Turkish Journal of Zoology

Volume 34 | Number 4 Article 4

1-1-2010

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TÜBİTAK

Research Article

Turk J Zool
34 (2010) 461-470
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doi:10.3906/zoo-0903-25

Life history features of the nonindigenous three-spined stickleback (*Gasterosteus aculeatus* Linnaeus, 1758) in the Gomishan wetland (southeast Caspian Sea, Iran)

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Received: 25.03.2009

Abstract: The Caspian Sea forms the southern limit of the distribution range of the three-spined stickleback (*Gasterosteus aculeatus*), but little is known about its life history in this area. A total of 362 specimens were collected from the Gomishan wetland (southeast Caspian Sea, Iran) to describe the stickleback's life history characteristics. Samples were taken monthly between February and July of 2008. The maximum ages of the population observed were 2+ years for males and 3+ years for females. The length-weight relationship (LWR) was estimated as $W = 0.0042TL^{3.711}$ for immature specimens, $W = 0.0095TL^{3.1328}$ for males, and $W = 0.0057TL^{3.4678}$ for females. The sex ratio was 1:2.63, in favor of females. Reproduction of the three-spined stickleback in the wetland occurred around March-June, with the highest average value of 2.82 for males and of 17.12 for females in April. Two kinds of eggs were found in the ovary: small white opaque eggs with a mean diameter of 0.549, and large yolk-filled eggs with a mean diameter of 1.317. The number of small eggs ranged from 311 to 4709, and of large eggs from 128 to 885. The mean absolute fecundity was 1241.69 eggs, while the mean relative fecundity was 535.24 eggs/g of body weight.

Key words: *Gasterosteus aculeatus*, size, growth, reproduction, life history, Iran, Caspian Sea

Introduction

Investigation of introduced species in new habitats can offer unique insight into life history variation, permitting determinations of the degree, direction, and rate of evolutionary change at the population level. In the southern Caspian Sea, the three-spined stickleback, *Gasterosteus aculeatus*, represents such a situation as one of the recent nonindigenous species in the south Caspian basin. It is distributed widely throughout the Holarctic region at latitudes ranging from 35° to 70° (Wootton, 1984), which comprises numerous differentiated allopatric populations displaying a large degree of variation in life history (Baker, 1994; Bell and Foster, 1994). The Iranian coast of the Caspian Sea forms the new distribution range of the three-spined stickleback and is inhabited by populations belonging to the fully plated (*Trachurus*) form, occurring in rivers, reservoirs, and coastal wetlands along most of the basin (Abdoli, 1993; Coad and Abdoli, 1993; Kiabi et al., 1999b). The mode of introduction of this nonindigenous species to Iran is unknown.

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Even though the three-spined stickleback has received attention for its life history patterns within its distribution range, to our knowledge, no detailed studies have been conducted in the southern Caspian basin. The references with very limited data on this fish from this basin are those of Abbasi et al. (1999), Abdoli (2000), and Naderi and Abdoli (2004), dealing with some morphological and biological characteristics. Given the climatic differences between the southern Caspian region and other distribution areas of the three-spined stickleback, the southern Caspian populations of this species are probably subject to different environmental conditions and may show habitat-specific adaptations in their life history traits. These adaptations could be attributed to recent adaptive responses of individual populations to their particular environments.

Therefore, for a better understanding of the life history characteristics of this species from the southeastern Caspian basin, this paper attempts to provide the first detailed information on its size and age structure, growth, sex ratio, gonadosomatic index (GSI), spawning duration, fecundity, and ova diameter, which provide insight into the life history of this species outside of its natural range.

Material and methods

The present study was carried out in the Gomishan wetland, which is a representative natural coastal wetland complex in the southeastern Caspian region. It has an area of 20,000 ha, including 4,850 ha of a large area of shallow brackish lagoons (S‰ = 15-22), with a maximum depth of 2.5 m and marshes covering at least 5,000 ha, at the extreme southeastern corner of the Caspian Sea (E53°54′34″-53°58′54″, N37°09′09″- 37°20′02″). The northern part of the wetland has been designated as a protected area. In the west, the wetland is bounded by low coastal dunes with typical sand dune vegetation bordering the Caspian beach. The bed formation consists of soft clay and mud. Aquatic macrophytes include *Ceratophyllum demersum*, *Callitriche palustris*, *Aeluropus littoralis*, *Myriophyllum spicatum*, *Phragmites australis*, *Potamogeton pectinatus*, *Juncus effusus*, *Typha angustifolia*, and *Zannichellia palustris* (Scott, 1995; Kiabi et al., 1999a).

Sampling was carried out monthly in the northern part of the wetland from February 2008 to July 2008, in the last week of each month on different days. The drag line of one wing of a beach seine net was fastened to the beach, while the net was taken out in a wide arc and then brought back to the beach. Outside of the collection period of February to July, three-spined sticklebacks were extremely scarce; one could hardly even capture a few specimens. In the field, all fish specimens were immediately preserved in a 4% formaldehyde solution.

The following measurements were taken at the wetland monthly: pH (Corning 410 pH meter), temperature (°C), and salinity (‰) (water quality checker U-10).

In the laboratory, total length (TL) was measured to the nearest millimeter. Total weight, weight of gonads, and subsamples were recorded with an electronic analytical balance to the nearest 0.01 g. Age was determined from opercula taken from both sides and validated by otolith readings. Opercula were reviewed for banding patterns 3 times, each time by a different person using a binocular microscope under reflected light at 20×-30×.

The relationship between the total length and total weight was determined by fitting the data with the equation $TW = aTL^b$, where TW is the weight in grams, TL the total length in centimeters, and a and b are the parameters to be estimated, with b being the coefficient of allometry based on the Pauly t-test (1984). Age-specific lengths were estimated using the equation $L_i = S_i S_c^{-1}(L_c - c) + c$, where L_i is the total length of the fish at age i, L_c the total length of the fish at capture, S_i the largest radius of the operculum at age i, S_c the largest radius of the operculum at capture, and c the intercept of the regression of body lengths on the operculum radii (Johal et al., 2001).

Sex was determined by visual examination of the gonad tissue either by eye or with the aid of a stereomicroscope. The gonadosomatic index, GSI % = (gonad weight/total body weight) × 100, was calculated for each fish, and all values were averaged for each sampling date. In order to estimate absolute and relative fecundities, we used the ovaries of 165 ripe females of maturity stage IV (Nikolsky, 1963), caught between March and June. Ovaries were removed, weighed, and then placed in Gilson's fluid for 3-4 weeks to harden the eggs and dissolve the ovarian membranes. The absolute fecundity (AF) was estimated by gravimetric method, using 3 pieces removed from the ovary. The relative fecundity index was calculated as $RF = AF/TW$, where AF is absolute fecundity and TW the total weight of the ovaries (Bagenal and Tesch, 1978). Average egg diameter was examined by measuring 30-40 eggs taken randomly from pieces of the ovaries of 165 ripe females caught in March-June. Measurements were made to the nearest 0.05 mm with an ocular micrometer microscope.

Using log-transformed data of $TW = aTL^b$ (as log TW = log a + b log TL), an analysis of covariance (ANCOVA) was performed to test significant differences in the weight-length relationships between sexes. The overall sex ratio was assessed using the chi-square test (Zar, 1984). Comparison of GSI values during the reproductive period and their temporal variation in each sex was carried out by analysis of variance (ANOVA). Statistical analyses were performed with the SPSS 11.5 software package and a significant level of 0.05 was accepted.

Results

Observations and fish frequency

In the coastal area of the wetland, during this study, water temperature ranged from 9.02 to 30.50 °C, salinity from 20.07‰ to 24.12‰, and pH from 8.14 to 8.59, and the fish fauna consisted of 15 fish species, including *Alburnus alburnus*, *Atherina boyeri*, *Bentophilus stellatus*, *Carassisus auratus*, *Clupeonella cultriventris*, *Gambusia holbrooki*, *Gasterosteus aculeatus*, *Hemiculter leucisculus*, *Knipowitschia caucasica*, *Liza saliens*, *Neogobius caspius*, *N. fluviatilis*, *N. melanostomus*, *N. syrman*, and *Syngnathus abaster*.

Based on beach-seine catches, the adult three-spined stickleback enters the wetland seasonally and stays in the coastal areas of the wetland from February to July. We observed individuals in advanced stages of maturity (greater than 40 mm TL, including spawning females), and also immature specimens (27-40 mm TL). The frequency of the fish peaked in April (Figure 1), when temperature was 14.5 °C, salinity 20.15‰, and pH 8.21. Dead specimens were found in the coastal area of the wetland in June and July.

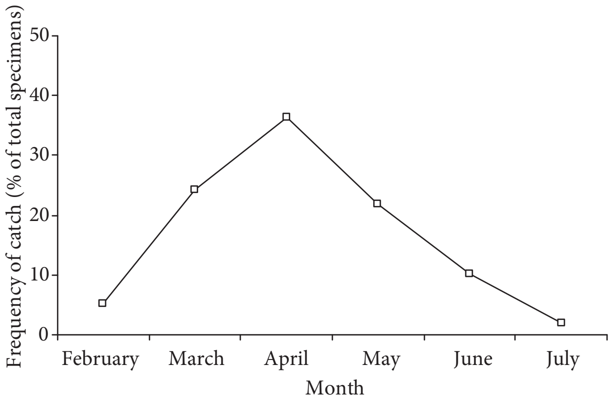

Figure 1. Monthly dynamic of catches of three-spined stickleback *G. aculeatus* in the Gomishan wetland (southeast Caspian Sea, Iran).

Size, age structure, and growth

During the sampling period, a total of 362 specimens of *G. aculeatus* were caught, ranging in total length from 27 to 73 mm and in total weight from 0.15 to 6.33 g. Males ranged from 46 to 62 mm and 1.15 to 3.09 g, while females ranged from 45 to 73 mm and 1.05 to 6.33 g. Opercula readings revealed that the older ages recorded were 3+ years for both sexes. Length frequency distribution of the fish (Figure 2) indicated that the most frequent size classes in the samples were 33-34 mm for immature specimens, 57-58 mm for males, and 53-54 mm for females. Males were absent in the length classes larger than 65-66 mm.

In the population, observed length-at-age differed between the sexes. Females were longer and heavier than males (Table 1) (ANCOVA, $P < 0.05$). Length-weight relationships were significant with a high regression coefficient (Figure 3).

The coefficients of the calculated regressions were significantly different between each of the considered groups. The b-values of the considered groups imply that the fish show positive allometric growth (t-test, $t_{immature} = 28.46$, $t_{male} = 2.94$, $t_{female} = 8.53$, $P < 0.05$).

Sex ratio

All individuals were sexed; the overall ratio of males to females was 1:2.63 and chi-square analysis showed significant differences from the ratio 1:1 ($\chi^2 = 49.48$, df = 1, $P < 0.05$). Females were more prevalent

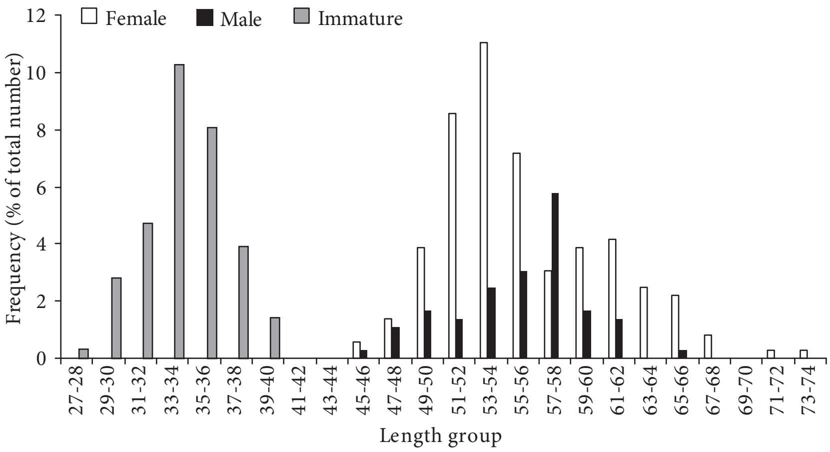

Figure 2. Total length (mm) frequency of immature, male, and female three-spined stickleback *G. aculeatus* in the Gomishan wetland (southeast Caspian Sea, Iran).

Table 1. Mean observed and back-calculated total lengths (cm) at age for male and female three-spined stickleback *G. aculeatus* in the Gomishan wetland (southeast Caspian Sea, Iran).

Age (years)	1+	2+	3+
Male	n = 48	n = 21	-
Mean observed TL (cm)	50.33 ± 2.24	57.58 ± 2.29	-
Back-calculated TL (cm)	51.09 ± 3.05	59.17 ± 3.44	-
Female	n = 118	n = 60	n = 2
Mean observed TL (cm)	52.5 ± 2.31	61.33 ± 2.91	72.00 ± 1.41
Back-calculated TL (cm)	51.97 ± 3.46	63.04 ± 3.60	73.08 ± 2.85

than males in all length groups, except in the 57-58 mm length group. Immature specimens were observed in length groups smaller than 39-40 mm.

Gonadosomatic index

Significant changes were observed in the temporal variation of gonad activity (ANOVA, females: $F_{5,256} = 14.12$, males: $F_{5,940} = 6.07$, $P < 0.05$). The GSI values of males were significantly lower than those of females (ANOVA, $F_{1,361} = 265.13$, $P < 0.05$). A period of low values of GSI in February was succeeded by a period of very rapid increase in the index in March. The highest average recorded values of GSI were observed in April for both sexes: 2.82 ± 0.43 (SD) for males and 17.12 ± 5.69 (SD) for females (Figure 4). Considering the high percentage of IV-V fish in March-June and the seasonal cycle of the gonadosomatic index, the reproductive period for this species in the wetland extended from March to June. Specimens that had fully spawned were caught in July.

Ovum diameter

Two kinds of eggs were found in the ovary: small white opaque eggs measuring between 0.20 and 0.83 mm with a mean value of 0.549 ± 0.109, and large yolk-filled eggs ranging from 0.77 to 1.96 mm with a mean value of 1.317 ± 0.233 (SD). The size distribution of the eggs indicated that the majority of small and large oocytes ranged from 0.5 to 0.6 mm and 1.4 to 1.5 mm, respectively (Figure 5). For the wetland stickleback, the diameter of small eggs was negatively correlated with fish size (length and

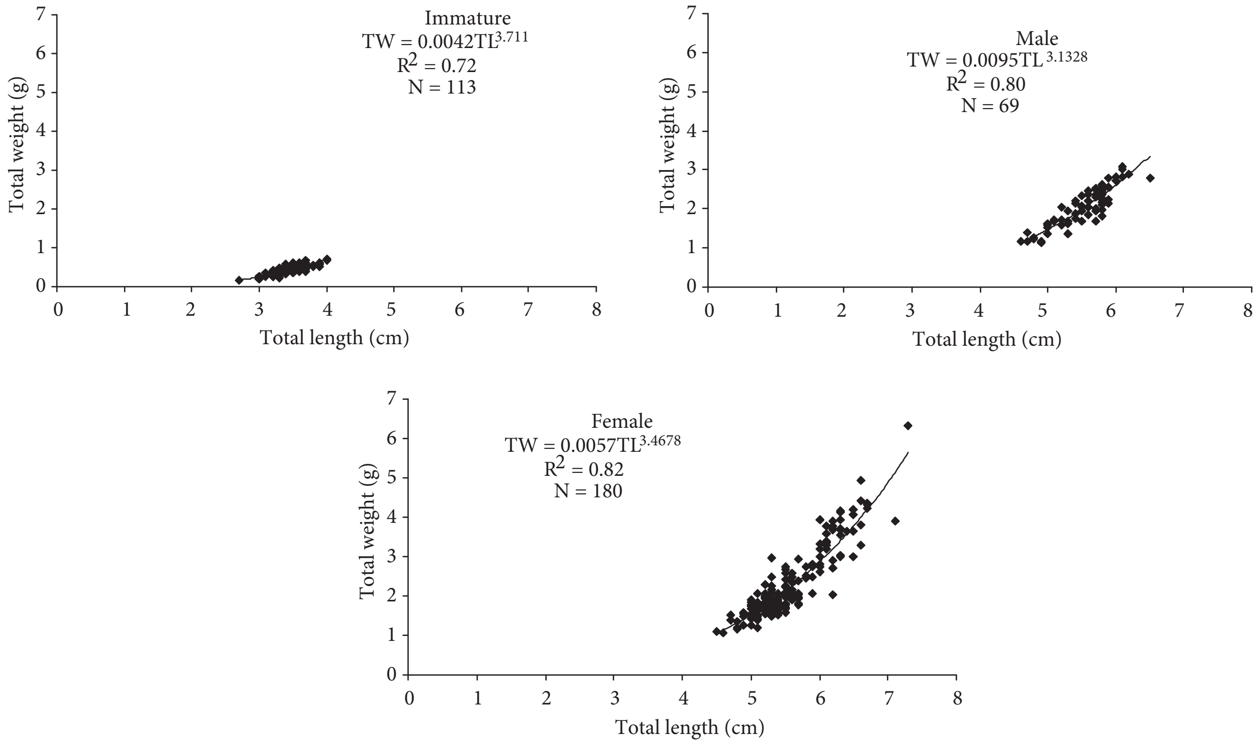

Figure 3. Relative growth curves (total length-total weight) for immature (top), male (middle), and female (bottom) three-spined stickleback *G. aculeatus* in the Gomishan wetland (southeast Caspian Sea, Iran).

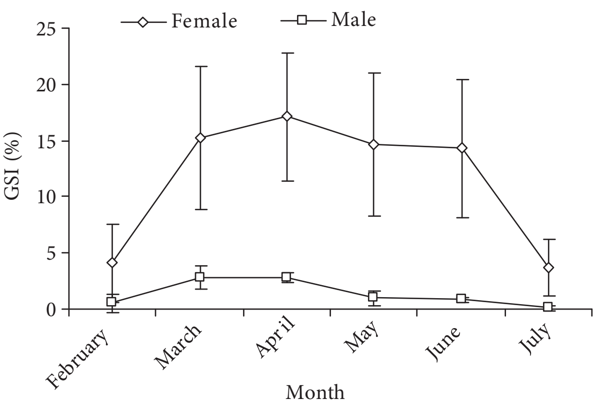

Figure 4. Monthly distribution of GSI in three-spined stickleback *G. aculeatus* in the Gomishan wetland (southeast Caspian Sea, Iran).

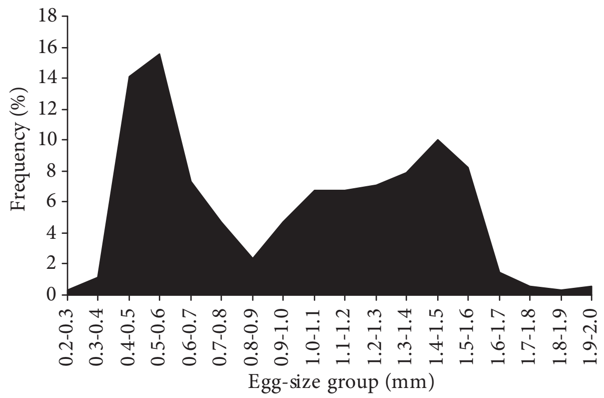

Figure 5. Size frequency distribution of the oocyte diameter of female three-spined stickleback *G. aculeatus* in the Gomishan wetland (southeast Caspian Sea, Iran).

weight), while diameter of the large eggs was positively correlated with the total length and weight of the fish (Figure 6). Even though the correlation coefficients of the regressions were low, the correlations were significant.

Fecundity

The analysis showed a positive significant effect of fish size on fecundity. A minimum value of 161 eggs was observed in a female of 1+ years weighing 1.82 g, and a maximum value of 4,130 eggs was observed in

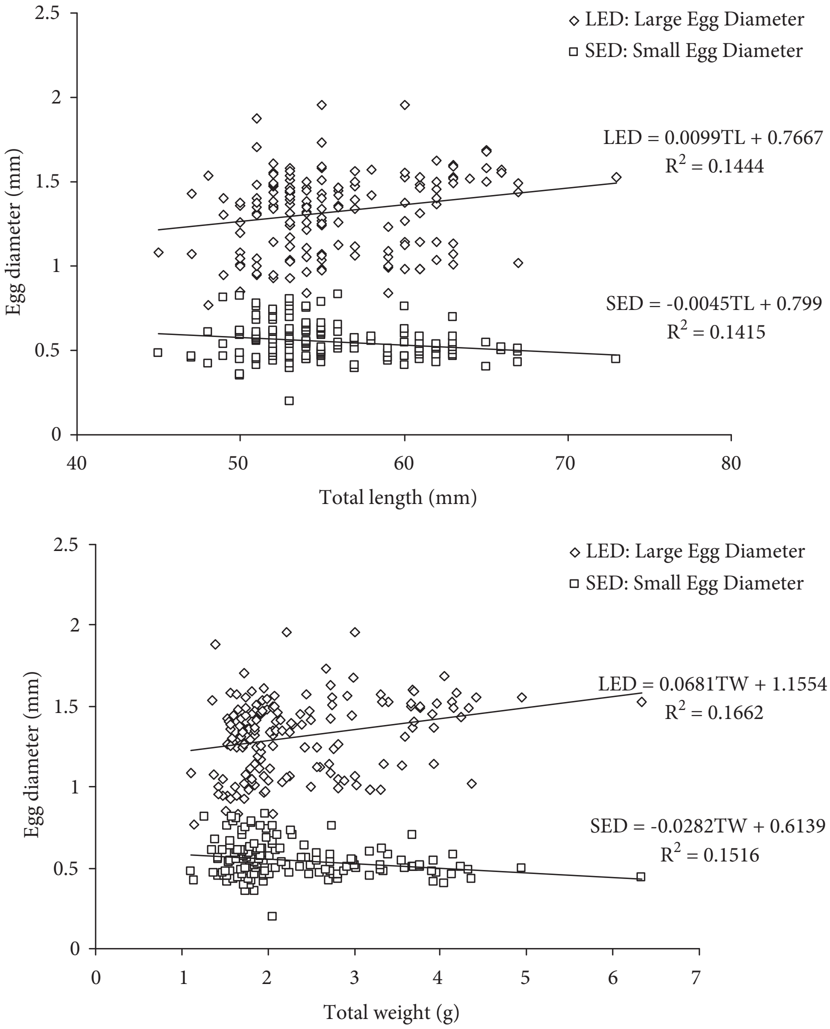

Figure 6. Relationship between ova diameter and total length (mm) and total weight (g) of female three-spined stickleback *G. aculeatus* in the Gomishan wetland (southeast Caspian Sea, Iran).

a fish of 3+ years weighing 3.19 g. The mean value of absolute fecundity was 1,241.69 ± 963.17 (SD) eggs/female. The linear function appropriately described the fecundity-total weight (TW, g) and fecundity-total length (TL, mm) relationships (Figure 7). All of the correlation coefficients calculated between fecundity and each of independent variables were judged to be moderate and statistically significant (TL: $F_{1,163} = 57.35$, TW: $F_{1,163} = 68.99$, $P < 0.05$).

Fecundity relative to total weight (g) fluctuated from 88.46 to 2,048.48 eggs/g, with a mean value of 535.24 ± 364.68 (SD), and relative to total length (mm) from 2.93 to 114.79 eggs/mm, with a mean value of 22.86 ± 114.79 (SD). The relationships of relative fecundity with body size (either to length or weight) were also found to be significantly positive, but correlation coefficients were low (Figure 8).

Discussion

As far as we know, life history variables of organisms often vary among habitats because of predictable changes in important environmental factors. The investigation of this variation is an important task in fish ecology. The *G. aculeatus*

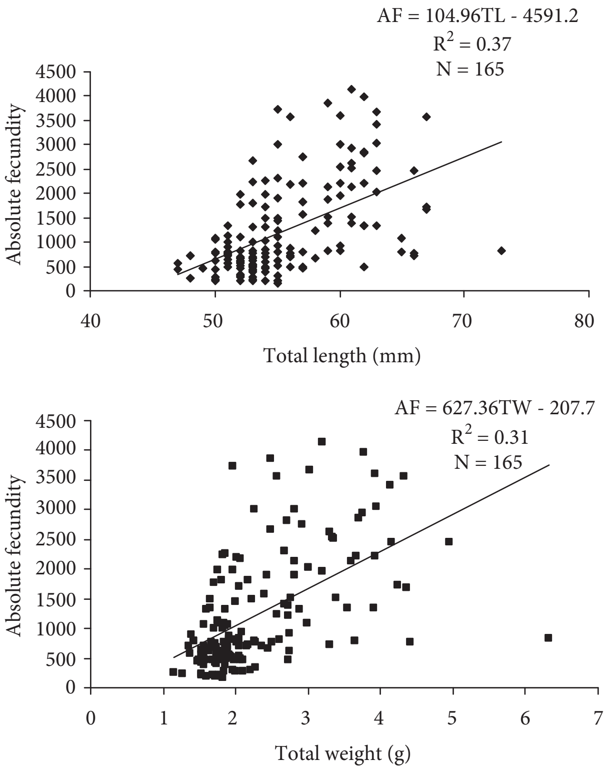

Figure 7. Relationship between absolute fecundity and fish total length (mm) and total weight (g) of female three-spined stickleback *G. aculeatus* in the Gomishan wetland (southeast Caspian Sea, Iran).

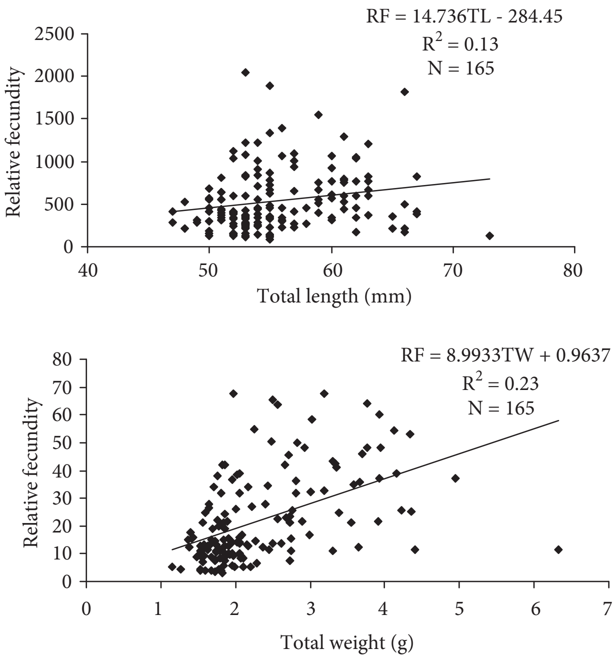

Figure 8. Relationship between relative fecundity and fish total weight (mm) and total length (g) of female three-spined stickleback *G. aculeatus* in the Gomishan wetland (southeast Caspian Sea, Iran).

population established in the Gomishan wetland represents the most southerly population in the nearly circumpolar range distribution within the Northern Hemisphere. Life history characteristics of populations living at range margins may deviate considerably from populations living in the core of the distribution range. This can have important evolutionary consequences.

Migration between habitats is a common phenomenon in many species of sticklebacks, although it does not seem to be obligatory. Generally, it occurs from a deep-water overwintering area to a shallow-water breeding area (Wootton, 1984). Specimens were scarce before February and after July, indicating that the wetland population is at least partially migratory. Presence of immature specimens, fish in advanced stages of maturity, and spawning individuals provided sufficient evidence to conclude that maturation and spawning takes place in the wetland.

Comparison of the largest size (length and weight) of the three-spined stickleback population in this study with that of other populations of this species shows that the Gomishan wetland population is similar to the anadromous type (*trachurus* type), reaching a larger length than the resident freshwater *leiurus* type (Wootton, 1984; Mori, 1987). The differences in the maximum length and weight of the fish between the anadromous *trachurus* type and the resident freshwater form may be due to the greater availability of food resources in marine habitats, different growth rate, and natural selections that favor a large size in migrants (Snyder, 1991).

Observed maximum size and longevity differed significantly between sexes of the fish. Males were smaller than females and appeared to have a shorter life span than females, although individuals older than 2 years were poorly represented in the samples.

In the present study, differences between males and females in the TL-TW relationship are explained by the differences in size distribution of the 2 sexes as a consequence of intersexual differences in growth, suggesting the convenience of using the appropriate estimate proposed for each group when calculating weights by sexes. The b-values estimated in the studied population are different from those cited by Wootton (1984) and Crivelli and Britton (1987). This reflects a variation in body form among populations. It seems that geographical location and associated environmental conditions can significantly affect the value of *b* in *G. aculeatus*. A b-value larger than 3 in the three-spined stickleback populations shows that large specimens have increased in height or width more than in length, such that the fish becomes less round as length increases.

In the Gomishan wetland, the overall sex ratio was biased in favor of females, and there was a noticeable trend in female dominance with age. This is probably the consequence of either the higher survival rate and greater longevity of females, or of the greater endurance of females to environmental variability. In terms of the sex ratio, the three-spined stickleback population in the wetland is "investing" in females, leading to more offspring. This strategy could help the species to establish itself rapidly in the ecosystem.

In the studied population, the breeding season extends from March to June, a prolonged breeding season of approximately 4 months. It is reported that the length of the breeding season of the three-spined stickleback appears to range from 2 to 5 months, varying with locality over the wide range of this species (Coad and Power, 1973). It seems that the high reproductive investment by females (as expressed by GSI) and the prolonged breeding season are important parameters in the reproductive strategy of this fish.

It is generally known that the freshwater population of *G. aculeatus* has larger egg sizes than the anadromous populations (*trachurus* form), which have large numbers of small-sized eggs representing adaptation to the rich food supply in marine waters (Wootton, 1984). In the population under consideration in this study, the mean size of large eggs (1.317 mm) is considerably smaller than those recorded in other populations (Table 2), and the degree of size variability (SD = 0.23 mm) exhibited by the Gomishan wetland population is greater. This variability, coupled with the large number of ova, could be considered as a reproductive strategy by the population of three-spined sticklebacks in the wetland. However, the reason for such a reproductive strategy remains unclear. The large heterogeneity in the size of the eggs may be also indicative of the release of a new clutch of large eggs generated from the remaining small eggs, which is common in the three-spined stickleback (Baker, 1994). A negative effect of fish size on the diameter of small eggs was observed, while larger spawners were able to increase the size of large eggs with growth. This means that the total energetic investment in large, ripe eggs tends to increase with increasing fish size.

Table 2. Comparison of the size of large eggs among three-spined stickleback *G. aculeatus* populations studied in its range distribution.

Localities	**Water Category**	**Egg Diameter (mm)**	**Reference**
Mayer Lake (western Canada)	Freshwater	1.87	Moodie, 1972
Matamek River (eastern Canada)	Freshwater	1.56	Coad and Power, 1973
St. Lawrence estuary (Canada)	Brackish water	1.39	Craig and FitzGerald, 1982
Camargue wetland (France)	Brackish water	1.49 ± 0.02	Crivelli and Britton, 1987
Yamayoke River (Japan)	Freshwater	1.46 ± 0.84	Mori, 1987
Tsuya River (Japan)	Freshwater	1.72 ± 0.85	Mori, 1987
Jizo Creek (Japan)	Freshwater	1.81 ± 0.111	Mori, 1987
Navarro River upstream (California, USA)	Freshwater	1.70 ± 0.01	Snyder, 1991
Navarro River estuary (California, USA)	Freshwater	1.73 ± 0.02	Snyder, 1991
Navarro River inland freshwater (California, USA)	Freshwater	1.77 ± 0.02	Snyder, 1991
Gomishan wetland (Iran)	Brackish water	1.31 ± 0.24	Present study

Table 3. Comparison of absolute fecundity among three-spined stickleback *G. aculeatus* populations studied in its range distribution.

Localities	Water Category	Absolute Fecundity (min.-max.)	Reference
River Rheidol (UK)	Freshwater	86.5 (40-295)	Wootton, 1973
Yamayoke River (central Japan)	Freshwater	168 (48-304)	Mori, 1987
Tsuya River (central Japan)	Freshwater	122 (41-236)	Mori, 1987
Jizo Creek (central Japan)	Freshwater	172 (109-298)	Mori, 1987
Kahoku-gata (central Japan)	Freshwater	401 (203-578)	Mori, 1987
Lake Towada (northern Japan)	Freshwater	395 (204-790) in 1985	Mori and Takamura, 2004
Lake Towada (northern Japan)	Freshwater	406 (213-541) in 1992	Mori and Takamura, 2004
Gomishan wetland (Iran)	Brackish water	1,241.69 (161-4130)	Present study

A wide range of values for the fecundity of the three-spined stickleback has appeared in the literature. When the egg production by female three-spined sticklebacks observed in this study is compared with that of previous reports, it is clear that the observed fecundity is higher than reported by Wootton (1973), Mori (1987), or Mori and Takamura (2004) (Table 3). The comparison is complicated because of the existence of 2 forms of the stickleback, the anadromous *trachurus* form with high absolute fecundity, and the freshwater *leiurus* form, which has considerably less fecundity. Even among *trachurus* populations, however, it looks like the Gomishan wetland population has a very high fecundity.

A significant effect of fish size on relative fecundity was observed for the fish. It can be hypothesized, however, that the largest spawners were able to increase the quantity of eggs per unit of somatic weight proportionally to the absolute number of eggs. This means that the total energetic investment in reproduction tends to be higher in the larger fish. Consequently, the proportional energetic investment in reproduction (as energy allocation per unit of fish size) also seems to increase with fish size.

In conclusion, it is clear that this three-spined stickleback population from the Gomishan wetland displays a number of different life history patterns. These traits may represent genetically based or plastic adaptations to the environmental conditions caused by the southern Caspian climate. It can be concluded that the life history patterns of this species are habitat-specific and greatly vary throughout its geographical range. Future studies may reveal whether the observed variation in growth and reproduction has a plastic or a genetic basis. This will contribute to our understanding of the processes underlying adaptation at range margins.

References

Abbasi, K., Valipour, A.R., Talebi Haghighi, D., Sarpanah, A.N. and Nezami, S. 1999. Atlas of Fishes of Iran, Inland Water of Guilan Province, Novin Press Co., Rasht. (In Persian).

Abdoli, A. 1993. Three-spined stickleback in southern basins of the Caspian Sea. Abz. 4: 10-13. (In Persian with English abstract).

Abdoli, A. 2000. The Inland Water Fishes of Iran, Iranian Museum of Nature and Wildlife, Tehran.

Bagenal, T. and Tesch, F. 1978. Methods for Assessment of Fish Production in Fresh Waters, IBP Handbook 3, Blackwell, Oxford.

Baker, J.A. 1994. Life history variation in female threespine stickleback. In: The Evolutionary Biology of the Threespine Stickleback (eds. M.A. Bell and S.A. Foster), Oxford University Press, UK, pp. 144-187.

Bell, M.A. and Foster, S.A. 1994. Introduction to the evolutionary biology of the threespine stickleback. In: The Evolutionary Biology of the Threespine Stickleback (eds. M.A. Bell and S.A. Foster), Oxford University Press, UK, pp. 1-27.

Coad, B.W. and Abdoli, A. 1993. Exotic fish species in the fresh waters of Iran. Zool. Mid. East 9: 65-80.

Coad, B.W. and Power, G. 1973. Observation on the ecology of lacustrine population of the three-spined stickleback (*Gasterosteus aculeatus* L. 1758) in the Matamek River system, Quebec. Nat. Can. 100: 437-445.

Crivelli, A.J. and Britton, R.H. 1987. Life history adaptation of *Gasterosteus aculeatus* in a Mediterranean wetland. Envir. Biol. Fish. 18: 109-125.

Johal, M.S., Esmaeili, H.R. and Tandon, K.K. 2001. A comparison of back-calculated lengths of silver carp derived from bony structures. J. Fish Biol. 59: 1483-1493.

Kiabi, B., Abdoli, A. and Ghaemi, R.A. 1999a. Wetland and riverian ecosystems of Golestan province, Department of the Environment Protection, Golestan Province, Gorgan.

Kiabi, B.H., Abdoli, A. and Naderi, M. 1999b. Status of the fish fauna in the south Caspian Basin of Iran. Zool. Mid. East. 18: 57-65.

Moodie, G.E.E. 1972. Predation, natural selection and adaptation in an unusual three-spined stickleback. Hered. 28: 155-167.

Mori, S. 1987. Divergence in reproductive ecology of the three-spined stickleback, *Gasteroseus aculeatus*. Jap. J. Ichthyol. 34: 165-175.

Mori, S. and Takamura, N. 2004. Changes in morphological characteristics of an introduced population of the threespine stickleback *Gasterosteus aculeatus* in Lake Towada, northern Japan. Ichthyol. Res. 51: 295-300.

Naderi, M. and Abdoli, A. 2004. Fish species atlas of south Caspian Sea basin (Iranian waters), Iranian Fisheries Research Organization, Tehran. (In Persian and English).

Nikolsky, G.V. 1963. The Ecology of Fishes (trans. L. Birkett), Academic Press, London.

Pauly, D. 1984. Fish population dynamics in tropical waters: a manual for use for programmable calculators, ICLARM Studies and Reviews 8.

Scott, D.A. 1995. A directory of wetlands in the Middle East, IUCN, The World Conservation Union.

Snyder, R.J. 1991. Migration and life history of the threespine stickleback: evidence for adaptive variation in growth rate between populations. Envir. Biol. Fish. 31: 381-388.

Wootton, R.J. 1973. Fecundity of the three-spined stickleback, *Gasterosteus aculeatus* (L.). J. Fish Biol. 5: 683-688.

Wootton, R.J. 1984. A Functional Biology of Sticklebacks, Croom Helm, London.

Zar, J.H. 1984. Biostatistical Analysis, Prentice Hall, Englewoods Cliffs, NJ.