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ICHTHYOLOGY

Caspian Anadromous Shad *Alosa kessleri kessleri* (Grimm, 1887) from the Akhtuba River, Lower Volga River Basin: Biological and Morphological Features

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Abstract—Data on the dynamics of anadromous migration, age composition, body length, body weight, and morphometric characteristics of Caspian anadromous shad from the Akhtuba River are presented. Currently, Caspian anadromous shad from the Akhtuba River is monomorphic; no temporal groups have been identified. The population is represented by medium-sized young early-maturing (age of 2–3 years) fish with life longevity less than 5 years. Generally, according to the most important diagnostic signs, first and foremost, to the number of gill stamens and some plastic signs, Caspian anadromous shad from the Akhtuba River falls within the range of the diversity that is typical for the form.

Keywords: Caspian anadromous shad, Akhtuba River, Lower Volga River Region, upstream migration, external morphology

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INTRODUCTION

In the past, anadromous shad of the *Alosa* genus were characterized by a high abundance; they used the Volga River basin for breeding, migrating upstream to the Kama and Oka rivers, and thus played a very important role in the fishery (Berg, 1948; Svetovidov, 1952; Kazancheev, 1981). However, since 1958, when the Volgograd hydroelectric power station was put into operation, large-scale changes in the ecosystem of the entire Volga River basin took place. Anadromous shad lost most of its reproduction areas, suffered a catastrophic decline in abundance, and the diversity of their intraspecific forms has decreased. At the end of the 20th and beginning of the 21st century, there has been some increase in the abundance of only one of the forms of migratory herring, namely Caspian anadromous shad *Alosa kessleri kessleri* (Grimm, 1887), and it even became the object of a small fishery in the delta sections of the Volga River (Vodovskaya, 1998, 2001; Kim, 2012; Pyatikopova, 2019). At the same time, the degree of knowledge of the Caspian anadromous shad in modern conditions is insufficient; data on the characteristics of its biology and morphology need to be clarified.

The available literature on the Caspian anadromous shad of the Lower Volga River basin is mainly devoted to the species group inhabiting the delta and mainstream of the Volga River, where the fishing and monitoring of this species is currently underway (Vodovskaya, 1998, 2001; Fomichev, Taradina, 2006; Vasil'eva et al., 2012; Voinova, 2012, 2016; Pyatikopova, 2019). However, there is no data on the Caspian anadromous shad from the Akhtuba River in the works performed in 20th–21st centuries, although it is an important component of the complex Volga–Akhtuba system and is important for fisheries (Nikolaev, 1962; Zvolinskii et al., 2015).

The purpose of the work is to study the features of anadromous migration of the breeders of the Caspian anadromous shad; their size, age, and gender composition; and morphological characteristics the Akhtuba River at the present status.

MATERIALS AND METHODS

The material was collected in May–July, 2014—2018, in the Akhtuba and Volga rivers, in the Kharabalinskii District of Astrakhan oblast. The sampling sites are located 150 km upstream from the upper boundary of the Volga River delta and 300 km upstream from the dam of the Volgograd hydroelectric station. In the studied section, the Volga and Akhtuba rivers flow in parallel channels; the width of the floodplain between them is 2–4 km. The width of Akhtuba River (at low water) varies from 190 to 420 (an average of 313) m; the depth in the reaches 10–11 m and, in the channel pits, ≤22 m. The mainstream is greatly meandering, a sharp dump of depth down to 8–11 m is formed at the reaches, and the opposite river bank is shallow with a smooth increase in depth to the channel edge at a depth of 6–8 m. The studied sections of the Akhtuba River do not differ in structure from those upstream and downstream (Nikolaev, 1962). In 2014–2018, annual observations of the breeder migration and fish behavior after spawning were performed; data on size, gender, and age composition and morphology were obtained on the basis of the samples taken in 2018.

A fixed ordinary scale mounted on the coastal gabions was used to determine the water level; the water temperature was determined every hour using Vemco Minilog T8K 8bit DataLogger automatic electronic recording sensors.

Caspian anadromous shad breeders were caught during their anadromous migration (from late April to late June) using a pole-and-line with six hooks (locally called a *samodur*) and a rubber shock absorber; all water layers from the bottom (6–8 m) to the surface were monitored. The migration intensity of the breeders was estimated by the catches of six operators (six tackles, one tackle per person, in accordance with the Rules of Sport and Recreational Fishing in the Astrakhan oblast), which carried out the capture in a fixed place throughout the entire period of work. The *samodur* has low selectivity (specimens with a body length of 12–15 to 50 cm are caught with equal success), thus the ratio of fish with different body lengths in the catch adequately reflects their ratio among migratory schools. The migration intensity was evaluated by catch per unit of effort, expressed as kg/h with an effort of six gears of six hooks each (36 hooks in total).

Unbiased samples were used when the entire control catch (15 L in total) was analyzed. In total, two samples were taken for the study: one was collected on May 18–21, 2018 (peak of the breeder migration) and the other on June 2–6, 2018 (end of the migration). The samples were studied separately; subsequently, their comparative analysis was carried out to identify phenetic diversity during the spawning period. The volume of material used for different types of analysis is presented in the corresponding tables and figures.

The length and body weight were measured for all fish that were caught; a scale sample was taken under the dorsal fin to determine the age; the specimen sex and the gonad maturity stage were visually determined at autopsy (Pravdin, 1966). A classical instrumental (manual) morphometric analysis was performed using 25 plastic and 6 meristic signs to study morphological features (Berg, 1948; Svetovidov, 1952; Pravdin, 1966). In order to avoid a system error (Reshetnikov, Popova, 2015; Reshetnikov, Tereshchenko, 2017), all fish measurements were performed under standard conditions by one operator.

The age of the Caspian anadromous shad was determined by analyzing the scales in accordance with Chugunova's method (Chugunova, 1959) and taking into account the recommendations of Yilmaz and Polat (Yilmaz, Polat, 2002) on acrylate plates using the electronic images for the analysis (image-capture system, Leica DMLS microscope with a set of lenses with magnifications from ×2.5 to ×10, digital camera Canon X500-D).

The dataset was processed by standard methods of univariate statistical analysis.

RESULTS

Anadromous migration of breeders. The Caspian anadromous shad started to migrate along the Akhtuba River at the collection point on May 9–12, when the water warmed up to >12°C. The peak of the migration occurred in the third decade of May; in the last days of May, the migration intensity of the Caspian anadromous shad dropped sharply until the end at June 10–12 (Fig. 1). Despite the significant fluctuations in the daily average temperature, sometimes caused by heavy rains and a short cold snap, the migration of the Caspian anadromous shad did not noticeably change (Fig. 1).

The migration of the Caspian anadromous shad takes place at a depth of 1–3 m along the steep banks of the river at a distance of 3–8 m from the water edge; the schools of Caspian anadromous shad pass wide and shallow areas with a troughlike profile of the riverbed along the intersect in the middle of the river. Even during mass migrations, the schools of Caspian anadromous shad never give themselves away by splashing, which differs from the data of Svetovidov (Svetovidov, 1952). No migration of the Caspian anadromous shad was recorded in the dark; at night, large schools of the Caspian anadromous shad disintegrate into small clusters confined to small river boils with whirlpools that form at the river promontories at high washed-out spring banks. The formation of large schools of Caspian anadromous shad and their movement upstream begins at dawn, which corresponds to the data of previous years (Pavlov, 1979).

At the beginning and end of the migration, the Caspian anadromous shad moves in separate, sometimes small schools; the interval between them may reach several hundred meters. During the peak of the migration, the Caspian anadromous shad migrates as a continuous mass, and there is almost no interval between the schools. In most cases, other fish species are absent in the schools of Caspian anadromous shad, but sometimes, especially in dry years, sichel *Pelecus cultratus* (L., 1758) migrates upstream along with the Caspian anadromous shad. In 2014 and 2015 there were cases when the sichel abundance migrating upstream was comparable that of Caspian anadromous shad, but the sichel moved in the surface-water

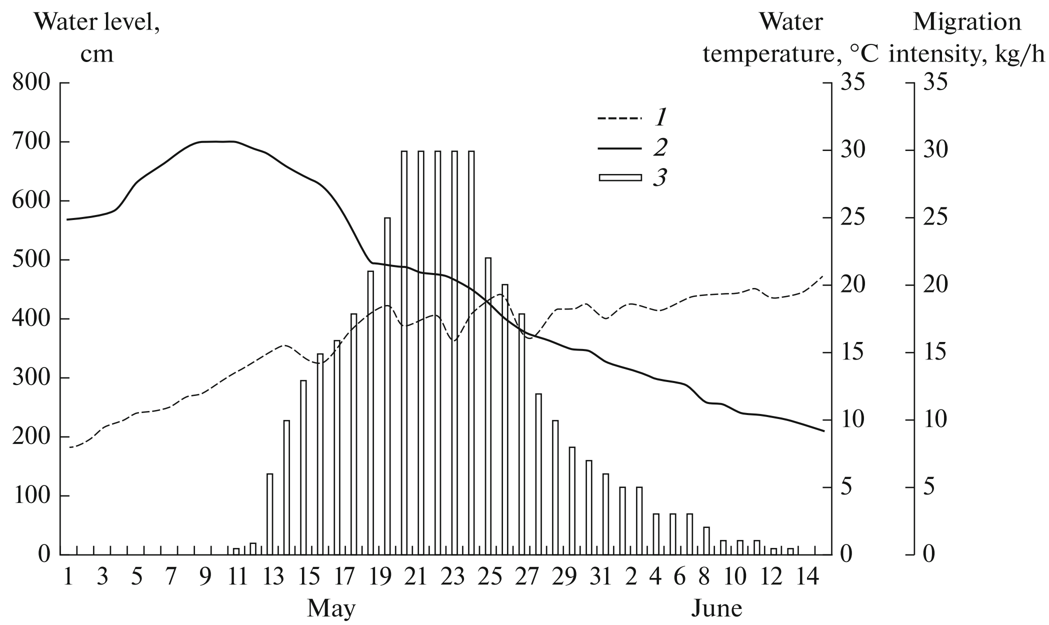

Fig. 1. Dependence of the migration intensity of the Caspian anadromous shad along the Akhtuba River in the study area on the temperature and water level in 2018: (*1*) Average daily water temperature, °C; (*2*) water level; (*3*) migration intensity of the Caspian anadromous shad breeders.

layers and the Caspian anadromous shad moved at a depth of ~3 m.

No spawning of the Caspian anadromous shad was found in the surveyed area, namely, in the course of the Akhtuba River from the village of Bugor to the village of Kharabali (~40 km) and in the Volga River from the village of Kopanovka to Kapitanskii Island (~50 km). In particular, no dense accumulations of the fish were found at the surface in the channel sections of the Volga or Akhtuba rivers, in the river backwaters, or canals, and no breeders were observed jumping out of the water and splashing at the surface in evening hours, which is characteristic of the spawning Caspian anadromous shad belonging to the Volga River grouping (Berg, 1948; Svetovidov, 1952).

Downstream migration of the spawned breeders. The spawned specimens of Caspian anadromous shad appears in the Akhtuba and Volga rivers in the study area on June 21–25, the highest migration intensity of the living and the transport of dying and dead fish is observed in the first week of July. By July 12–15, the after-spawning migration ends. The dead and dying specimens of Caspian anadromous shad are carried by the current into the backwaters or small bays, where they may accumulate in large quantities. For example, in 2018, in a small backwater of the Volga River at the Chub Island, more than 3000 dead specimens accumulated near the surface on an area of 200 × 100 m. During the downstream migration of the spawned fish, predators actively eat them, first and foremost, pikeperch *Sander lucioperca* (L., 1758) and catfish *Silurus glanis* (L., 1758). In the last week of June and the first week of July, the dying Caspian anadromous shad serves as the basis for pikeperch nutrition; its frequency of occurrence is 100% in the stomachs of the specimens with a body length >35 cm (2014–2018, n = 830). Pikeperch with a body length of 50–55 cm can swallow five to six shads with a body length of ~30 cm (n = 112). In the end of June, the frequency of occurrence of Caspian anadromous shad in the stomachs of small catfish weighing ≤20 kg reaches ~100% (n = 78); for large individuals weighing >50 kg, the frequency of occurrence does not exceed 40% (n = 44). At the same time, the Caspian anadromous shad is almost absent in the diet of pike *Esox lucius* (L., 1758) (n = 64); no cases have been recorded for the asp *Aspius aspius* (L., 1758) (n = 96).

Description. The body is elongated, without a sharp narrowing in the caudal part of the body, moderately high (the greatest height is 18–23% of the body length by Smith (Lsm)). The body is slightly compressed laterally in the anterior part and is swollen in the caudal region. The head is large, 20–26 (average 22.8)% Lsm, interorbital distance 19–27 (20.8)% of head length (C), moderately high, 13–19 (15.2)% Lsm or 65–75 (70.5)% C, the eye horizontal diameter 17–22 (19.7)% C. The jaws are either of equal length (in 43% of the studied fish), or the lower jaw is protruding forward (in 57% of the studied fish); both variants are found in both small (<250 mm) and large individuals. The pectoral fins are short, 11–16 (12.9)% Lsm. The bases of the ventral fins in all studied fish are located behind the vertical, passing through the beginning of the dorsal fin.

Table 1. Body length, the number of gill setae in the Caspian anadromous shad of different groups, and statistical estimation of differences between groups

Characteristic	Groups of fish with different lengths and shapes of gill stamens				Assessment of differences, T_{st}/M-U		
	I $n = 19$	II $n = 68$	III $n = 160$	IV $n = 109$	I : II	I : III	I : IV
Lsm, mm	258 ± 13.3 198–336	266 ± 10.2 202–367	282 ± 8.2 201–370	277 ± 11.6 199–365	0.47 –	1.53 –	1.07 –
Sp. br	70.5 ± 0.24 64–86	70.3 ± 0.21 61–84	70.1 ± 0.19 59–82	70.0 ± 0.20 57–81	0.63 0.8234	1.31 0.6352	1.60 0.4416

Lsm is the fish body length by Smith; Sp. br is the number of gill setae. Numbers above the line are the mean and the error of the mean; limits of variation are below the line. T_{st} is Student's test; M-U is the Mann–Whitney *U*-test.

The number and shape of gill stamens are characterized by significant variability. In the pooled sample ($n = 356$), not a single individual was found with broken, bent, or serrated gill stamens, which was indicated by different authors as a characteristic feature of the Caspian anadromous shad (Berg, 1948; Svetovidov, 1952; Kazancheev, 1981). However, four morphs may be distinguished by the length of the gill stamens and the shape of their outer edge. In morph I (5.8%), the gill stamens are long, exceed the gill petals in length, and their outer edge forms a convex arc; in morph II (19.3%), the branchial stamens are equal in length to the branchial petals, and their outer edge is slightly convex and wavy; in morph III (44.3%), the branchial stamens are equal in length to the branchial petals and the outer edge is straight; in morph IV (30.6%), the branchial stamens are shorter in length than the branchial petals; their outer edge is straight. Different lengths and shapes of gill stamens are found in both small and large individuals, during the peak of migration and at its end. Despite some differences in the limits of variation in the number of gill stamens and their length, there are no significant differences between groups in the number of gill stamens and body length (Table 1).

Age and gender composition. During the peak of migration, the age composition of males and females is generally similar: in the combined sample ($n = 186$), specimens at the age of 3 years dominate (85.2%), specimens at the age of 4 years (8.4%) take the second place, and individuals aged 2 (5.2%) and 5 (3.2%) years old are found in a small amount. At the end of the migration, the age composition of the Caspian anadromous shad is somewhat simpler: specimens at the age of 3 (97.5%) and 4 (2.5%) years were found in the sample ($n = 170$). At the peak of the migration, males slightly dominate; their share is 52% but, at the end of the migration, the numbers of females become significantly larger and the proportion of males drops down to 24%. During the peak of migration, almost all females have gonads at stage IV of maturity; some individuals carried fluid oocytes in the caudal part of the ovaries. A similar picture was observed in males, when most individuals had testes at stage IV of maturity and 15.2% of males had signs of stage V in the caudal part of the testes. A somewhat more complex picture was at the end of the upstream migration. During this period, 9.5% of females had ovaries at stage III–IV of maturity and the remaining females at stage IV–V; among males, specimens with testes at stage IV–V of maturity prevailed.

Body length and body weight. The body length of the Caspian anadromous shad in the combined sample ($n = 356$) varies from 198 to 370 (average 264.9) mm and body weight from 92 to 489 (average 146.6) g. The average length and body weight of the females significantly exceeded those of males in the same age classes (Table 2). Throughout the entire period of anadromous migration of Caspian anadromous shad, males were smaller than females, but no significant differences have been found (males, age 3 years, peak of migration: end of migration, $T_{st} = 1.05$, $p < 0.95$; females, age 3 years, peak of migration: end of migration, $T_{st} = 1.38$, $p < 0.95$; males age 4 years, peak of migration: end of migration, $T_{st} = 1.29$, $p < 0.95$).

Morphometric characteristic. Analysis of sexual dimorphism by plastic and meristic signs did not reveal significant differences between males and females in any of the 32 plastic and six meristic signs. In addition, no significant differences were found between the samples of the peak of the migration ($n = 161$) and the end of the migration ($n = 112$). The analysis of the distributions of the values in the combined sample showed that all plastic and meristic signs are characterized by a normal distribution: the asymmetry (*As*) and excess (*Ex*) indicators do not reach threshold levels in any case (Table 3). In this regard, the data on the pooled (males and females, peak and end of the migration) sample are provided in Table 3.

DISCUSSION

Our results relate to a separate section of the Lower Volga River basin—the Akhtuba River—which had not

Table 2. Body length and body weight of Caspian anadromous shad

Age, years	Migration peak		End of migration	
	Males $n = 100$	Females $n = 89$	Males $n = 41$	Females $n = 133$
2	206 (198–215) [8] / 96 (92–102)	218 (195–230) [5] / 112 (93–141)	–	–
3	249 (209–286) [78] / 127 (97–204)	277 (205–343) [69] / 177 (96–310)	239 (220–251) [31] / 105 (97–203)	258 (234–285) [99] / 112 (92–206)
4	284 (231–327) [10] / 205 (108–311)	319 (269–365) [11] / 303 (185–472)	279 (230–302) [10] / 181 (100–295)	302 (276–325) [34] / 167 (145–189)
5	316 (293–337) [4] / 309 (206–388)	325 (312–370) [4] / 332 (293–489)	–	–

Average body length, mm, is shown above the line; average body weight, g, is under the line. Min–max values are given in parentheses; number in squares is the sample size, ind.

previously been studied for the migratory forms of herring. The significance of the Akhtuba River for the reproduction of the Caspian anadromous shad is extremely rarely mentioned in published works; there is fragmentary information that ~12% of the local school reproduced in the river in the 1960–1980s (Vodovskaya, 2001). Data on the morphological and biological features of the Caspian anadromous shad inhabiting the Akhtuba River are missing.

The results of our study allow us to conclude that at present the Caspian anadromous shad from the Akhtuba River is monomorphic; no temporal groups have been identified. According to the most important diagnostic features, first and foremost, according to the number of gill stamens and some plastic signs, the Caspian anadromous shad from the Akhtuba River as a whole corresponds to the variability series typical of the form.

At the same time, it seems important to conduct a comparative analysis of the results obtained by us on the Caspian anadromous shad from the Akhtuba River with historical data. We carry out such a comparison with caution, since almost all of them belong to the regions of the delta of the Volga River (Berg, 1948; Svetovidov, 1952; Kazancheev, 1965, 1981; Vodovskaya, 1974, 2001; Pyatikopova, 2019). Temporal changes in many parameters of the Caspian anadromous shad were revealed (Table 4). In particular, the body length and body weight have significantly decreased and the proportion of younger fish in the spawning school has increased. This is especially noticeable for the period from the 1960s to the 1970s, when large older (7–8 years) individuals with a body length >50 cm and a body weight ≤2 kg disappeared from the catches. Apparently, this was due to a sharp reduction in the routes of anadromous migration in the Volga River. Even Svetovidov (Svetovidov, 1952) pointed out that, before the dams appeared, the largest individuals of the Caspian anadromous shad migrated farthest up the river, reaching the mouth of the Oka River.

The trend towards a decrease in the body size and body weight of Caspian anadromous shad continues to the present (Pyatikopova, 2019). Our data confirm the trends observed by other researchers: in 2018, sexually mature males and females were observed for the specimens at the age of 2 years, which had not been previously noted, and not a single specimens over the age of 5 years has been caught (Table 4).

Changes affected also the shape and number of gill stamens (Table 4). Until 1959 and in the 1960–1970s, the individuals of the Caspian anadromous shad were often present with short, broken off, and curved branchial stamens (Vodovskaya, 1974). In our samples obtained in 2018 in the Akhtuba River, no such individuals were found. After regulating the flow of the Volga River in the 1970s, the maximum registered number of the gill stamens per specimen was >90 (Vodovskaya, 1974; Kazancheev, 1981), and in our sample it was 86 (2018). It is possible that changes in the number and structure of gill stamens reflect changes in the nature of its nutrition. According to Svetovidov (1952), Kazancheev (1981), and Vodovskaya (1984, 2011), Caspian anadromous shad is a predator and feeds on small fish and crustaceans in the sea. It is possible that feeding fish could lead to the deformation and breakage of gill stamens. According to Svetovidov (1952) and Kazancheev (1981), broken stamens were much more common in large specimens, which consumed mainly fish. Perhaps the absence of the specimens with broken stamens at present is a consequence of changes in the nutrition of the Caspian anadromous shad in the sea, but this aspect is not actually covered in the up-to-date literature.

Table 3. Morphometric characteristics of Caspian anadromous shad the Akhtuba River, pooled sample ($n = 273$)

Characteristic	Parameter				
	M ± *m*	*SD*	*Lim*	*As*	*Ex*
Lsm	262.7 ± 1.1	18.2	198–338	0.34	0.10
Plastic signs, % Lsm					
C	23.83 ± 0.09	0.63	22.3–25.3	0.02	0.26
ao	6.36 ± 0.05	0.36	5.6–7.3	0.11	0.25
o	4.69 ± 0.05	0.37	3.9–5.5	0.27	–0.58
op	12.98 ± 0.07	0.51	11.0–14.1	–0.24	0.32
io	4.96 ± 0.04	0.33	4.4–6.4	0.25	0.71
hcz	16.77 ± 0.07	0.55	15.6–17.7	–0.27	–0.75
hco	12.65 ± 0.09	0.66	11.5–14.1	0.30	–0.47
lm	11.93 ± 0.07	0.56	10.8–13.9	0.20	0.76
hmx	3.21 ± 0.04	0.27	2.5–3.7	–0.16	–0.36
lmd	14.65 ± 0.10	0.69	13.0–16.0	0.15	–0.25
H	22.13 ± 0.15	1.09	20.3–24.8	0.13	–0.13
h	6.75 ± 0.06	0.39	6.2–8.0	0.15	0.41
pl	14.25 ± 0.11	0.81	12.4–16.2	0.02	0.22
lD	12.58 ± 0.10	0.67	11.3–14.1	0.24	–0.15
hD	10.92 ± 0.14	1.01	9.6–14.0	0.24	0.79
lA	15.24 ± 0.10	0.68	13.7–16.7	0.17	–0.40
hA	6.86 ± 0.09	0.62	5.4–8.1	0.13	–0.21
lP	14.27 ± 0.09	0.64	12.2–15.8	–0.29	0.24
lV	8.85 ± 0.06	0.44	8.1–10.0	0.26	0.42
aD	44.75 ± 0.17	1.17	42.3–47.9	0.23	0.48
pD	41.34 ± 0.14	0.98	39.1–43.7	0.31	–0.22
aV	47.13 ± 0.14	0.97	44.6–49.0	–0.31	–0.17
aA	67.66 ± 0.15	1.04	65.6–70.1	0.15	0.04
P–V	24.03 ± 0.12	0.89	22.0–25.8	–0.27	–0.49
V–A	21.39 ± 0.16	1.12	19.3–23.8	0.09	–0.65
Plastic signs, % C					
ao/C	26.62 ± 0.21	1.52	23.8–29.7	0.19	–0.66
o/C	19.69 ± 0.20	1.40	16.7–22.2	–0.09	–0.72
op/C	54.47 ± 0.24	1.67	49.3–58.1	–0.12	0.66
io/C	20.86 ± 0.22	1.51	18.8–24.3	0.19	–0.71
hcz/C	70.41 ± 0.34	2.35	64.7–74.6	–0.10	–0.45
lm/C	50.06 ± 0.25	1.74	45.9–54.7	–0.12	0.16
lmd/C	61.45 ± 0.29	1.75	55.8–65.6	–0.16	0.24
Meristic signs					
D	14.47 ± 0.06	0.78	12–16	–0.07	0.48
A	18.54 ± 0.09	1.18	16–22	0.21	–0.08
P	14.80 ± 0.07	0.95	11–17	–0.14	0.72
V	7.76 ± 0.04	0.49	6–9	–0.20	0.53
sp. br	70.20 ± 0.44	5.62	57–86	0.24	–0.48
vert.	52.13 ± 0.10	1.01	50–54	–0.11	–0.22

Lsm is the body length by Smith; **C** is the head length; **ao** is the snout length; **o** is the horizontal eye diameter; **op** is the postorbital distance; io is the interorbital distance; **hcz** is the head height at the back of the head; **hco** is the head height at the orbit level; **lm** is the upper jaw length; **hmx** is maxillary bone height; **lmd** is mandible length; **H** is largest body height; **h** is caudal peduncle height; **pl** is caudal peduncle length; **lD** is dorsal fin base length; **hD** is dorsal fin height; **lA** is the length of the anal fin base; **hA** is the anal fin height; **lP** and **lV** are the lengths of the pectoral and ventral fins; **aD, pD, aV, aA, P–V** and **V–A** are the antedorsal, postdorsal, anteventral, anteanal, pectoventral and ventroanal distances; **D, A, P**, and **V** are the numbers of branched rays in the dorsal, anal, pectoral, and ventral fins; **vert.** is the number of vertebrae. ***Ex*** and ***As*** are indices of excess and asymmetry, respectively; ***Lim*** is the limits of variation; ***SD*** is the standard deviation; ***M* ± *m*** is the mean value and the standard error of the mean. Other designations are the same as in Table 1.

Table 4. Comparative analysis of biological and morphological parameters of Caspian anadromous shad in different years

Parameter	Historical period, localization of places and references		
	Until 1959, the delta and lower reaches of the Volga River (Berg, 1948; Svetovidov, 1952)	1960–1970s, delta and lower reaches of the Volga River (Kazancheev, 1965, 1981, Vodovskaya, 1974, 1977, 2001)	2016–2018, the Akhtuba River, ~300 km upstream from the Caspian Sea (original data)
Dates of anadromous migration	End of April and beginning of July. During the migration, several peaks were observed, usually in mid-May and mid-June	April 10–20 to early/mid-June (according to some references, until early July). One peak in the second half of May	First decade of May to the first decade of June; the peak of the migrations lasts for ~9 days (May 20–28)
Body length, cm	30–52 (40–42)	24–46 (33)	19–37 (26)
Body weight, g	300–2000 (500–600)	200–1000 (460)	90–490 (146)
Age, years	3–7, mostly 4, 5	2–8, mostly 3, 4, 5	2–5, mostly 3
Number of gill stamens	59–92 (72.4)	51–96 (74.6)	52–86 (72.0)
Shape of the gill stamens	In large fish, they are thick and coarse—some of them are broken off, some are curved—with lateral spines. Gill stamens are shorter than petals, forming a straight line	In large fish, strong, thick, rarely planted, often broken off; in small fish they are thinner and shorter	Straight, not curved or broken off, smooth, more often equal in length to gill lobes. Form a straight line, less often a convex arc. No dimensional variability detected
Number of vertebrae	47–50 (48.9)	49–54 (51.8)	50–54 (52.1)
C, % Lsm	22–25.0 (23.1)	22–26 (23.2)	20–26 (22.8)
lP, % Lsm	13.7–15.9 (14.9)	13–16 (14.6)	11–16 (12.9)
H, % Lsm	20–28 (23.9)	20–28 (23.8)	18–23 (22.1)
io, % C	18–23 (20.3)	–	19–27 (20.8)
hcz, % Lsm	15–18 (16.5)	15–19 (17)	13–19 (15.2)

Designations of signs are given in Table. 3. The limits of variation are given and the numbers in parentheses indicate average value.

The number of vertebrae is another sign affected by significant changes. Over a 60-year period, the number of vertebrae has naturally increased, and not only have the limits of variation expanded, but a significant shift in the variation curves has also occurred. At present, the limits of variation of the trait are 50–54, whereas they were 47–50 in the first half of the 20th century (Berg, 1948; Svetovidov, 1952). It is likely that such a significant shift in the trait is caused by a change in the reproduction conditions; namely, the complex of hydrogeomorphological parameters of the Middle Volga River, where the Caspian anadromous shad had been reproducing before the dams of the Volgograd and Saratov hydroelectric power plants were put into operation, differs significantly from those in the Lower Volga River basin. In addition, changes were also revealed in some plastic signs; in particular, at present, the head height and body height of Caspian anadromous shad are smaller than before.

Obviously the shifts in the biology and morphology of the Caspian anadromous shad, as well as a catastrophic decline in its abundance, are a consequence of changes in the conditions for the anadromous herring species of the Volga River due to river-flow regulation. As a result of this flow regulation, a radical reorganization took place under the spawning conditions of the Caspian anadromous shad and the course of the early freshwater phase of its life cycle. Before the regulation of the river by dams, the developed fry migrated to the North Caspian Sea from the Volga River (Pavlov, 1979; Vodovskaya, 1990, 1994, 1996; Pyatikopova, 2019); currently, larvae predominate. The natural reproduction efficiency of Caspian anadromous shad has declined 10–11 times under the new conditions (Vodovskaya, 2001); therefore, despite a slight increase in the number of Caspian anadromous shad, the conditions of its natural reproduction are considered unfavorable (Vodovskaya, 2001; Voinova, 2012, 2013, 2016; Pyatikopova, 2019). In fact, the population of Caspian anadromous shad is currently in a state of stress and is very vulnerable to any adverse external factors, for example, to the low volume of Volga River flow (Vodovskaya, 1996, 2001; Pyatikopova, 2019). The high vulnerability of the Caspian anadromous shad is confirmed by the fact of its rapid decline in the early 2000s as a result of even small amounts of fishing, which had to be urgently stopped (Voinova, 2013; Lepilina et al., 2016).

CONCLUSIONS

The environmental parameters for the existence of the Caspian anadromous shad are far from optimal, and the process of developing local adaptations for its sustainable survival in modern changing conditions is still ongoing. In this regard, there is a reason to consider the identified changes in biological and morphological characteristics a reflection of active microevolutionary processes aimed at the effective adaptation of the form/species to the newly changed ecosystem conditions of the Lower Volga River basin. At the same time, the results suggest further studies of the structure and diversity of the Caspian anadromous shad group from the Lower Volga River basin. In particular, it seems important to conduct an extended differential analysis of the parameters of the structure of the Caspian anadromous shad population from the Volga and Akhtuba rivers, including by molecular genetic analysis.

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COMPLIANCE WITH ETHICAL STANDARDS

Conflict of interests. The authors declare that they have no conflict of interest.

Statement on the welfare of animals. All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

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