

ORIGINAL ARTICLE

Life history characteristics of Threespine Stickleback (*Gasterosteus aculeatus*) from an estuarine area of the southern Caspian Sea, Iran

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Abstract

To fill the knowledge gap on Caspian population of stickleback (*Gasterosteus aculeatus*), a total of 405 specimens caught near the mouth (in a distance of about 500m from the sea) of the Siahroud River (a small stream), and examined for the population-specific life history. The growth type was allometric negative for the studied population of the species. The stickleback's lifespan was estimated to be 3.45 and 4.69 years for males and females, respectively. The Von Bertalanffy Growth Curve estimated as $L_t = 8.11(1 - \exp(-0.87(t + 0.46)))$ for males, and $L_t = 10.31(1 - \exp(-0.64(t + 0.47)))$ for females. The total mortality rate was 3.47 year⁻¹ for males, and 2.20 year⁻¹ for females. Sex ratio was not significant from the ration 1:1. The reproduction period extended from April to June (late spring-early summer), with a peak in May. There were two kinds of ova, small colorless ova (0.43±0.08 mm) and large yolk-filled ones (1.16±0.29mm). Number of all ova ranged from 311 to 4709 and 128 to 885, respectively. The estimated absolute fecundity varied in a wide range from 235 to 5460 oocytes per ovary with a mean value of 1837.34±1028. The relative fecundity varied from 84 to 2441 eggs/g. The mean relative fecundity (eggs/g) was 799.

Keywords: Threespine Stickleback, Growth, Mortality, Reproduction, Siahroud River, Caspian Sea.

INTRODUCTION

The Gasterosteidae family comprises two closely related species in Iranian waters; ninespine stickleback (*Pungitius platygaster*) as native stickleback to the Caspian Sea and Threespine stickleback (*Gasterosteus aculeatus*) as non-indigenous "marine" form of the stickleback in the southern Caspian basin (Coad & Abdoli 1993; Esmaeili et al. 2014; Joudaleh-Roudbar et al. 2014; Eagdei et al. 2022). The distribution of Threespine stickleback includes a wide range throughout the Holarctic region between 35° and 70° latitude (Wootton 1984) and involves various isolated populations exhibiting differentiated life histories within its large geographic and ecologically diverse range (Bell & Foster 1994; Baker 1994; Paepke 2001). In the habitat range of the species in northern Eurasia, beside Syria, the southern coastal Caspian habitats is located in its southeastern range distribution, occurring in most of estuaries of the rivers and wetlands of this area (Abdoli 1993; Coad & Abdoli 1993; Kiabi et al. 1999). According to the literature review, this species has unknown mode of

introduction into Iran.

Even though, the threespine stickleback has been investigated for its biological aspects in the distribution range (e.g. east Russia, USA, Canada, Alaska, Japan and European areas), to the best of our knowledge, no comprehensive study on the species has been conducted in the estuarine habitats of the southern Caspian basin, northern Iran. The only reference on the biological aspects of the stickleback in this area is that of Patimar et al. (2010). Additionally, Abbasi et al. (1999), Abdoli (2000), Naderi and Abdoli (2004) and Mouludi-Saleh & Eagderi (2022) provided some limited information on the species, dealing with its biology and morphology.

The new established populations of a non-indigenous species often face environmental conditions that differ from the habitats of the parent stock, and the main characteristics producing the highest fitness in the original population will probably no longer do so in the new habitats (Wade & Kalisz 1990). The life history characteristics of newly established populations will depend on the new environment condition (Land & Arnold 1983), and it

Table 1. Average of some environmental factors (min–max) of study area from estuarine area of Siahroud River (south Caspian Sea-Iran).

Characteristics	$\bar{x}$ (min– max)
Depth (cm)	85.4 (0-134)
Width (cm)	625 (222-1400)
Bottom substrate	Clay
Water velocity (m/s)	0.81 (0.31-0.98)
Water t ^{°c}	12.08 (8.1-13.2)
DO (mg/l)	7.21 (6.8-8.2)
PH	7.14 (6.8-8.55)
EC	12.6 (1.11-16.05)
Salinity (‰)	0.84 (0.22-1.98)
Turbidity (NTU)	112.4 (24-124)
Po ₄ ⁻ (mg/l)	1.03 (0.14-2.07)
No ₃ ⁻ (mg/l)	2.35 (2.02-2.98)

has been demonstrated that adaptation in life history of fish populations is the response to environmental conditions (Nikolsky 1962; Kume et al. 2003; Poumpalie et al. 2000).

We hypothesized that the estuarine habitats of the southern Caspian Sea result in habitat-specific life history of the stickleback. Therefore, to develop the knowledge about life history variability of the threespine stickleback, the present paper provides the first more-in-depth information on characteristics of an estuarine population of the species. These parameters provide a better understanding on the stickleback to test whether an estuarine habitat has promoted locally differentiated demographic parameters of this model species.

MATERIAL AND METHODS

Many surveys (hereafter the corresponding author's survey) performed in many areas of the southern Caspian Sea to provide estimates of fish species status during last decade (2010-2020). These surveys provided valuable measures about trends in population traits of the species, which are essential for ecosystem conservation programs. The data collected through these surveys on a riverine population of the threespine stickleback was used in the present work. The samples collected out near the estuary of Siahroud stream (in a distance of about 300 m from the sea with Latitude: N36°, 43', 46.08", Longitude: E52°, 51', 07.52", average depth: 0.75m) which lies in the north of the Elburz Mountains, and entering to the Caspian

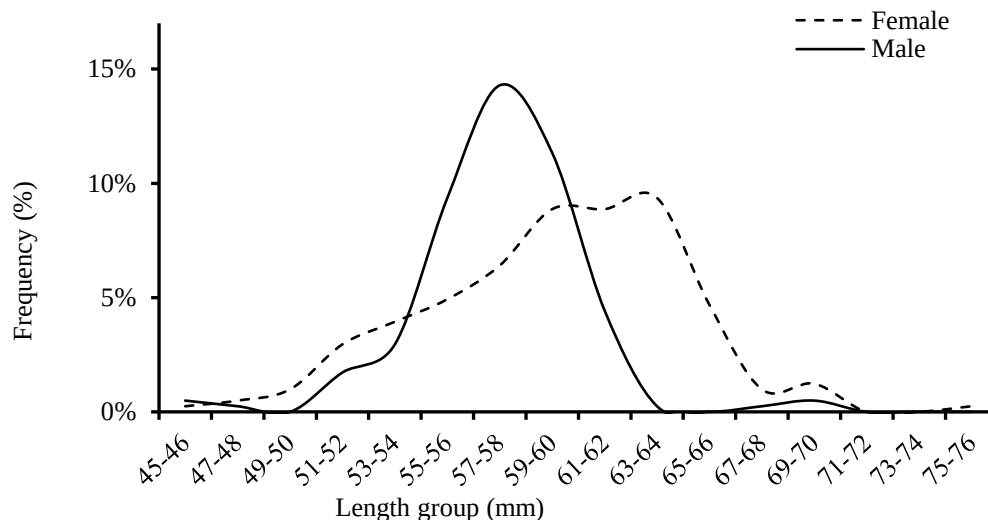
Sea through its southern coast (Mazandaran Province). The river is certain kind of small permanent stream of the southern Caspian humid climate (Afshin 1994; Kiabi et al. 1999). Table 1 shows some physical and chemical characteristics of the sampling area (estuarine habitat of Siahroud River- southern Caspian coast). In the laboratory, basic biometric data including total length (to the nearest millimeter), total weight (to the nearest 0.01g), weight of gonads and its sub-samples (to the nearest 0.005g) were recorded for all specimens. The specimens aged from opercula and validated by the otoliths readings in about 10% specimens using a stereomicroscope at magnifications of 20-30×. The observed lengths at age were back calculated for all specimens (Johal et al. 2001).

The growth type (allometry or isometry) determined using power regression of length-weight. The difference between b being the coefficient of allometry and 3 (isometric value) checked with the t-test adopted by Pauly (1984).

The age-length relationship was described using the parameters of L_{∞} mm, K year⁻¹, and t_0 year using ELEFAN I method in FiSAT-II package (Pauly 1987; Gayanilo et al. 2005). Since ELEFAN does not define the t_0 -value, it was estimated using Pauly's equation: $\log(-t_0) = -0.3922 - 0.2752(\log(L_{\infty})) - 1.038(\log(K))$ (Sparre & Venema 1997). The results of L_{∞} and K values were used to estimate of the ϕ' - index (Munro & Pauly 1983; Pauly & Munro, 1984). In order to estimate lifespan (t_{max}), we used the following formula (Taylor 1958; Pauly 1984): $t_{max} = (2.996/K) + t_0$, where K is the growth coefficient

Table 2. Mean observed and back-calculated total lengths (mm) at age for males and females of Threespine stickleback *G. aculeatus* from estuarine area of Siahroud River (south Caspian Sea-Iran).

Age (years)	1+	2+	3+
Male			
Mean observed TL (mm)	52.22±5.34	58.34±1.71	69.33±1.16
Mean back-calculated TL (mm)	51.08±4.77	58.01±1.66	65.99±1.09
Female			
Mean observed TL (mm)	53.04±2.41	61.67±3.05	86.50±16.26
Mean back-calculated TL (mm)	52.00±2.40	59.89±2.78	85.54±14.12

**Fig.1.** Total length (mm) frequency of males and females of Threespine stickleback *G. aculeatus* from estuarine area of Siahroud River (south Caspian Sea-Iran).

(year⁻¹). The method of length-converted catch curve in FiSAT II (FAO-ICLARM-Stock Assessment Tools) was used to determine the total mortality (Z) rate (Pauly 1984; Sparre & Venema 1997; Gayanilo et al. 2005). The specimens had all been sexed accurately based on the examination of the gonads either with eye or with the stereomicroscope at magnifications of 30-40×. To determine spawning period, the GSI (%) was estimated and averaged for each month. to estimate fecundity and egg diameter, 57 ripe ovaries with stage of IV maturity caught between April and June used, all eggs counted, and absolute and relative fecundities calculated. The size (diameter) of ova determined by measuring (to the nearest 0.05mm) 30-40 ova randomly taken from the ovary using an ocular micrometer stereomicroscope.

Analysis of co-variance (ANCOVA) was performed to test significance differences between weight-length regressions of males and females. Chi-square test (χ^2) applied to test whether overall sex ratio is significantly different from 1:1 ratio (Zar 1984). Any difference in the mean GSI values among the

months (temporally) and between males and female (inter-sex) checked out by ANOVA. In all statistical analysis, the level of significant (alpha) is taken at 0.05.

RESULTS

A total of 405 specimens of *G. aculeatus* were caught and analyzed. In all specimens, lateral plates extend in lateral midline from the head to the caudal peduncle where they form a keel; therefore, the studied population is monomorphic for the completely plated form. The largest male had 70mm TL and 3.58g weight, while the maximum total length and weight of females were 98mm and 4.02g, respectively. Age readings indicated that the maximum age recorded in the population is 3+ in both males and females. The measurements showed that females are heavier and longer than males, implying significant difference between length and weight of sexes (Table 2) (ANCOVA, $F=141.1$, $P<0.05$). Regarding length frequency distribution (Fig. 1), the highest frequent length group in the population was 57-58mm length

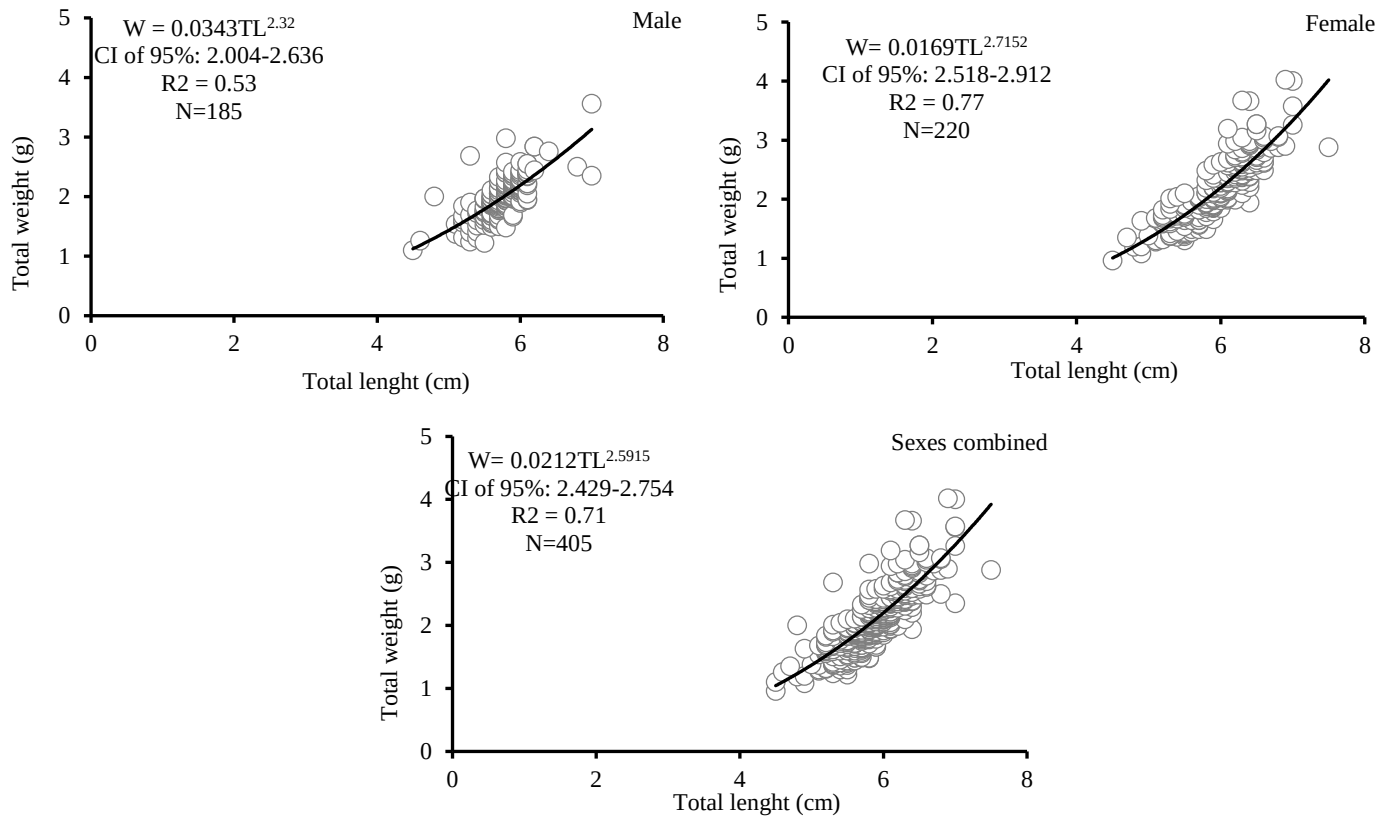


Fig.2. Relative growth curves (Total length-Total weight) for males, females and sexes combined of Threespine stickleback *G. aculeatus* from estuarine area of Siahroud River (south Caspian Sea-Iran).

Table 3. VBGF parameters and estimated longevity of of Threespine stickleback *G. aculeatus* from estuarine area of Siahroud River (south Caspian Sea-Iran).

	L_{∞}	K	t0	Tmax
Male	8.11	0.87	-0.46	3.45
Female	10.31	0.64	-0.47	4.69

class in males and 63-64mm in females, respectively. Males were absent in the length class of 70-71mm and beyond.

All length-weight relationships (LWRs) were found significant (Fig. 2). The allometry coefficients (the slope of regressions) imply that growth type is a kind of negative allometric for males and females, and whole population as well (t-test, $t_{\text{male}}=21.8$, $t_{\text{female}}=7.2$, $t_{\text{population}}=13.0$, $P<0.05$). In spite of similarity in the growth type, there were significant differences among the coefficients of allometry (t-test, $P>0.05$).

In the monthly adjusted growth parameters, males and females displayed differences in best-fitting von Bertalanffy growth curves by sex. The estimated results showed that L_{∞} of males is smaller than that of females, and K of females has slightly lower values than that of males, thus the males get their L_{∞} in a shorter time than female individuals (Table 3). The

index of ϕ' indicated the correctness of the VBGF estimations with the least possible errors in the calculations. As expected, the estimated theoretical longevity was longer for females than males, and females enjoyed greater longevity than males. Based on length-converted catch curves, the estimated total mortality (Z) (Fig. 3) was 2.20 (CI: 0.46-3.14) year^{-1} for females and 3.47 (CI: 1.56-4.49) year^{-1} for males, showing the longer lifespan of females of the stickleback. When the total mortality rate is converted into a percentage, the mortality estimated as high as 88.9% for females and 96.8% for males by the end of the first age, giving evidences for the shorter lifespan of males of the stickleback.

Despite the fact that the observed ratio of male: female was 1:1.2, the statistical analysis revealed no significant difference from 1:1 ration ($\chi^2=3.0$, $P>0.05$). Regarding the length group distribution (Fig.

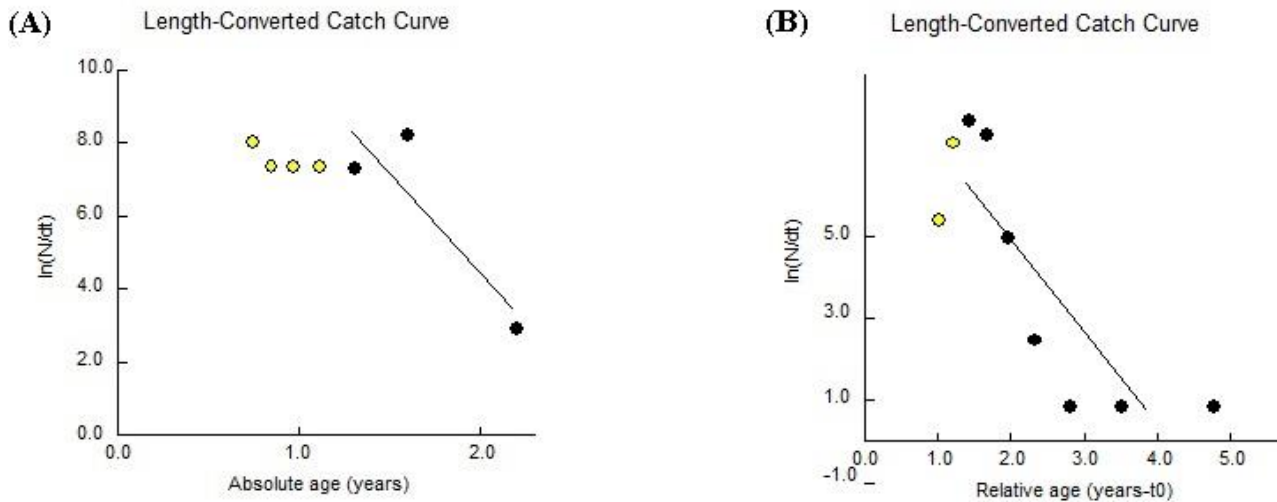


Fig.3. Length converted catch curve of (A) male and (B) females of Threespine stickleback *G. aculeatus* from estuarine area of Siahroud River (south Caspian Sea-Iran).

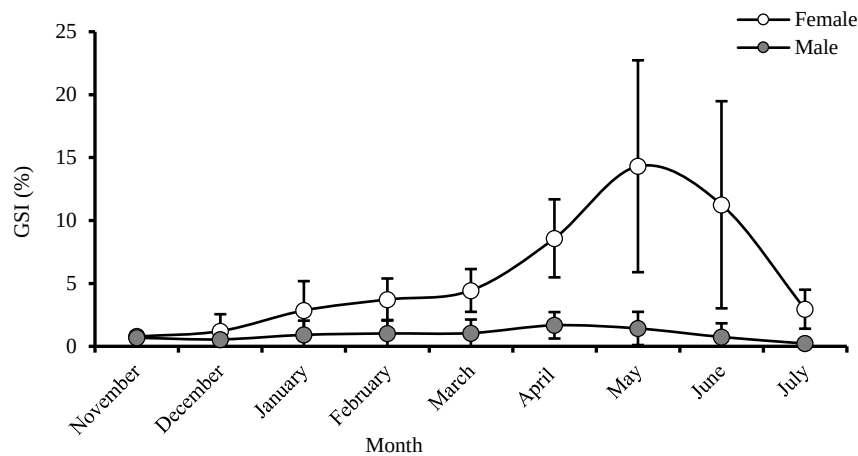


Fig.4. Monthly distribution of GSI in Threespine stickleback *G. aculeatus* from estuarine area of Siahroud River (south Caspian Sea-Iran).

1), the male: female ratio was unequal among the length classes, where males dominated in medium lengths of 55- 60mm.

The females had significantly larger gonadosomatic index (GSI) than males (ANOVA, $F=281.0$, $P<0.05$). In both sexes, monthly variation of this index (ANOVA, $F_{\text{female}}=21.1$, $F_{\text{male}}=5.2$, $P<0.05$) was approved during reproductive season. The highest GSI values were recorded in May as 14.3 ± 8.4 (SD) for females, and in April as 1.7 ± 1.0 (SD) for males. Based on the monthly cycle of the GSIs (Fig. 4), the spawning season for the estuarine population of the stickleback in the area of the southern Caspian Sea extended from April to June. Regarding colour and size, there were two kinds of ova, small colorless ova ranging from 0.32 to 0.66mm with an average of 0.43 ± 0.08 mm (S.D.), and large yellow yolk-filled

ones ranging between 0.60 and 2.15mm with averaged size of $1.16\text{mm}\pm 0.29$ (S.D.) (Fig. 5). For the estuarine population of the Caspian stickleback, size of both ova (small and large eggs) correlated negatively to the length and weight of fish, meaning increase in size (length and weight) of females would lead to decrease of diameter of eggs (Fig. 6). The results of the examination of the eggs showed that the numeric range of small ova was from 311 to 4709 per female with an average of 1513 ± 904 (SD), while that of large ova had a mean 454 ± 195 (SD) ranging from 128 to 885 egg per female.

Since there is no report on this species regarding being a batch spawner, the fecundity (both absolute and relative) was estimated based on the calculation of the total number of ova in the ovary.

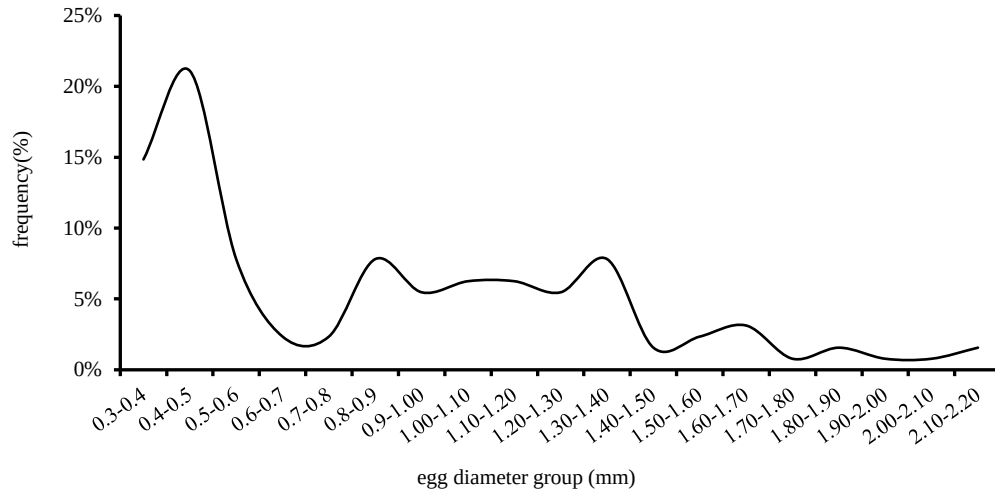


Fig.5. Size frequency distribution of oocytes diameters of female Threespine stickleback *G. aculeatus* from estuarine area of Siahroud River (south Caspian Sea-Iran).

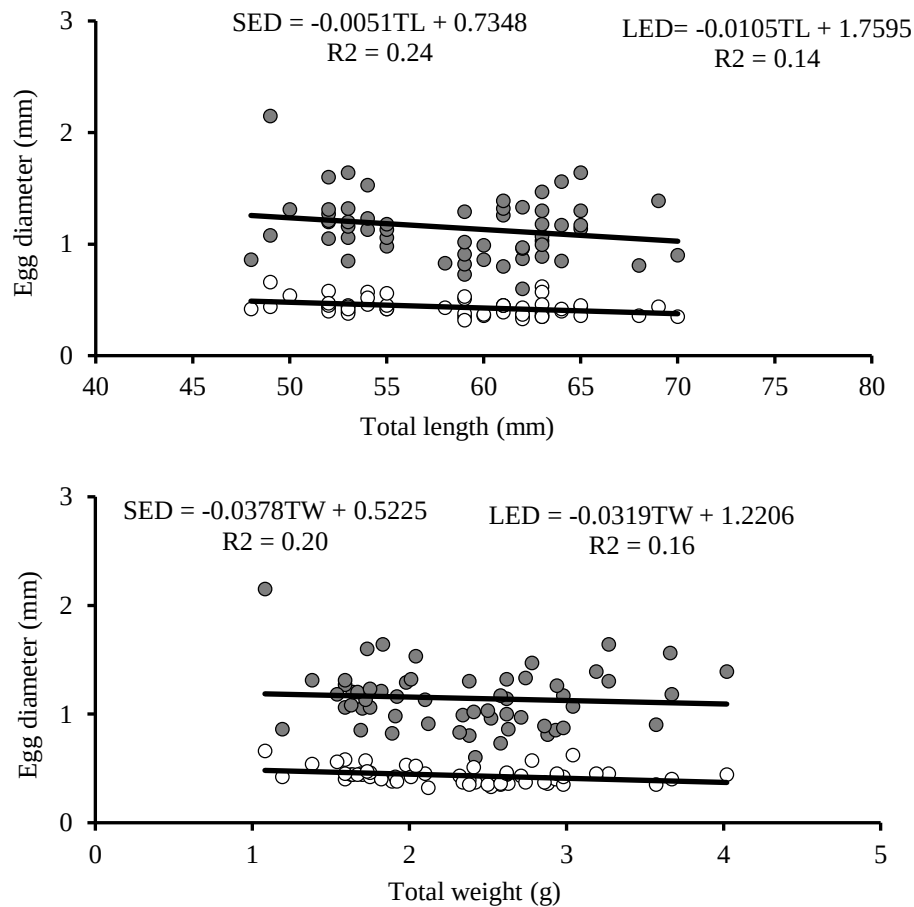


Fig.6. Relationship between ova diameter (SED: small egg diameter, LED: large egg diameter) with total length (mm) and total weight (g) of female Threespine stickleback *G. aculeatus* from estuarine area of Siahroud River (south Caspian Sea-Iran).

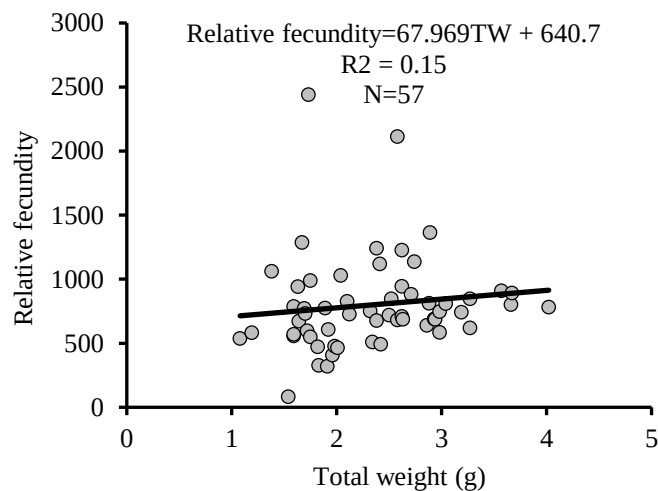
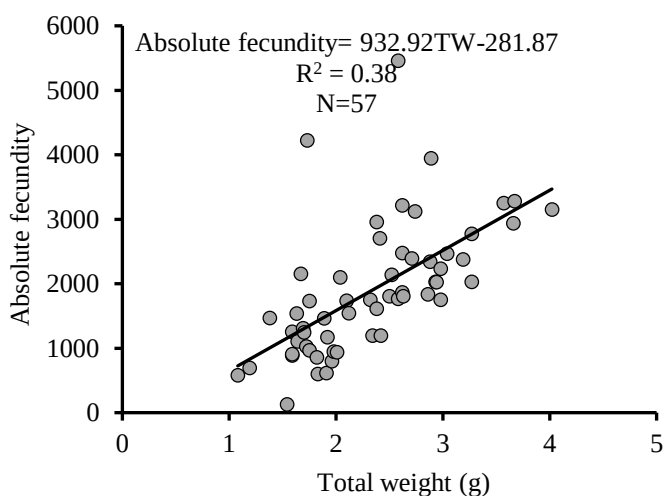
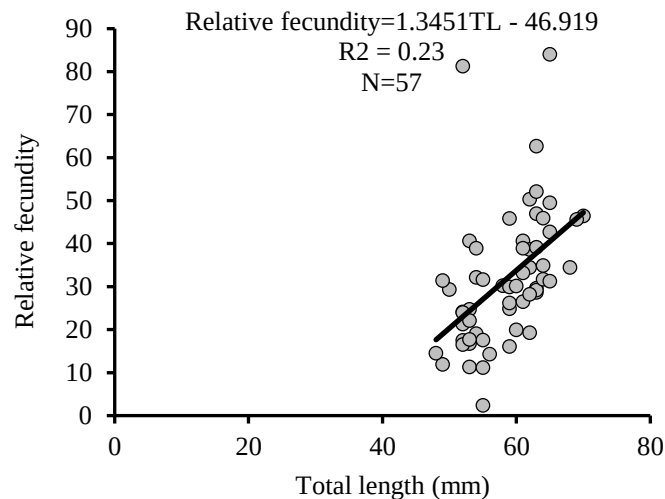
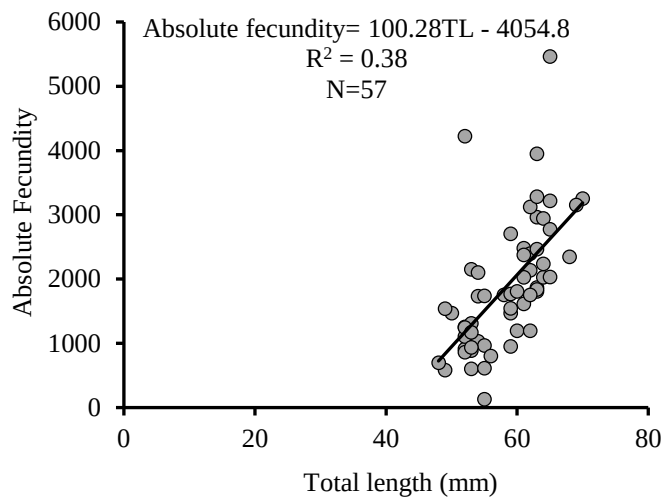


Fig.7. Relationship between absolute fecundity and fish total length (mm) and total weight (g) of female Threespine stickleback *G. aculeatus* from estuarine area of Siahroud River (south Caspian Sea-Iran).

Fig.8. Relationship between relative fecundity and fish total length (mm) and total weight (g) of female Threespine stickleback *G. aculeatus* from estuarine area of Siahroud River (south Caspian Sea-Iran).

The lowest absolute fecundity (AF) was 235 in a female weighing 1.96g and 1+ years old, while the highest AF observed was equal to 5460, which belongs to a female specimen with 3+ age and 2.56g of weight, and its mean value was 1837.34 ± 1021 (S.D.). The absolute fecundity showed a positive linear correlation with fish length and weight (Fig. 7). The regressions were statistically significant ($F_{TL}=21.9$, $F_{TW}=18.8$, $P<0.05$) with moderate correlation coefficients (AF~TL & AF~W: $R^2=0.38$).

Fecundity relative (RF) to fish weight (g) ranged between 84 and 2442 eggs per gram of females' weight, averaged out 799 ± 374 eggs/gram (SD), while its relative to the fish length fluctuated from 2 to 84

eggs/mm, with an average of 32 ± 15 (SD). It should be noted that relationships between the relative fecundity and fish size (length and weight) also were statistically significant, but had low correlations (RF~TL: $R^2=0.23$; RF~W: $R^2=0.15$) (Fig. 8).

DISCUSSION

The threespine stickleback developed three plate morphs in Europe: completely-plated, partially-plated and low-plated. Black Sea populations belong to the completely-plated morph (Paepke 2001); without doubt, southern Caspian basin population is also monomorphic completely plated form of this species. Therefore, the present work reports characteristics of

an estuarine monomorphic type this species from the southern Caspian Sea, and is important with respect to demographic parameters that generates variation in life history among populations of a species.

The parameters of the estuarine population consisted of four age groups being evident (minimum age: 0⁺ and maximum age: 3⁺). This age corresponds to age reported for this species from Gomishan wetland- SE Caspian Sea (Patimar et al. 2010; Izadi et al. 2021). Paepke (2001) noticed that members of the completely plated morph appear more frequently among the relatively old individuals than members of the low plate and partially plated morphs. Maximum ages observed in this study are in agreement with those of European completely plated morph populations. It can be concluded that longevity of threespine stickleback has minimum variance within this morph; it is almost independent of habitats.

Many studies show that the life histories of geographically distinct populations of a species vary considerably across the species distribution range (e.g. Lobon-Cervia *et al.* 1991 and 1996). Compared to the stickleback populations outside the Caspian Sea, the estuarine population of this species is similar to marine type form, which reaches a larger size than the freshwater inhabitant forms (Mori 1987; Wootton 1984; Paepke 2001). Different maximum size (length and weight) of a species between freshwater and marine types may be due to environmental variables remain constant and greater availability of food resources, suggesting the existence of higher growth rate in marine habitats that favors large length and weight in in marine forms (Snyder 1991; Coad & Power 1973). It seems that members of the completely plated morph (Caspian marine form) grow faster than those of the low and partially plated morphs. Another biological fact is that there is inter-sex difference in length and weight of the species. In the studied population, the general picture is that maximum size differed significantly between sexes of the studied population of the species. Males possess smallish size than females and appear to have a marked size, with females being significantly larger than males, although both males and females with 3⁺ years old are poorly represented in the population.

In the present study, the coefficient of allometry of length-weight relationship of *G. aculeatus* from an

estuarine area showed that the species grows allometrically, being negative allometry type for the studied population. The difference between sexes in the growth (regarding coefficients of allometry) can be explained by the differences in inter-sexual differences of growth. These results show that any estimation related to length and weight should be considered separately for each gender. The allometry coefficients (b of LWRs) of the estuarine population had considerable differences with previously reported values from the southern Caspian Sea (Esmaeili & Ebrahimi 2006; Patimar et al. 2010; Izadi et al. 2021), and from European waters (Wootton 1984; Crivelli & Britton 1987; Tarkan et al. 2006; Verreycken et al. 2011; Wilhelms 2013). This variability of the coefficient could be explained as a result of different habitat conditions forming local fish populations. This ecological evolutionary force is reflected as a change in form of body with populations. It can be stated that that different habitats and its ecological parameters have a significant impact on the value of coefficient of allometry in *G. aculeatus* populations. Totally, in the estuarine population from the study river, the b-value smaller than 3 (as isometric value) indicates that large individuals of the species have increased in length more than height or width, and the fish becomes more elongated as length increases.

The estimated VBGF parameters were different from those of population from Gomishan wetland- SE Caspian Sea. Izadi et al. (2021) reported the age-length growth model as $L_t = 7.10(1 - e^{-0.62(t+0.38)})$ for males and $L_t = 7.81(1 - e^{-0.41(t+0.60)})$ for females from Gomishan wetland. The estimated asymptotic length of the estuarine population of the species is remarkably higher than that of the studied population from the Gomishan wetland (southeast Caspian Sea). Dissimilarity in VBGF parameters among populations from different locations of range distribution of a species can be induced by varied ecological parameters. It is worth noting that these parameters vary between the males and females of this species. Therefore, like many of these fishes, these results indicate the presence of sexual dimorphism in this species. So far there is no published information on maximum lifespan of the stickleback in the literature. However, given the results, the maximum age for both sexes was 3⁺ in the estuarine population.

Regarding the observed maximum age in the studied population, the longevity of both males and females sounds reasonable for the species and, is not overestimated.

To the best of our knowledge, there is no report on mortality and survival rate of the species in the literature. However, it may seem that the estimates of Z to lie in a upper range of total mortality rates, and assume that the total mortality rate can vary among the populations of the species. Therefore, the estimated Z rate is specific to the estuarine population of the stickleback.

In the estuarine area of Siahroud River, the sex ratio didn't differ significantly from parity and was unlike that observed in Gomishan wetland- SE Caspian Sea (Patimar et al. 2010; Izadi et al. 2021). Wootton (1984) reported that the presence of highly geographical variations in sex ratio throughout the species range distribution. Since survival rate and longevity is different between males and females, the sex ration of 1:1 implies that that more males enter the estuarine area of the studied. In addition, the even-sex ratio in the estuarine population of a river from the southern Caspian Sea is probably the result of favorable environmental conditions for both sexes in the estuarine habitat. An observable notable fact in sex ration is dominance of males in a certain length group, which may be males defending the nests in the habitats while females are schooling outside the estuarine area.

Based on the recorded GSI (the mean highest value of 14.3 for females), it is apparent that total energy invested in gamete production by females, as opposed to somatic growth, is much lower in the southern Caspian basin than in European regions. Based on Paepke (2001), in Europe, the weight of the gonad's accounts for 25.6% of a female's body weight and in extreme cases, it can reach 56.4%. Even though female's GSI of southern Caspian basin population is lower than that of Europeans, inter-sex comparison of GSI shows that investment in reproduction (as energy allocation in gonads) by females much higher than males, a general fact for more than 80% of the fishes. It seems that higher reproduction investment (given as GSI) and relatively protracted spawning period (~3 months) of the stickleback females are important reproductive parameters, which, in turn, promotes high abundance and wide distribution of this species

as a successful species in the introduction pathway into new environments.

It is acknowledged that the freshwater threespine sticklebacks has larger eggs than the marine forms which have small sized eggs of large number evidencing a kind of adaptions to high availability of food items in sea environments (Wootton 1984; Paepke 2001). In the studied estuarine population, without considering the small sized white opaque eggs that is recruitment stock eggs, the large eggs had considerably smaller size than that of reported for other populations of this species (Coad & Power 1973; Craig & Fitzgerald 1982; Crivelli & Britton 1987; Mori 1987; Snyder 1991) and occurs in lower range of egg diameter that varies from 1.1 to 1.8 mm (Paepke 2001). Another notable thing related to the size of the ova is that the size variability of the ova produced by the estuarine population is larger. The high variability combined with smallish ova might be considered as the species induced variety in larvae of an estuarine population of the Caspian marine form of the threespine stickleback in the southern Caspian Sea. A reverse effect of fish length and weight on ova diameter was recorded for the estuarine population of species, an increase in length and weight of females caused a decrease of ova diameter. It could be supposed, however, that the larger females are incapable of increase the size of ova with length and weight growth. Therefore, this implies that invested energy in individual oocyte decreases with increasing in female size.

Fecundity is one of important biological traits in understanding life history of a species, which determines the base of population ability to produce viable offspring (eggs and larvae). It has been reported the fecundity, varied in a wide range, of this species in the literature. Comparison of egg production (hereafter fecundity) of the studied population of the species with previous reports shows that estuarine population of stickleback far more fecund (Wootton 1973; Mori 1987; Mori & Takamura 2004). When comparing egg production of the stickleback, it should be taken into consideration that in general the species has two forms: the freshwater and marine forms, with low and high fecundity, respectively. Regarding this, it is evident that the studied estuarine population is a marine form of the species.

Assessment of effect of fish length and weight on relative fecundity is fundamental in determination of species/population life history. In the present work, the weight and length-specific relative fecundity was confirmed and significant. This case is rarely observed in fish populations. To the best of the knowledge, there is no previous study about significance of the effect of fish size on relative fecundity in the stickleback populations. In the estuarine population, however, the larger females can increase the number of ova according to weight unit proportionally to the total fecundity. This implies that beside higher investments of total energy in producing offspring by the larger females (i.e. absolute fecundity), its proportional investment in reproduction (the energy allocation per unit of length and weight) tends to be significant with increasing in length and weight of females.

In conclusion, it has been shown that the estuarine population of the stickleback displays a few unique demographic parameters. These parameters relating to life history may be interpreted as a kind of growth-reproductive plasticity and adaptation to habitat conditions. Such plasticity and adaptation in the level of population can enhance the number and distribution of the stickleback in a wide range of areas in the southern Caspian basin and European waters as well.

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مقاله کامل

ویژگی‌های تاریخچه حیات ماهی سه‌خاره (*Gasterosteus aculeatus*) در یک ناحیه مصبی در بخش جنوبی دریای کاسپین، ایران

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چکیده: به منظور رفع خلأ موجود در دانش مربوط به جمعیت ماهی سه‌خاره (*Gasterosteus aculeatus*) در دریای کاسپین، در مجموع ۴۰۵ نمونه از این گونه در نزدیکی دهانه رودخانه سیاه‌رود (یک رودخانه کوچک)، در فاصله تقریبی ۵۰۰ متری از دریا، صید و از نظر ویژگی‌های اختصاصی تاریخچه حیات جمعیت مورد بررسی قرار گرفتند. الگوی رشد جمعیت مورد مطالعه، آلومتریک منفی بود. طول عمر ماهی سه‌خاره برای نرها و ماده‌ها به ترتیب ۳/۴۵ و ۴/۶۹ سال برآورد شد. پارامترهای رشد براساس مدل رشد فون برتالانفی برای نرها به صورت $L_t = 8.11(1 - \exp[-0.87(t + 0.46)])$ و برای ماده‌ها به صورت $L_t = 10.31(1 - \exp[-0.64(t + 0.47)])$ برآورد گردید. نرخ مرگ‌ومیر کل برای نرها ۳/۴۷ در سال و برای ماده‌ها ۲/۲۰ در سال به دست آمد. نسبت جنسی تفاوت معنی‌داری با نسبت ۱:۱ نشان نداد. دوره تولیدمثل از آوریل تا ژوئن (اواخر بهار تا اوایل تابستان) ادامه داشت و اوج آن در ماه مه مشاهده شد. دو نوع تخمک در تخمدان‌ها شناسایی شد: تخمک‌های کوچک و بی‌رنگ با میانگین قطر 0.43 ± 0.08 میلی‌متر و تخمک‌های بزرگ و سرشار از زرده با میانگین قطر 1.16 ± 0.29 میلی‌متر. تعداد تخمک‌ها در این دو گروه، به ترتیب در دامنه ۳۱۱ تا ۴۷۰۹ و ۱۲۸ تا ۸۸۵ قرار داشت. باروری مطلق برآوردشده دامنه وسیعی از ۲۳۵ تا ۵۴۶۰ تخمک به‌ازای هر تخمدان داشت و میانگین آن ۱۸۳۷/۳۴۱±۱۰۲۸ تخمک بود. باروری نسبی نیز از ۸۴ تا ۲۴۴۱ تخمک به‌ازای هر گرم وزن بدن متغیر بود. میانگین باروری نسبی ۷۹۹ تخمک به‌ازای هر گرم محاسبه شد.

کلمات کلیدی: ماهی سه‌خاره، رشد، مرگ‌ومیر، تولیدمثل، رودخانه سیاه‌رود، دریای کاسپین