and temporal dimensions, reshaping the structure and functioning of marine ecosystems amid a complex interplay of local and global pressures (Mackinson & Daskalov 2007). Decreasing sea surface levels and increasing seawater temperatures are key environmental drivers that are reshaping the Caspian ecosystem, affecting fish population dynamics and community composition (Beyraghdar Kashkooli *et al*. 2017; Fazli *et al*. 2021a, 2022a). The fisheries within the CS hold significant importance for both the local ecosystem and the economy, particularly species of kilka: *Clupeonella engrauliformis*, *C. grimmi*, and *C. caspia*. These pelagic fish species are essential components of the food web, serving as a critical food source for various marine predators and supporting local fishing activities (Mamedov 2006; Azizov *et al*. 2015; Fazli *et al*. 2020). Between 1995-96 and 1999-2000, there was an increase in the catch of kilkas, rising from 41,000 to 95,000 tons, driven by heightened fishing efforts in the Iranian coastal zones. During this time, *C. engrauliformis* and *C. grimmi* accounted for over 90% of the total catch. However, following the introduction of *Mnemiopsis leidyi* in 2000 (Pourang *et al*. 2016), the catch plummeted to below 16,000 tons in the 2003-2004 period, remaining relatively stable between 15,500 and 26,000 tons from 2005 to 2021. This invader species was triggered to decline *C. engrauliformis* and *C. grimmi* (Mamedov 2006; Pourang *et al*. 2016; Shiganova *et al*. 2023), while other environmental variables such as sea surface level (SSL) and seawater surface temperature (SST) have also contributed to this decrease (Fazli *et al*. 2021a). During this period, *C. caspia* gradually emerged as the dominant species, constituting over 95% of the total catch. According to Amiri *et al*. (2018), using Time Series SARIMA models, it was forecasted that under the current fishing effort, the performance of kilka fishing (*Clupeonella* spp.) in the southern part of the CS will be relatively stable by 2021, although the study did not differentiate between the three *Clupeonella* species, *C. caspia*, *C. engrauliformis*, and *C. grimmi*. The presence of *M. leidyi*'s has significantly altered the zooplankton community in the CS (Pourang *et al*. 2016; Roohi *et al*. 2024). This change in the zooplankton community has subsequently affected the population of two kilka fish species (*C. engrauliformis* and *C. grimmi*). Conducting time series studies on the biological data of aquatic populations is essential for effective ecosystem management. Such analyzes are instrumental as they establish baseline metrics and offer insight into the underlying patterns of population dynamics and their influencing factors. A comprehensive understanding of how environmental fluctuations and human-induced stresses shape the long-term dynamics of populations is crucial for the conservation and management of both ecosystems and species. Employing multivariate time-series analyses facilitates the interpretation of long-term population trends. Dynamic Factor Analysis (DFA) serves as a robust methodology for evaluating ecological time series and identifying shared population trends. Additionally, DFA can assess the covariance among multiple ecological time series (Zuur *et al*. 2003). Numerous studies have successfully applied DFA to investigate the effects of environmental parameters on ecological metrics (Jorgensen *et a*l. 2016; Barber *et al*. 2019; Bitetto *et al*. 2019). In a recent investigation conducted in the southern CS, DFA was employed to evaluate the impact of environmental factors on sturgeon populations (Fazli *et al*. 2022b). However, the application of DFA to pelagic fish stocks in this ecosystem has not yet been explored. The purpose of this study was to examine the trends in biological indicators for *C. caspia* in the southern CS. We employed DFA to evaluate the relative synchrony of total catch, abundance, spawning stock biomass (SSB), the proportion of immature and mega spawners (Mega), and the relative condition factor (Kn). The objectives of this study were: (i) to analyze the trends in biological indicators; and (ii) to investigate the impact of various environmental factors such as SSL, SST, East Atlantic-West Russian pattern (EA_WR), river discharges (RD), and one human activity, fishing effort (E) on the variability of *C. caspia* bio-indicators over the past 27 years. The results of this study are intended to enhance our comprehension of the ecosystem and contribute to the development of effective fisheries management in the CS.

MATERIALS AND METHODS

Study area and sampling

The CS is typically categorized into three sections: northern, central, and southern. This particular study focuses on the deeper regions of the southern CS, specifically in Iranian waters, where 74 vessels operated across three kilka landing sites: Anzali, Amirabad ports, and Babolsar harbor (Fig. 1). The kilka were captured at depths between 40 and 100 meters using conical lift nets that were fitted with underwater electric lights. Typically, the diameter of the liftnet's hoop measures between 2.5 and 3 meters. Each net is equipped with two underwater electric lamps (around 2 kW). The mesh size between the knots is 7–8 mm. All fishing vessels utilize conical lift nets of similar size and design, ensuring uniformity across the fleet. These vessels are relatively small, with a capacity lower than 100 tons, and fishing activities primarily take place at night (Fazli *et al*. 2007). The fishing season commences throughout the whole year in the years 1995 to the early 2000s (Fazli *et al*. 2007). Thereafter, due to the spawning season, the catch was closed from April to June. A total of 118,604 specimens of *C. caspia* were collected from 1995 to 2021 and used as input data. Researchers from the Caspian Ecology Research Center (CSERC) and Inland Waters Aquaculture Research Center (IWARC) also conducted field sampling during this period. Following the identification of species, they randomly selected up to 200 specimens of *C. caspia* every two weeks in each province (Fazli *et al*. 2007, Janbaz *et al*. 2020). Each individual was measured to the nearest 1 mm in fork length and the nearest 0.1 g in body weight. Age was determined using sagittal otolith reading. For each sex, 5-10 otoliths were collected from each 5 mm size class.

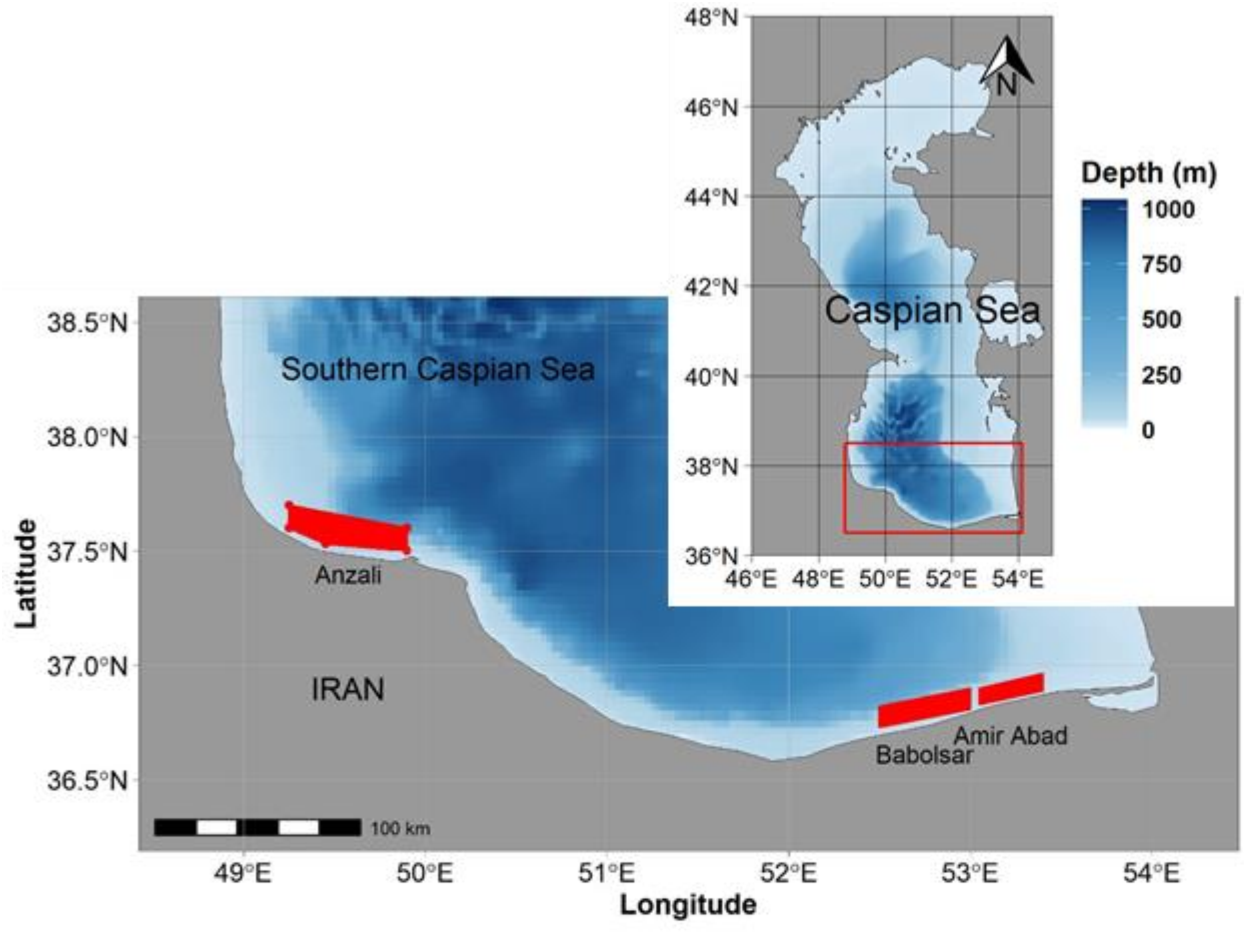

Fig. 1. Map of the study area, and the green-filled circles show the beach seine locations.

Biological variables

This study examined six response variables associated with stock indices for *C. caspia* from 1995 to 2021, including total catch, abundance, SSB, and the percentage of immature (Immature) and mega spawners (Mega), as well as the relative condition factor (Kn; Table 1). Kn was used to evaluate the health of different fish species and is computed using the formula: Wo/Wc, where Wo represents the observed weight and Wc is the calculated weight derived from the length-weight relationship (Table 2). According to Froese (2004), the percentages of Immature and Mega act as indicators of stock health, defined as the proportion of fish samples with lengths shorter than $Lm_{50\%}$ (the mean length at 50% maturity) and the proportion of fish exceeding the length Lopt (optimal length) plus 10%, respectively (Table 2). The maturity ogive for female *C. caspia* was determined to be 0.18, 0.68, 0.95, and 1.0 at ages 1, 2, 3, and 4, respectively (Fazli *et al*. 2007). Time-series data for both abundance and SSB were sourced from fish stock assessments conducted by the Iranian Fisheries Scientific Research Institute (IFSRI) utilizing biomass-based cohort analyses (Zhang & Sullivan 1988). SSB estimates, expressed in metric tons, were derived by multiplying biomass by the female maturity index. Catch data were provided by the Iranian Fisheries Organization (IFO).

Explanatory Variables

The study analyzed the impact of four environmental variables on long-term trends in fish stock indices of *C. caspia* from 1995 to 2021. These included one global variable with broad influence, EA_WR, two regional variables, SST and SSL, and one local variable, which comprised the cumulative river discharges from Sefidrood, Polrood, Chalos, and Haraz (RD). The analysis also incorporated an anthropogenic variable (E), representing fishing effort (vessels per night). Monthly averaged SST data from 1995 to 2021, with a resolution of $0.1^{\circ} \times 0.1^{\circ}$, were obtained from the NOAA website (https://neo.sci.gsfc.nasa.gov). Monthly averages for SSL and RD, along with fishing effort data (from the IFO), were sourced from the Caspian Sea National Research Center (CSNRC) and EA_WR data (available at https://catalog.data.gov; Table 3). The EA-WR pattern, characterized by pressure/height anomalies centered on the CS and western regions of Europe (Lim 2015), plays a significant role in influencing weather conditions across Eurasia.

Table 1. Summary of the biological indices and source of data.

Variable	**Period**	**Source**
Catch	Monthly	Iranian Fisheries Organization
Abundance	Annually	Produced by the authors, using the archival data from the Iranian Fisheries Science
Spawning stock biomass (SSB)	Annually	Research Institute
Percentage of immature (Immature)	Annually	
Percentage mega spawners (Mega)	Annually	
Relative condition factor (Kn)	Annually	

Table 2. The length-weight relationship values, $Lm_{50\%}$, and L_{opt}, were used to estimate the relative condition factor and percentage of immature and mega spawners for two benthopelagic fish species in the Caspian Sea.

a **(constant)**	***b*** **(slope)**	***Lm*** $_{50\%}$ **(cm)**	***L*** $_{opt}$ **(cm)**	**Reference**
0.000034	2.688	80.0	87.0	Fazli *et al*. (2013)

Table 3. Summary of the monthly environmental variables and source of data.

Scale	**Variable**		**Source**
Global	EA-WR	East Atlantic-West Russian	https://catalog.data.gov
Regional	SST	Sea surface temperature	https://neo.sci.gsfc.nasa.gov
Regional	SSL	Sea surface level	Caspian Sea National Research Center
Local	RD	River discharge	Caspian Sea National Research Center
	E	Fishing effort	Iranian Fisheries Organization

The corresponding explanatory variables time-series data show large annual fluctuations (Fig. 2). The summarized statistics (average ± SD) for SSL, SST, RD, and EA_WR were -26.4 ± 0.42 (m), 19.1 ± 0.41 (°C), 3602.6 ± 1502.1 (MCM, a million cubic meters), and -0.19 ± 0.36. The average of E was 12463.4 ± 6188.3 (vessels × night). The annual SSL time series showed a clear decrease. The annual SST displayed an increasing trend over the entire period. The E increased to the highest in 2002 and then followed a decreasing trend. The RD and EA_WR displayed a negative long-term trend (Fig. 2).

Univariate analysis

Annual time series data for each fish stock variable and related environmental factors were analyzed. The breakpoints technique was applied to this annual data using the "strucchange" package, where an algorithm was utilized to identify structural changes and assess interannual variability. The Bayesian information criterion (BIC) guides the determination of the optimal number of segment partitions, facilitating the identification of significant changes (Zeileis *et al*. 2002). Additionally, a Pearson correlation matrix was generated to analyze relationships between response variables and five explanatory factors, utilizing the "corrplot" package for the species.

Dynamic factor analysis (DFA)

The DFA model comprises four components: common trends (M), explanatory variables, a level parameter, and a noise component (Zuur *et al*. 2003). In this research, four hypotheses regarding the covariance matrix (R) of observational errors were tested: diagonal-equal, diagonal-unequal, equal variance-covariance, and unconstrained models. Various DFA models were evaluated, incorporating between one and three common trends (1, 2, and 3). All response and explanatory variables were standardized to have a mean of zero and an SD of one. To test the DFA model configuration, which included six response variables and three common trends, five explanatory variables were incorporated with variable numbers of covariates (ranging from 0 to 5) for each fish species, resulting in a total of 324 models being tested. The environmental variables included SSL, SST, RD, E, and EA_WR. Model efficacy was assessed using the Akaike Information Criterion (AICc) as per the methodologies outlined by Burnham & Anderson (2002), Zuur *et al*. (2003), and Holmes *et al*. (2021). To identify trends within the series, a cutoff loading level of 0.2 was arbitrarily established based on recommendations by Zuur *et al*. (2003). The assumptions of normality and independent observation errors for residuals from the selected models were evaluated for model validation (Fig. 3). R software (R Core Team 2020) was employed for univariate analyses alongside the strucchange (Zeileis *et al*. 2002), corrplot (Wei & Simko 2021), and ggplot2 (Wickham 2016) packages, while the MARSS R package (Holmes *et al*. 2021) was used for conducting the DFA analysis.

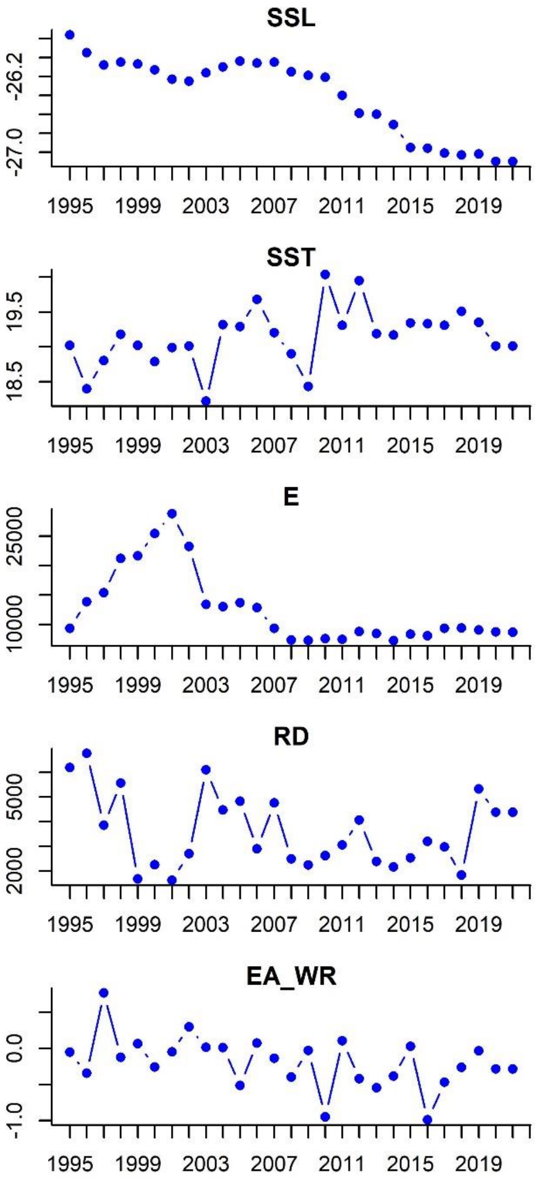

Fig. 2. Time-series environmental parameters of sea surface level (SSL), sea surface temperature (SST), fishing effort (E), river discharge (RD), and East Atlantic West Russia (EA_WR), the period 1991-2020. The green curve is the loess-smoothed trend.

RESULTS

Biological time series data

The annual sample size and mean, min (minimum), max (maximum) length, and weight of *Clupeonella caspia* from 1995 to 2021 are presented in Table 4. During the period, the fork length and weight of *C. caspia* ranged from 47.5 to 142.5 mm and from 0.5 to 25.3 g and averaged (± S.D.) 97.0 (± 13.8) mm and 7.6 (± 2.7) g, respectively (Table 4). The mean ± SD of catch, abundance, SSB, immature, Mega, and Kn were 15800 ± 1332.2 t, 14544 ± 6095.2 10^6 ind., 45002 ± 21786.4 t, 1.5 ± 2.4%, 17.7 ± 11.2%, and 1.02 ± 0.10, respectively (Fig. 4). Catch attained the max at 26745 t in 2010, and the min at 969 t in 1996, indicating three increasing breakpoints in 1999, 2004, and 2009 (Fig. 4). The max abundance and SSB were observed to be 25120.3×10^6 ind. and 70119.2 t in 2009 and 2010, while the min was 2955.7×10^6 ind. and 1106.5 t in 1996, respectively. Four discontinuities were detected for abundance (in 1999, 2003, 2007, 2011, and 2018). In addition, the SSB showed three breakpoints in 1999, 2004, 2008, and 2012 (Fig. 4).

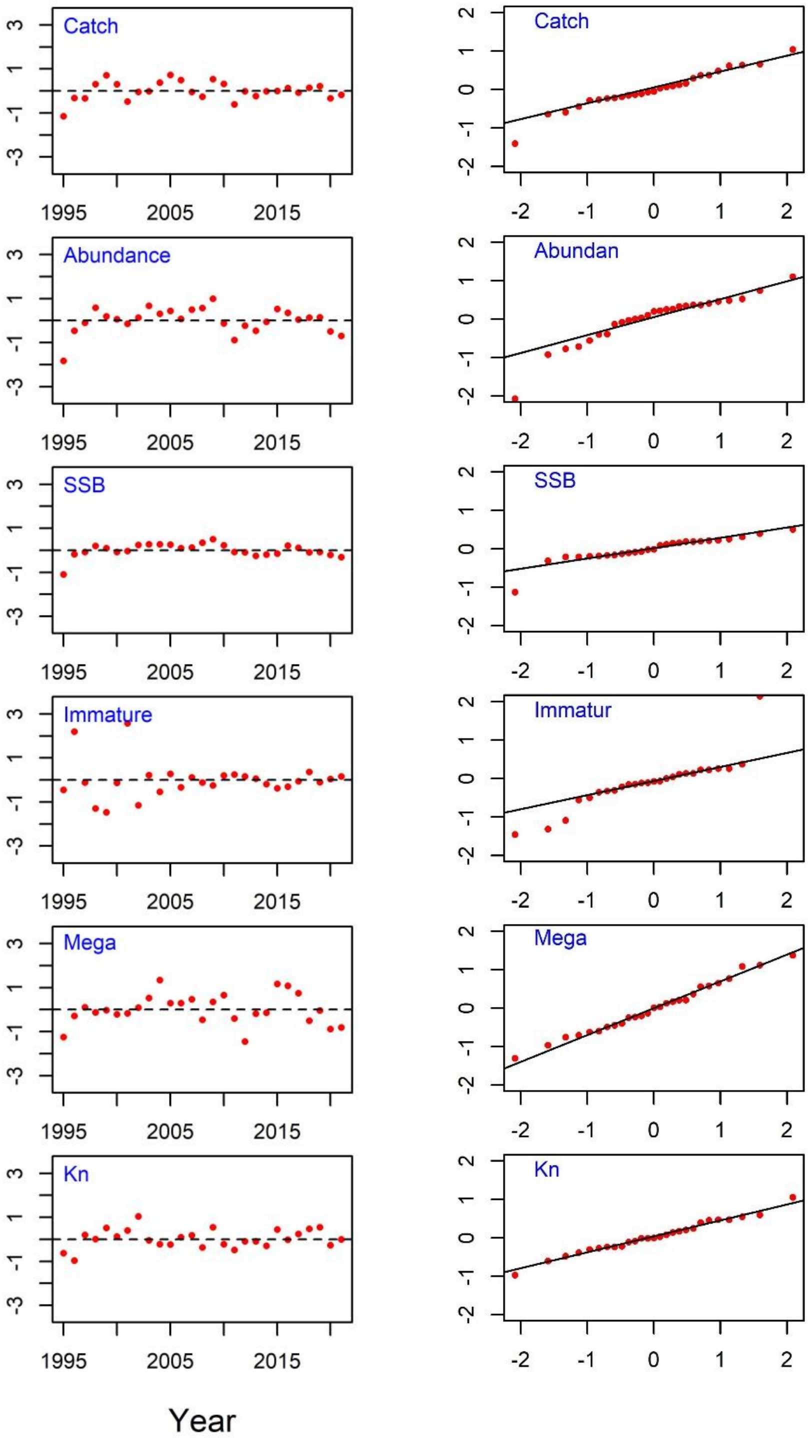

Fig. 3. Model innovations (left) and quantile-quantile plots (right) for the best-fitting DFA model with two trends and a covariate of SSL explaining temporal variability in annual catch, abundance, spawning stock biomass (SSB), percentages of immature (Immature) and mega spawners (Mega), and relative condition factor (Kn) of *Clupeonella caspia*.

Table 4. Mean ± SD (standard deviation) min-max (minimum and maximum) lengths (mm) and weight (g) of *Clupeonella caspia* sampled in the Iranian region of the Caspian Sea during 1995–2010.

Year	N	Fork length (mm)		Weight (g)	
		Mean ± SD	**Min_Max**	**Mean ± SD**	**Min_Max**
1995	1495	94.3 ± 15.5	57.5-122.5	6.7 ± 2.5	1.9-12.4
1996	2400	98.6 ± 14.2	47.5-127.5	7.6 ± 2.6	1.0-15.7
1997	1423	96.1 ± 13.2	67.5-127.5	6.9 ± 2.3	3.1-13.5
1998	970	93.4 ± 13.2	57.5-122.5	5.7 ± 1.9	1.4-10.2
1999	1914	84.7 ± 11.6	47.5-107.5	4.5 ± 1.5	0.8-8
2000	1322	82.7 ± 9.9	57.5-107.5	4.0 ± 1.2	1.5-7.5
2001	5108	86.8 ± 9.1	57.5-107.5	5.0 ± 1.3	1.7-10.9
2002	4290	87.2 ± 12.4	47.5-112.5	5.2 ± 1.7	0.5-10
2003	3091	88.1 ± 12.9	52.5-112.5	5.7 ± 2	1.3-10.1
2004	4426	92.7 ± 11.3	67.5-112.5	7.1 ± 2.3	2.8-13
2005	6664	94.7 ± 13.5	52.5-127.5	7.5 ± 2.6	1.2-16.5
2006	6616	98.5 ± 13.2	52.5-132.5	8.2 ± 2.7	1.4-18.6
2007	7074	98.5 ± 15.1	52.5-127.5	7.8 ± 2.9	0.8-15.6
2008	5808	100.7 ± 14.9	57.5-132.5	8.4 ± 3.1	1.6-19.9
2009	6292	101.1 ± 14.8	52.5-132.5	8.6 ± 3.2	1.2-17.1
2010	7836	99.4 ± 14.1	67.5-137.5	7.9 ± 2.8	2.1-18.2
2011	7506	102.0 ± 13.6	62.5-132.5	8.8 ± 2.8	1.9-18.4
2012	5800	102.3 ± 14	67.5-142.5	8.9 ± 3.2	2.4-23.5
2013	6737	103.4 ± 14.3	67.5-142.5	8.9 ± 3.2	2.2-28.3
2014	4294	100.2 ± 15	67.5-142.5	8.1 ± 2.8	2.5-20
2015	1870	102.8 ± 15.5	67.5-137.5	9.0 ± 4	2.3-26.5
2016	1596	104.9 ± 12.5	77.5-127.5	9.0 ± 2.7	3.2-16.4
2017	2032	103.2 ± 14.5	72.5-142.5	9.4 ± 3.1	2.1-19.3
2018	6289	102.6 ± 14.8	57.5-137.5	9.1 ± 3.3	0.9-26.1
2019	5863	99.6 ± 17.2	52.5-137.5	8.9 ± 3.8	1.0-25.2
2020	4366	99.4 ± 16.3	62.5-137.5	9.0 ± 3.5	1.9-20.3
2021	5522	101.0 ± 15.7	62.5-137.5	10.0 ± 3.8	1.9-25.5
Total	118604	97.0 ± 13.8	47.5-142.5	7.6 ± 2.7	0.5-28.3

The max and min of Immature were 9.8% in 1994 and 0.1% in 1995 and 2001, averaging 1.5 ± 2.4%, with two decreasing breakpoints in 2002 and 2008 for *C. caspia*, respectively. The Mega ranged between 0.8% in 2001 and 35.4% in 2015, averaging 17.7 ± 11.2%. One discontinuity was detected in 2003. Kn time series data displayed a clear increasing trend and showed two breakpoints in 2001 and 2018 (Fig. 4).

Correlation analysis

The Pearson correlation coefficient revealed numerous significant correlations between the response and explanatory variables (Fig. 5). Between the six response time series data of *C. caspia*, the catch, abundance, SSB, Mega, and Kn had a positive significant correlation with SST, and negative significant correlation with E of explanatory variables (except for the correlation of Immature and E, which was positive). Also, the catch, abundance, SSB, Mega, and Kn had a significantly negative correlation with SSL (Fig. 5).

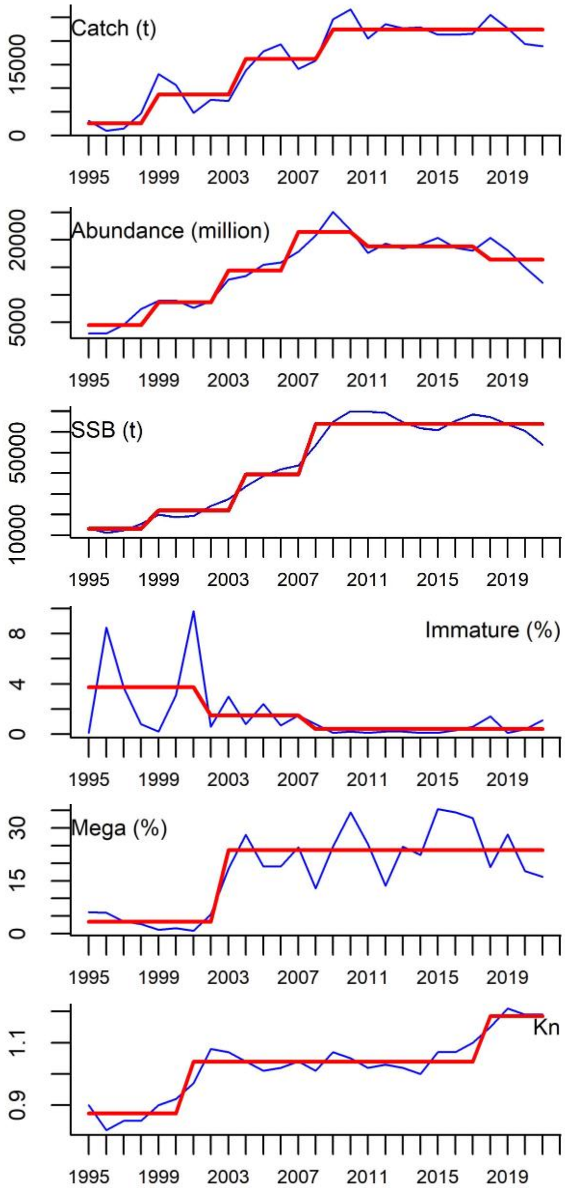

Fig. 4. Time-series annual catch, abundance, spawning stock biomass (SSB), percentages of immature (Immature) and mega spawners (Mega), and relative condition factor (Kn) of *Clupeonella caspia* of the Caspian Sea. The red lines represent the mean values between breakpoints.

Dynamic factor analysis

Various DFA models were developed that integrated five environmental variables to analyze the 'multispecies-covariate' relationship with six biological time series data of *C. caspia* in the CS. Among the 324 models assessed, the optimal model featured a "diagonal and unequal" R matrix, two common trends, and the exploratory covariate SSL (Table 5). The first trend demonstrated a steady increase from 1995 to 2009, followed by a decline until 2020 (Fig. 6). This common trend showed a strong positive correlation with catch, abundance, SSB, and Mega, while exhibiting a negative association with Immature. The second trend revealed a shorter period of increase between 1996 and 2001, followed by a decrease in 2014, and then a sharp rise in 2020. This trend was positively correlated only with Kn (Fig. 6). All the response time series exhibited substantial factor loading (exceeding ± 0.2) on at least one common trend, indicating that these trends were quite effective for the biological time series. Fig. 7 illustrates the standardized observed values alongside the model fitted to the stock condition indices time series, showing a high degree of concordance between the observed and predicted values.

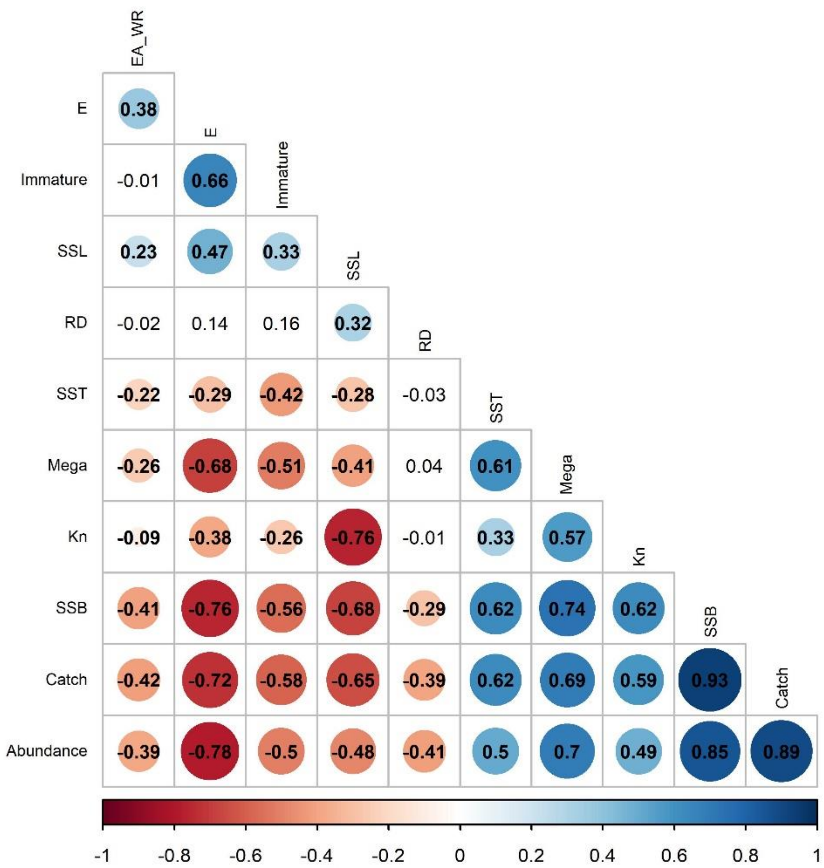

Fig. 5. Correlations between the time series data for *Clupeonella caspia*. The significant correlations (p<0.05) are indicated in bold-colored. See Figs 2 and 3 for a key to biological and environmental parameters.

DISCUSSION

Over the past three decades, various environmental and anthropogenic factors, such as invasive species, RD, SST, and SSL, have influenced the condition of the Caspian ecosystem (Pourang *et al*. 2016; Fazli *et al*. 2022a,b; Shiganova *et al*. 2023). Three pelagic species of kilka, which feed on zooplankton, may be impacted by shifts in the species composition and abundance within the zooplankton community of the CS (Roohi *et al*. 2024). Due to the scarcity of time series data on zooplankton quality and quantity in the study area, we employed a range of environmental and anthropogenic variables that impact both the production and structure of zooplankton and pelagic fish. In this research, we estimated six population indices for *C. caspia*, including catch, abundance, SSB, Immature, Mega, and Kn, from 1995 to 2021. These indices are valuable for assessing changes in their populations. The DFA model provided strong evidence supporting the hypothesis that the majority of biological indices for *C. caspia* display interannual patterns that are influenced by environmental variables. The selected models revealed two common trends associated with SSL in the data collected over the 27-year span since 1995. SSL is linked to the North Atlantic Oscillation (NAO), which plays a significant role in determining precipitation patterns in the Volga region (Arpe *et al*. 2000). A decline in SSL can lead to reduced habitats, resources, and food availability for fish, as certain prey species may struggle to thrive in shallower waters (Prange *et al*. 2020). Our findings indicate that SSL serves as a negative predictor for all response indices of *C. caspia*. This observation contrasts with previous research on environmental factors affecting the fisheries resources within the CS ecosystem (Arpe *et al*. 2000, Mamedov 2006, Beyraghdar Kashkooli *et al*. 2017, Seyedvalizadeh *et al*. 2020, Fazli *et al*. 2022a,b). This contradiction could be related to the fish species, which shows that *C. caspia*, classified as euryhaline and eurytherm (Prikhod'ko 1981), has different behavior to other species such as *C. engrauliformis*, *C. grimmi* (Mamedov 2006, Fazli *et al*. 2022a,b), *R. kutum*, and *C. aurata* (Beyraghdar Kashkooli *et al*. 2017). Kn serves as an important measure of environmental suitability, reflecting the overall health and feeding behavior of fish in a given aquatic ecosystem. When Kn falls below 1, it indicates a deterioration in condition and feeding activity (Bagenal & Tesch 1978, Anderson & Neumann 1996, Sutton *et al*. 2000). In our study, we observed that the Kn for *C. caspia* has been on the rise over recent years, remaining above 1 since 2001. This indicates that the overall health and fitness of *C. caspia* have been relatively good during this period. In contrast, during the period from 2013 to 2014, the Kn values for the two pelagic species, *Alosa braschnikowi* and *A. caspia*, varied. One species exceeded a Kn of 1, denoting good health, while the other fell below 1, suggesting compromised well-being in the Southeastern CS (Fazli *et al*. 2021b).

Table 5. The top 15 DFA models ranked in order of decreasing data support (increasing AICc). The "M" values are different numbers (1–3) of common trends, and "R" represents the different combinations of measurement error covariance matrix structures. Covariate abbreviations are defined in Fig. 2, and the best model is indicated in boldface.

M	Environmental covariates	R	AICc	Δ AICc
2	**SSL**	**diagonal and unequal**	**227.5**	**0.0**
2	SSL, RD	diagonal and unequal	230.5	3.0
2	SSL, E	diagonal and unequal	231.6	4.0
3	Nocov	diagonal and unequal	233.8	6.3
1	SSL	diagonal and unequal	235.4	7.9
2	SST, SSL	diagonal and unequal	235.7	8.2
2	Nocov	diagonal and unequal	236.4	8.9
3	E	diagonal and unequal	237.9	10.4
3	SST	diagonal and unequal	238.3	10.7
2	RD	diagonal and unequal	238.6	11.1
2	SSL, EAWR	diagonal and unequal	239.3	11.7
1	SSL, RD	diagonal and unequal	239.4	11.8
3	SSL	diagonal and unequal	239.4	11.8
2	SST, SSL, E	diagonal and unequal	239.9	12.4
1	SSL, E	diagonal and unequal	239.9	12.4

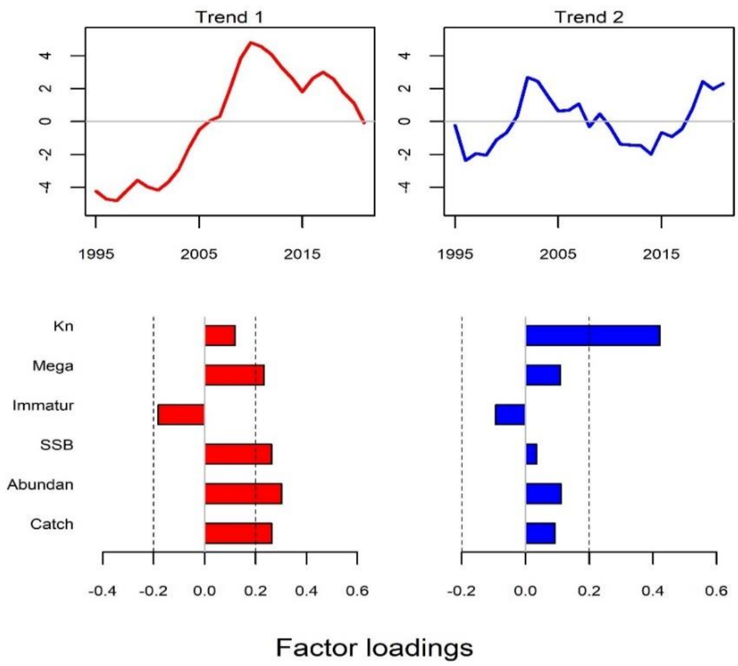

Fig. 6. Estimated trends (top row) and factor loadings per trend (bottom row) for the best-fitting model. Factor loadings for each species-biological loadings greater than ± 0.2 (horizontal dashed line), identify a time series of conditions that had a relatively strong influence on the common trend. See Figs. 2 and 3 for a key to biological parameters.

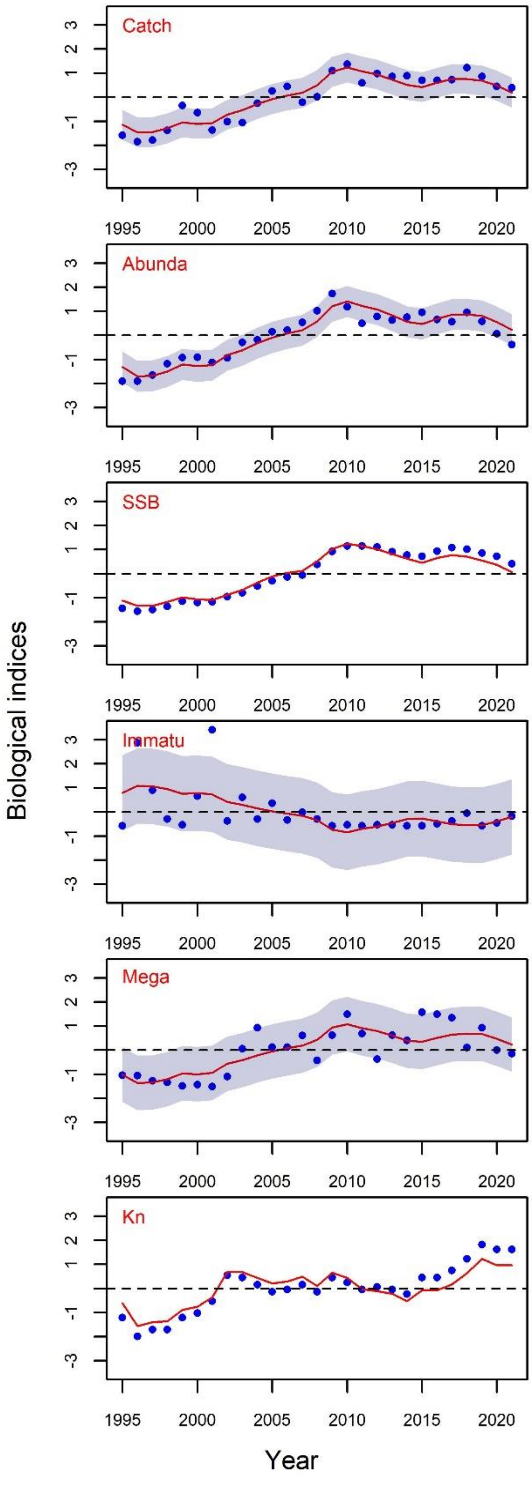

Fig. 7. Dynamic factor analysis results for the best-fitting model: model fitted values (red lines) and standardized biological observed data (filled blue circles) of *Clupeonella caspia*. Shading indicates the 95% confidence intervals of the model-fitted values. See Fig. 3 for a key to biological parameters.

Furthermore, the Kn values for the dominant sturgeon species, including *Acipenser persicus*, *A. stellatus*, and *A. gueldenstaedtii*, dropped below 1 during the 2000s and 2010s. This decline can likely be attributed to significant changes within the CS ecosystem and a regime shift occurring in the region (Fazli *et al*. 2022b). The different behavior observed in *C. caspia* compared to the other species could be related to its feeding strategies. *C. caspia* exhibits opportunistic feeding strategies by consuming a diverse array of prey, demonstrating adaptability to various environmental conditions (Prikhod'ko 1981). According to Fazli *et al*. (2020), the stocks of the two primary kilka species, *C. engrauliformis* and *C. grimmi*, have experienced a dramatic decline, categorizing them as Critically Endangered. This decline can be attributed to overfishing, the presence of invasive species (*M. leidyi*), and various global and regional environmental factors over the past two decades (Daskalov & Mamedov 2007, Pourang *et al*. 2016, Fazli *et al*. 2021a). Similarly, the populations of two benthopelagic species (*Rutilus kutum* and *Chelon aurata*) have negatively reacted to the changes in SST that occurred in the late 1990s (Beyraghdar Kashkooli *et al*. 2017). In contrast, our study reveals that *C. caspia* demonstrates a different pattern; despite decreasing SSL and increasing SST, catch, abundance, and SSB have all shown an upward trend (Fig. 4). It appears that *C. caspia* exhibits a distinct response to fluctuations in environmental and anthropogenic activities. While the rising Kn (suggests improved well-being and feeding activity), catch, abundance, and SSB over recent years, its differing behavioral responses to environmental changes may indicate unique adaptive strategies. This divergence highlights the complexity of species interactions within the CS ecosystem, suggesting that *C. caspia* may possess mechanisms that allow it to better withstand or adapt to these environmental shifts compared to other species. The contrasting behavioral responses among the three pelagic species of kilka can be further elucidated. *C. caspia* exhibits opportunistic feeding strategies by consuming a diverse array of prey, and it is classified as euryhaline and eurytherm, demonstrating adaptability to various environmental conditions (Prikhod'ko 1981). In contrast, *C. engrauliformis* and *C. grimmi* have more limited diets and face significant competition from the invasive *M. leidyi*, both of which are classified as stenohaline and stenotherm (Prikhod'ko 1981; Roohi *et al*. 2010; Pourang *et al*. 2016). Together, these insights underscore the differing ecological strategies employed by these species and their implications for survival in a dynamic ecosystem. Zuur *et al*. (2003) noted that the absence of certain covariates in the most effective models does not necessarily imply that these covariates lack influence on the data. In the present study, we observed a positive correlation between all biological indices and sea surface temperature (SST; Fig. 5), which contrasts with the effects seen in other fish species within the CS (Beyraghdar Kashkooli *et al*. 2017; Fazli *et al*. 2022a). Numerous global studies over recent decades have documented an upward trend in SST, which has had negative impacts on marine ecosystems (Barber *et al*. 2019; Bitetto *et al*. 2019; Feuilloley *et al*. 2020), a phenomenon often linked to climate change (Xu *et al*. 2021). Mega and Immature are key indicators of population structure. A healthy population is characterized by 30-40% Mega, with no upper size limit for captures, while the ideal target for Immature is 0% (Froese 2004). In this study, we found that the Mega of *C. caspia* has consistently exceeded 20%, while Immature has remained below 2% since 2002. These findings suggest that, according to these two indicators, *C. caspia* displays an approximately healthy population structure. E can have a range of impacts on fish populations. The interaction between catch and E, as well as abundance, can be affected by various factors, including the target fish species, fishing techniques, and management approaches (Mulazzani *et al*. 2015). In the CS, an increase in E has resulted in declines in the catch, abundance, SSB, and Mega, alongside a rise in Immature for *C. caspia*. This indicates that E should be reduced at a level lower than the current state.

CONCLUSION

The findings from this comprehensive study highlight the divergent response of the *C. caspia* population parameters to environmental factors like SSL and temperature, compared to other commercially important fish species in the dynamic Caspian ecosystem. Despite declining sea surface levels and rising temperatures, which have negatively impacted many other Caspian fish species, *C. caspia* exhibited increasing trends in key population parameters, including catch, abundance, SSB, and Kn. This suggests that the species has adapted well to the changing environmental conditions, likely due to its opportunistic feeding strategies and wide tolerance for environmental variability. In contrast, other pelagic and benthopelagic species, such as the two other kilka species (*C. engrauliformis* and *C. grimmi*), as well as *R. kutum* and *C. aurata*, have shown significant declines in response to the environmental shifts occurring in the CS. The distinct behavioral patterns of *C. caspia* underscore the complex species interactions and ecosystem dynamics within the Caspian region. These findings contribute valuable insights for informed decision-making and adaptive management strategies to support the resilience of the CS ecosystem in the face of ongoing environmental changes. Accounting for the unique ecological characteristics of *C. caspia* will be crucial to ensuring the long-term sustainability of this key fishery resource, which plays a vital role in the region's economy and food security. The divergent population trends observed in this study highlight the importance of species-specific management approaches to effectively conserve and manage the CS's diverse fisheries.

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