

# Reproductive Condition in the Caspian Anadromous Shad *Alosa kessleri kessleri* (Alosidae) during Spawning Migration in the Volga River

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**Abstract**—This paper describes the state of the gonads of Caspian anadromous shad, *Alosa kessleri kessleri* (Grimm, 1887), migrating for spawning in the Akhtuba River. In May of 2021, the peak of spawning was recorded at a water temperature of 17–18°C. Females and males had gonads at the developing and spawning-capable phases. The fork length (*FL*) of females averaged 254.1 mm, and their body weight was 178.9 g; for males, this was 209.9 mm and 87.5 g, respectively. Most females were over three years old, while males were between one and three years old. The gonadosomatic index (GSI) in females and males averaged 8.71 and 3.67%, respectively. Among the asynchronously developing secondary growth oocytes in the spawning capable gonads, three different-sized groups were distinguished for intending to spawn the same number of oocyte batches. The number of primary growth oocytes (26.7–59.4% of germ cells on sections) allows for considering these fish as iteroparous. The diameter of the tertiary vitellogenic oocyte was about 800 μm.

**Keywords:** Caspian Anadromous Shad *Alosa kessleri kessleri*, gametogenesis, life cycle, the Volga-Caspian fishery basin

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## INTRODUCTION

Anadromous shads of the genus *Alosa* were essential components of the ecosystem of the Volga basin in the past, when they used the riverbed of the Volga to the rivers Kama and Oka for breeding and were of great importance in the fishery (Berg, 1948; Svetovidov, 1952). In 1958, the start of the Volzhskaya hydro-based power plant's (Volzhskaya HPP) operation occurred, causing the Caspian anadromous shad losing access to the center of the Volga basin, where its main spawning grounds were located. As a result, there was a catastrophic drop in the stocks of this species.

At the end of the 20th century and the beginning of the 21st century, the shad population had recovered, but in smaller quantities than before the dam's construction (Vodovskaya, 2001; Voinova, 2012, 2016; Lepilina et al., 2016). At this time, a significant change was noted in several biological parameters, such as sex, age composition, and the morphological characteristics of individual fish. According to several researchers, the anadromous shad was able to adapt to modern conditions and master a new niche in the lower Volga half-century after the dam's construction (Voinova, 2016; Pyatikopova, 2019). This adaptation process likely continues into the present (Kuzishchin et al.,

2020). Moreover, a detailed study and monitoring of the biological parameters of the shad population are of interest not only from the point of view of the economic value of this species but also from the point of view of a fundamental study of microevolution processes in a modified habitat.

One of the most significant changes in the shad's biology is associated with its reproduction. The main spawning grounds are below the Volzhskaya HPP dam, between the Svetly Yar and Cherny Yar villages (Voinova, 2013, 2021; Lepilina et al., 2016). Accordingly, the spawning grounds below Volgograd, mastered by the shad, could not be considered equivalent to the former before dam construction (Lepilina et al., 2016; Pyatikopova, 2019). In addition, the discrepancy between the water and temperature regimes and the natural rhythms that existed before the dam's construction is observed (Voinova, 2013, 2016, 2021). In this regard, the current conditions for the existence of the shad are not optimal and, according to some researchers, negatively affect the spawning flock condition and gametes quality. Natural reproduction will not provide stable recruitment, and the species will again find itself in an even more depressed state if a decrease in reproductive ability continues for years (Voinova, 2021). Consequently, at the present

research stage, it is necessary to analyze the shad gametogenesis features to assess fish reproductive output and the quality of egg and sperm production. This work aims to explore the gonadal and gametogenesis features and to determine the Caspian anadromous shad spawner's condition accordingly.

## MATERIALS AND METHODS

The materials were collected in mid-May 2021 in the Akhtuba River on the territory of the Kharabalinsky district of the Astrakhan region. The collection point is 150 kilometers (km) upstream from the upper boundary of the Volga Delta and 300 km downstream from the Volzhskaya HPP dam. The site of Akhtuba, where the material was collected, does not differ in structure from those upstream and downstream (Nikolaev, 1962). Annual observations of the shad spawners were carried out here between 2016–2020, and the time of material collection was confined to the period with the most intensive anadromous migration among the species. Spawners were captured with fishing tackles with five hooks and a rubber shock absorber, catching all depths from surface to the bottom (6–8 m).

Once caught, the fish were placed in thermally-insulated containers with water and processed fresh directly in the laboratory. The biological analysis included fork length (*FL*) and body weight (*BW*) measurements, scale sampling under the dorsal fin for age determination, fish sex, and gonadal maturity stage visual identification. The scales determined the age, based on Chugunova (1959), and considering the recommendations of Yilmaz and Polat (2002), using electronic images of impressions on acrylate sheets (image-capture system, Leica DMLS microscope with a set of objectives from 2.5× to 10.0×, and a Canon X500-D digital camera). The gonadosomatic index (GSI) was measured as the ratio between gonad weight and *BW* without viscera. Fragments of gonads were fixed with Bouin's solution.

Histological processing was carried out according to standard for fish methods (Mikodina et al., 2009). The gonads of 14 females and 23 males were studied. The samples were dehydrated, cleared with xylol, embedded in paraffin, sectioned at 3–5 μm, and stained with hematoxylin and Ehrlich's eosin (Roskin and Levinson, 1957). The OLYMPUS BX45 microscope and Leica DC 100 digital camera were used for microscopy and photography. Image Processing and Data Analysis in Java (ImageJ) was used for measuring the diameters of germ cells and visualizing their structures (937 oocytes). The material was processed by the methods of standard univariate statistical analysis (Lakin, 1990). The Kruskal–Wallis one-way ANOVA was used to assess the significance of differences in the average values of oocytes diameters. The maturity of each gonad was classified, based on the most advanced oocytes stage observed in the histological sections

according to scale described in Brown-Peterson et al. (2011). The nuclear-cytoplasmic ratio (N/C, %) was calculated as the ratio of the nucleus diameter to the germ cell diameter.

## RESULTS

### *Biological Characteristics of Spawners*

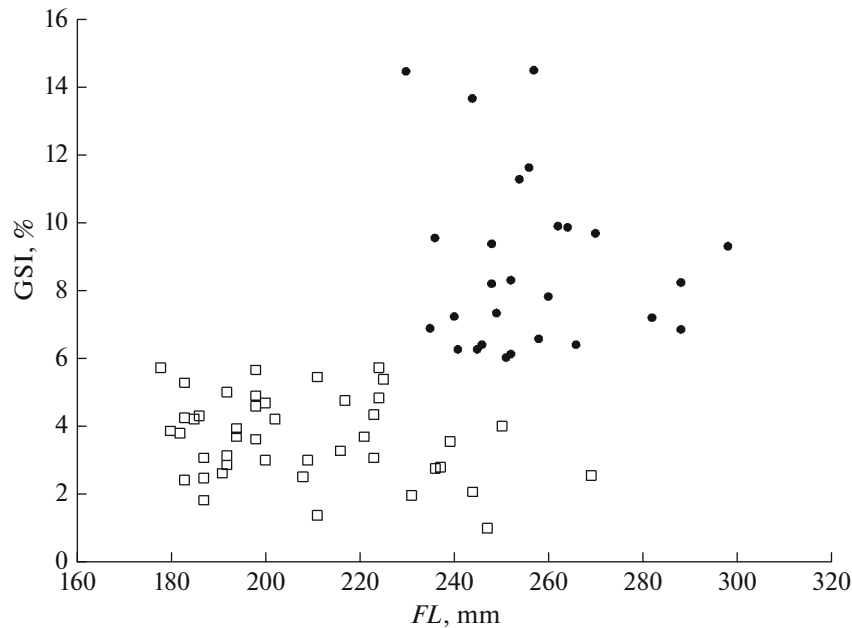
In 2021, the first specimens of Caspian anadromous shad appeared in the Akhtuba River on May 11–12. The spawning run was most intense during May 20–28, and its completion was at the end of the first week of June. Anadromous migration occurred against a rise in water temperature from 13°C at the outset to 22°C by the end. During the migration peak, the river's water temperature was 17–18°C. The first dead and surviving post-spawners of shad appeared in the Akhtuba River from June 27–28, and the mass downstream migration of post-spawners occurred in the first week of July. All investigated spawners had empty stomachs. The exact localization of the shad spawning grounds in the Akhtuba River is still being determined. According to some indirect data, the species spawns in the area from Leninsk to Srednyaya Akhtuba, meaning the distance from the material collection point to possible spawning grounds was ~250–280 km.

The *FL* of males in the sample ranged from 178 to 269 (average 209.9) mm, *BW* from 47.7 to 180.9 (87.5) g, and age was 2+ (39%), 3+ (56%), and 4+ (5%); the *FL* of females was 184–316 (254.1) mm, *BW* was 64–341 (178.9) g, and age was 3+ (91%) and 4+ (9%).

The GSI of males was less than that of females, <6 vs >6% (Fig. 1). The GSI values in males varied from 1.00 to 5.75 (average 3.67)%, and in females, from 6.02 to 14.49 (8.71)%. The highest GSI values were noted in smaller males and females. The significant variability of GSI in different females was apparently due to the different sizes of eggs in the ovaries due to the prolongation of their maturation and spawning in portions.

### *Gonadal Condition*

According to the results of histological analysis, the females had gonads at the developing and spawning-capable phases, in which oocytes at different stages of the primary growth (PG) and secondary growth (SG) were noted (Fig. 2). Oogonia and chromatin nucleolus oocytes were not present in large numbers. The diameter of PG oocytes varied from 32 to 194 μm; their N/C was 29.6–70%. Oocytes with a diameter of ~190 μm entered the SG and were characterized by the appearance of vacuoles in the peripheral cytoplasm; oil droplets were absent. The number of vacuoles increased as the oocyte grew and formed approximately four rows, filling the cytoplasm to its middle. The small yolk globules appeared in oocytes with a diameter of 200–372 μm; they were usually localized



**Fig. 1.** Variation in the gonadosomatic index (GSI) in Caspian anadromous shad *Alosa kessleri kessleri* males (□) and females (●) in relation to the fork length (FL).

under the oocyte membrane and between vacuoles. The oocyte N/C was 20.7–45.9%. Zona radiata was already noticeable, with a thickness of 1.5–2.0  $\mu\text{m}$ . In larger oocytes with a diameter of 319–551  $\mu\text{m}$ , yolk globules with a diameter of 8–18  $\mu\text{m}$  were also located in the cytoplasm, free from vacuoles. The N/C was 16.3–42.3%, and the thickness of the zona radiata was 3.5–4.7  $\mu\text{m}$ . The largest germ cells (with a diameter of 519–785  $\mu\text{m}$ ) were tertiary vitellogenic oocytes, yolk granules filled the entire cytoplasm in them (Figs. 2a, 2b); their N/C was 11.6–28.2%, and the thickness of the zona radiata was 6.5–8.0  $\mu\text{m}$ .

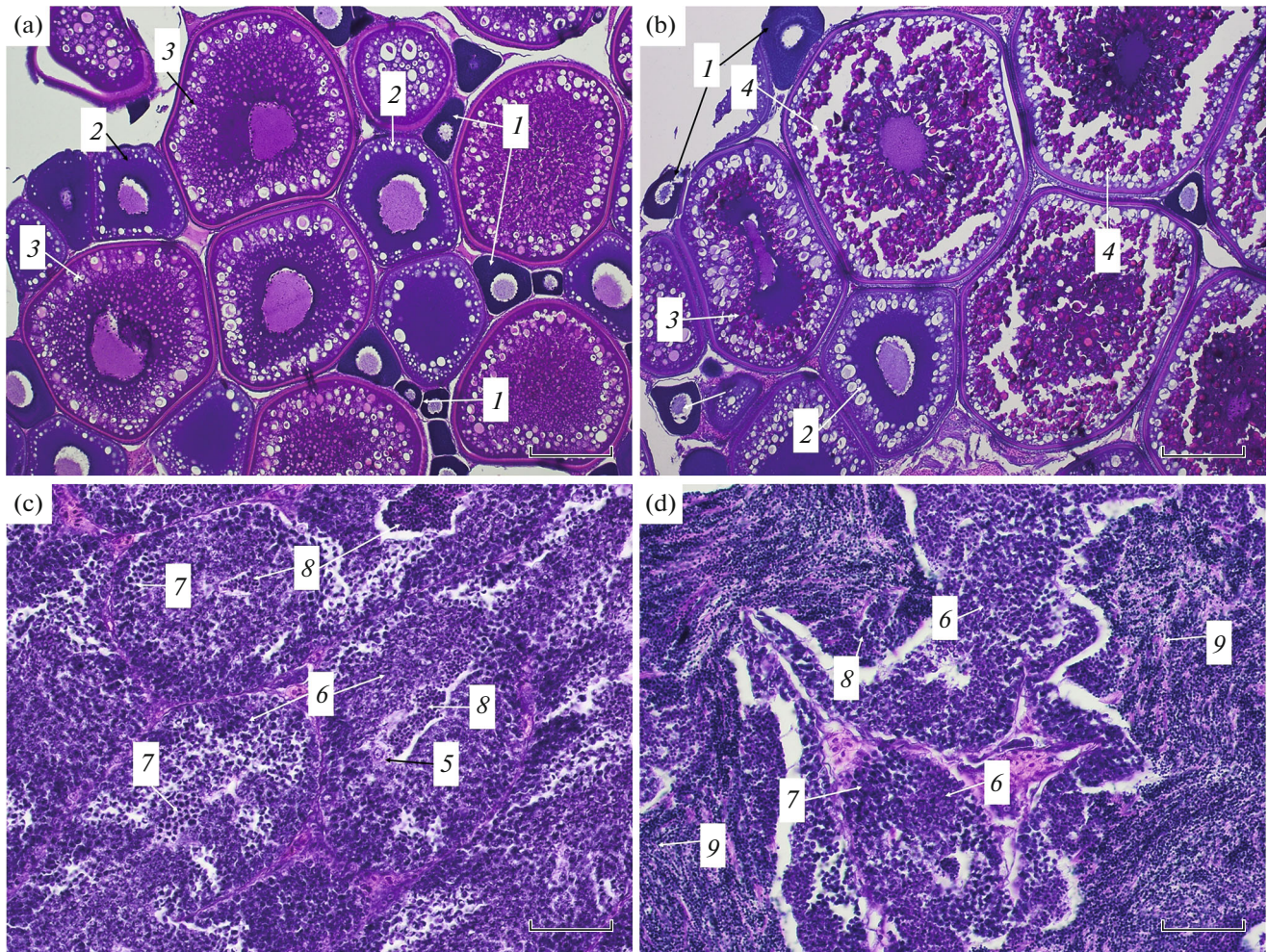
Gonads of all females contained many PG oocytes (26.7–59.4% of all oocytes on studied samples sections), which were oocyte reserve. The development of the SG oocytes proceeded asynchronously (Fig. 3). Two groups of SG oocytes were observed in developing ovaries, i.e., primary vitellogenic (~19%) and secondary vitellogenic (22.6%). In spawning-capable ovaries, three groups were present, i.e., primary (13.3%), secondary (24.4%), and tertiary vitellogenic oocytes (35.6%).

The male gonads were at the developing and spawning capable phases of maturity. Male germ cells of all developmental stages were noted, including spermatozoa (in spawning-capable gonads) located in different parts of the testes (Figs. 2c, 2d). The diameters of germ cells of different developmental stages in the ovaries and testes differed statistically ( $p < 0.001$ ) among themselves, except for spermatids and spermatozoa (Fig. 4).

## DISCUSSION

In the ovaries of the Caspian anadromous shad migrating to the spawning grounds in the Akhtuba River, there are PG and SG oocytes. Three different-sized groups, obviously intended for the release of three batch of eggs, were identified among the asynchronously developing SG oocytes in the spawning-capable gonads (Fig. 3). Early works on the oogenesis of this species (Ivanov, 1953; Ivanov and Dodzina, 1957) reported the presence of four to five batches being spawned within 1.0–1.5 months. The interval between the release of oocytes in the next batch is very short (6–8 days).

Many anadromous representatives of the Alosinae subfamily are characterized by batch spawning and indeterminate fecundity. These are species like *A. pseudoharengus* (Ganias et al., 2015), *A. sapidissima* (Olney et al., 2001; Hyle et al., 2014; McBride et al., 2016), *A. mediocris* (Murauskas and Rulifson, 2011), *A. fallax fallax* (Pina et al., 2003), and *A. macedonica* (Mouchlianitis et al., 2020). In the Caspian anadromous shad from the Akhtuba River, small PG oocytes predominate, and oocytes of all intermediate size classes between PG and the largest tertiary vitellogenic oocytes are present on histograms showing size composition (Fig. 3). This distribution indicates a continuous type of oogenesis and, as a result, indeterminate fecundity (Götting, 1961; Oven, 1976, 2004). Nevertheless, since the spawning period of the shad lasts ~1.5 months (Vodovskaya, 2001), it seems unlikely that PG oocytes recruit to SG and spawn in the cur-



**Fig. 2.** Caspian anadromous shad *Alosa kessleri kessleri* ovaries and testes: (a) developing ovary, *FL* of female is 262 mm, *GSI* 7.8%; (b) spawning capable ovary, *FL* of female is 272 mm, *GSI* 9.9%; (c) developing testis, *FL* of male is 191 mm, 4.1%; (d) spawning capable testis, *FL* male is 195 mm, *GSI* 4.5%. Microscopic characteristics include: 1—primary growth, 2—secondary growth (primary vitellogenic), 3—secondary vitellogenic, 4—tertiary vitellogenic oocytes; 5—spermatogonia; 6—primary spermatocytes, 7—secondary spermatocytes; 8—spermatids, 9—spermatozoa. Scale: (a), (b)—200  $\mu$ m; (c), (d)—50  $\mu$ m.

rent season. It is possible that some part of PG oocytes may enter second growth, but is subsequently resorbed at its early stages. The resorption of different-sized SG oocytes of shad was noted (Ivanov, 1953; Ivanov and Dodzina, 1957; Belyaeva and Vasilchenko, 1965) and associated with a change in spawning migrations due to the Volga flow regulation (Belyaeva and Vasilchenko, 1965) or with ecologically unfavourable habitat (Dubovskaya, 2020).

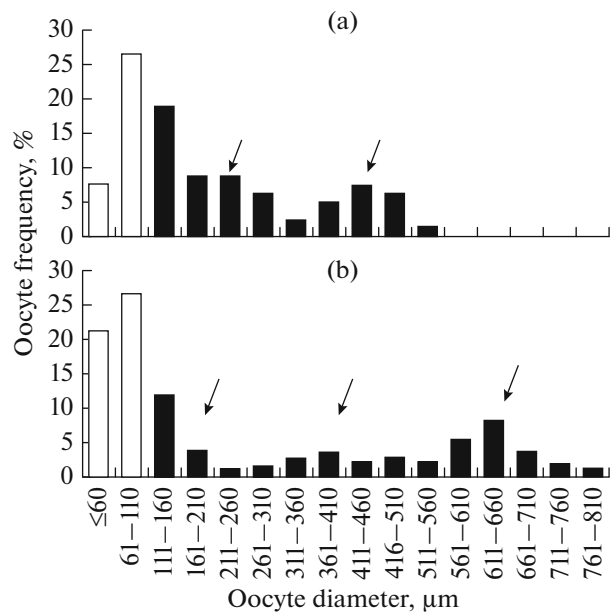
Asynchronous oocyte development and batch spawning were noted for *A. fallax fallax* in the rivers of southern Portugal (Pina et al., 2003). An analysis of the distribution of germ cells by diameter in fish before the start of the spawning season did not reveal the absence of any size classes between PG and SG oocytes, which, in the opinion of the authors, indicated the possibility of recruitment to the SG at the expense of PG oocytes. This species is iteroparous,

and PG oocytes are plentiful, as reflected in the histograms and micrographs in the above-noted publication.

The American shad *A. sapidissima* from the north-western coast of the Atlantic is also an iteroparous species with asynchronous development of SG oocytes and batch spawning (Mylonas et al., 1995; Olney et al., 2001). After the spawning in the York River is completed, partially depleted (70% of fish) and completely exhausted individuals (subsequently dying) back into the ocean. In partially depleted individuals, only a part of the SG oocytes is realized; the rest are subjected to resorption, providing an energy resource for fish restoration. Such individuals can return to spawn in the next season, ensuring the iteroparity of this species, which can increase the stability of the population in case of unpredictable environmental conditions (Olney et al., 2001).

A representative of the same genus, *A. pseudoharengus*, breeding in the lakes of Connecticut, spawns three batches (Ganias et al., 2015). In fish returning to the ocean after spawning, in addition to empty follicles, the ovaries have only one batch of oocytes less than in individuals those only going to spawn. This suggests oocyte recruitment from PG to SG during individuals stay in the lake. All batches of unspawned oocytes are subsequently resorbed. The fecundity of this species is likely indeterminate. However, it is unusual since the fish do not feed during migration. The combination of anadromous migration and indeterminate fecundity is quite controversial. Some researchers believe that fish with indeterminate fecundity (largely inhabitants of low latitudes) can easily regulate the number of SG oocytes due to the flexible redistribution of energy that is consumed during the breeding season since they feed at this time (McBride et al., 2015). Indeterminate fecundity makes it possible to more flexibly distribute the energy accumulated earlier during marine feeding and increase the number of spawned egg batches as much as possible while there are enough internal resources. This corresponds to the extended spawning period of the shad in the Volga River (Vodovskaya, 2001; Pyatikopova, 2019). Therefore, individuals with indeterminate fecundity must achieve a balance between recruitment of PG to the SG, which requires ongoing energy costs, and saving resources for life support. This was shown to be the case for *A. aestivalis* in the Connecticut River, an anadromous species with batch spawning and indeterminate fecundity (Mouchlianitis et al., 2021). The energy balance is created by reducing the oocyte recruitment intensity and fecundity during spawning. In *A. macedonica*, recruitment to the SG with new groups of maturing oocytes occurs only during the ovulation periods of the leading group of germ cells (Mouchlianitis et al., 2020). The highest individual fecundity and recruitment intensity can be observed in the middle of spawning compared to its beginning and end.

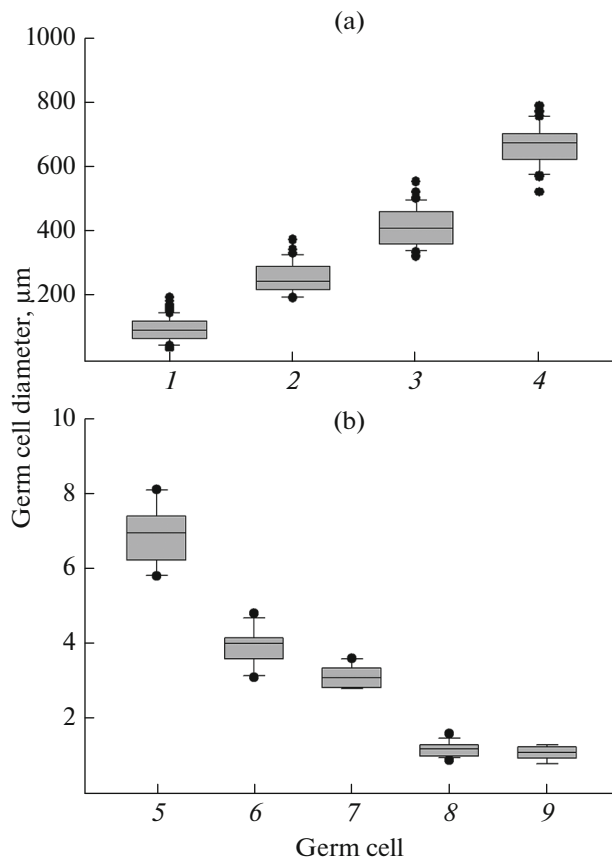
In *A. alosa*, spawning in the Mondego River of Central Portugal, the number of PG oocytes is deficient and significantly decreases during the breeding season (Mota et al., 2015, cited in Mouchlianitis et al., 2019). Repeated breeding individuals are < 6.5%, which, according to the authors, indicates an obligate tendency towards semelparity of *A. alosa* (Mouchlianitis et al., 2019). Thus, a specific reproductive strategy has been noted in shads, at least in several species, which includes the regulation of recruitment of PG oocytes to the SG and individual fecundity during spawning. Several authors point to the high plasticity of the reproductive strategy in anadromous shad of the genus *Alosa*, which is expressed through a change in the proportion of first-time and repeatedly maturing fish, the duration of the spawning period, changes in fecundity, and egg size (Tanasychuk, 1962; Leggett and Carscadden, 1978; Glebe and Leggett, 1981;



**Fig. 3.** Oocyte size–frequency histograms of ovarian development representative of developing (a) and spawning capable (b) phase in female Caspian anadromous shad *Alosa kessleri kessleri*: (□)—primary growth reserve, (■)—secondary growth oocytes; (↓)—batches of oocytes.

Vodovskaya, 1994, 1996, 2001; Blaber et al., 1999; Grice et al., 2014; Ganias et al., 2015; Voinova, 2021).

Significant changes in the reproductive strategy of anadromous alosines have also been observed due to the anthropogenic impact on river systems (Carscadden and Leggett, 1975; Blaber et al., 1999; Catalano and Allen, 2011; Gilligan-Lunda et al., 2021). The conditions for the existence and reproduction of the shads in the Volga basin changed dramatically in 1958–1959 after the construction of the Volzhskaya HPP. The conditions for spawning and downstream migration of larvae deteriorated sharply, and the quality of eggs changed; these became partially over-ripe, and a vast amount of non-developing eggs were spawned (Vodovskaya, 2001). The above factors led to a sharp decrease in shads (and remains the case), despite some restoration of stocks (Katunin et al., 2000; Vasilyeva et al., 2012; Pyatikopova, 2019). Many of the shad's biological parameters have changed compared to before the dam's construction. There is a decrease in body length and weight, and spawning occurs at lower ages (Vodovskaya, 2001; Voinova, 2013; Pyatikopova, 2019). As our studies have shown, changes have also affected the reproductive system of shad spawners. It was previously noted that up to five batches of oocytes matured in the gonads of females; our data indicate a reduction to three batches. Concurrently, there was a decrease in the egg diameters, particularly in the first batch. The observed changes in gametogenesis are most likely due to a significant decline in the length of the migration route to spawning grounds.



**Fig. 4.** Box plot of the relationship between oocyte diameter and histological stages of maturity for females (a) and males (b) of *Alosa kessleri kessleri*. The stages of oocyte development are 1—primary growth, 2—primary vitellogenic, 3—secondary vitellogenic, 4—tertiary vitellogenic oocytes; 5—spermatogonia; 6—primary spermatocytes, 7—secondary spermatocytes; 8—spermatids, 9—spermatzoa. The upper and lower parts of each box represent the first and third quartiles (the 25th and 75th percentiles), and the horizontal line is the median. The error bars indicate 1.5 times the interquartile range, and the black circles (●) represent values outside this range.

The changes in the population structure of alosines in the Volga basin, as noted by different researchers, indicate that at present (the early 2020s), its population is a completely transformed group compared to that before large-scale hydro construction. Our data fully confirm large-scale changes and indicate shifts in gametogenesis. The Caspian anadromous shad population is rapidly adapting to new conditions in the Caspian basin. The process of active changes may also result from large-scale climate shifts. The currently available information on shads requires in-depth research and elucidation of cause-and-effect relationships between environmental parameters and the biological characteristics of fish. This supports the need for monitoring the state of the species in the Volga River.

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## COMPLIANCE WITH ETHICAL STANDARDS

*Conflict of interests.* The authors declare that they have no conflicts 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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