Journal of Ichthyology, Vol. 43, No. 7, 2003, pp. 516–527. Translated from Voprosy Ikhtiologii, Vol. 43, No. 4, 2003, pp. 499–510.

Reproductive System of Amu-Dar Shovelnoses—Big Shovelnose *Pseudoscaphirhynchus kaufmanni* and Little Shovelnose *P. hermanni* (Acipenseridae)

V. B. Sal'nikov[1], N. V. Akimova[2], G. I. Ruban[2], R. L. Mayden[3], and B. R. Kuhajda[4]

[1]*National Institute of Deserts, Plant and Animal World, Ministry of Nature Conservation of Turkmenistan, Ashkhabad, Turkmenistan*

[2]*Severtsov Institute of Ecology and Evolution, Russian Academy of Sciences, Leninskii pr. 33, Moscow, 119071 Russia*

[3]*Department of Biology, 3507 Laclede Ave., Saint Louis University, St. Louis, MO63103-2010, USA*

E-mail: maydenrl @ SLU.EDU

[4]*Box 870344, Univ. of Alabama, Tuscaloosa, Alabama 35487-0345, USA*

E-mail: bkuhajda @ bama.ua.edu

Received February 13, 2003

Abstract—A study on gametogenesis in the big *Pseudoscaphirhynchus kaufmanni* and little *P. hermanni* Amu-Dar shovelnoses was performed. It was shown that processes of gameto- and gonadogenesis are similar in these species and proceed according to a scheme common to all acipenserids. In recent years, females and males of the dwarf form of *P. kaufmanni* are reaching sexual maturity at an earlier age (at 4–5 and 3–4 years, respectively), but at the same body length and relative gonad weight as before. For the first time, females of *P. kaufmanni* with gonad microstructure were found, which suggests their unusually early sexual maturation at small length and weight. Females of *P. hermanni* mature at an age of 4–5 years at a body length and weight similar to indices of the dwarf form of *P. kaufmanni*. Both species of shovelnoses spawn mainly in April at a water temperature of 13–20°C. In recent years, various anomalies in the micro- and macrostructures of gonads of the studied species have been recorded; in *P. kaufmanni*, their range is wider than in *P. hermanni*.

INTRODUCTION

The biological specific features of the big *Pseudoscaphirhynchus kaufmanni* and little *P. hermanni* Amu-Dar shovelnoses are described in few publications based on little material (Nikolsky, 1938, 1971; Dragomirov and Shmal'gauzen, 1952; Maksunov, 1968; Kozhin, 1970; Tleuov and Tleubergenov, 1974; Nikol'skaya, 1989; Shmal'gauzen, 1991). The most comprehensive data are cited in papers of Sagitov (1968a, 1968b, 1998c; 1969a, 1969b), and Tleuov and Sagitov (1973) in which it is shown that according to several morphological characters, as well as the growth rate and fatness, there are differences between individuals of *P. kaufmanni* from different areas of the Amu Darya. This indicates that several local populations of this species exist in this river. In *P. kaufmanni*, the so called "dwarf" form was described which differs from the "common" form in several morphological and biological characters. The common form of *P. kaufmanni* reaches sexual maturity at an age of 6–8 years at a body length of 40 cm. Its absolute fecundity varies from 3127 to 36 558 eggs. The dwarf form matures at the same age: males at 6–7 years (single individuals at 5 years); females, at 7–8 years (single individuals at 6 years). Its fecundity varies from 990 to 1910 eggs. The spawning of the big shovelnose takes place in the river channel on large-grained sandy shoals, mainly, in the first ten days of April at a water temperature of 14–16°C (Tleuov and Sagitov, 1973). The gametogenesis of *P. kaufmanni* was described in one publication based only on materials from 1964–1968 (Makeeva and Sagitov, 1979); data on the development of sexual cells and gonads of *P. hermanni* are lacking. A steady decline in the population size of Amu-Dar shovelnoses, a species endemic to the Aral basin, has taken on threatening dimensions and has put them on the verge of extinction (Tleuov *et al.*, 1989; Zholdasova, 1997; Kuhajda *et al.*, 2000; Salikhov *et al.*, 2001; Sal'nikov *et al.*, 2001).

The purpose of the present paper was to trace the processes of gameto-and gonadogenesis in the big (common and dwarf forms) and little Amu-Dar shovelnoses, as well as to elucidate changes in the processes of development and functioning of the reproductive system of *P. kaufmanni* over a thirty-year period from the time of the last study. Since a comprehensive description of the development of sexual cells and gonads of *P. kaufmanni* was performed previously (Makeeva and Sagitov, 1979), the present paper analyzes only those specific features of these processes that are lacking in the abovementioned publication.

MATERIAL AND METHODS

The material for histological study was collected in 1996–2002 in the middle reaches of the Amu Darya (Turkmenistan) on the section of the river from the settlement of Tashrabat to the settlement of Khalach extending 100 km. Three-walled drift nets with mesh sizes of 30 and 34 mm and a small drag seine with a 30-mm mesh were used. The body length (L) of fish was measured from the snout end to the last scute, bearing the crest, with an accuracy to 1 mm; body weight (Q), to 1 g; the age of fish was determined from saw cuts of marginal rays of the pectoral fin. A description of maturity stages of gonads was given following the scale of Nedoshivin (1928) for acipenserids with amendments made by Trusov (1964) and Serebryakova (1964).

In all, gonads from 146 individual big shovelnose (84 females, 60 males, and two juvenile individuals), 25 individual little shovelnose (14 females and 11 males), and from one individual that was assumed to be a hybrid of these species were examined under a microscope. Gonads were fixed with Bouin's fluid and 4% formalin. The histological treatment was performed according to common methods (Roskin and Levinson, 1957). Sections 5–10 μm thick were stained according to Mallory. In the present paper, the gonadosomatic index (GSI, the relation of gonads to the body weight without entrails) was mainly used as a more precise index. However, for a comparison of data with other authors, the coefficient of maturity (C_{mat}, the relation of gonad weight to the total weight of the fish) was also calculated.

RESULTS

Big Amu-Dar shovelnose *Pseudoscaphirhynchus kaufmanni*

In the middle reaches of the Amu Darya, a fairly large number of mature individual shovelnose of the dwarf form were found; their maturation occurs at a considerably smaller size than in other individuals of this species (Sagitov, 1969b; Tleuov and Sagitov, 1973). The issue concerning the existence of the dwarf form of shovelnose is complicated. In juvenile individuals, the growth rate of the common and dwarf forms is similar (Makeeva and Sagitov, 1979); therefore, it is not always possible to differentiate these forms based on the size of fish at an early age. Individuals of the dwarf form are visually distinguishable from the common form. The coloration of the dorsal side of their body is dark brown to blackish and the snout has a triangular form; the common form is light colored; muscular segments are viewed through integuments; the snout is broad, rounded, and blade-shaped. These forms also differ in a set of plastic and meristic characters (Sagitov, 1969b; Tleuov and Sagitov, 1973). According to our data, there is chiatus between these forms with respect to snout width at the barbel level (Fig. 1).

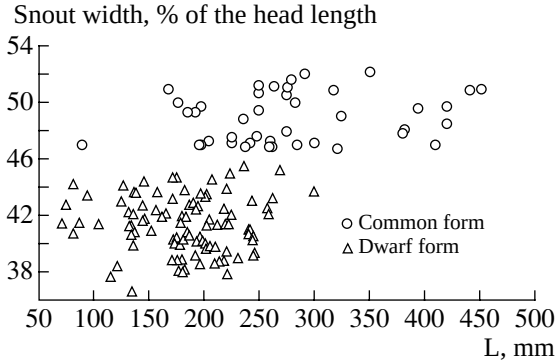

Fig. 1. Values of the relative (in % of the head length) snout width in individuals of the common and dwarf forms of *Pseudoscaphirhynchus kaufmanni*.

It is known that dwarf forms are designated as forms with a low growth rate and an earlier sexual maturation in comparison with other forms of the species (Koshelev, 1984). However, as was noted above, the common and dwarf forms of *P. kaufmanni* reach sexual maturity at the same age. According to our data, the average values of the body length of fish of the same size are different for these forms; however, there is a substantial overlapping in body length in the age classes (Table 1) to 4+. In our materials, individuals older than 4+ are scarce; therefore, it cannot be excluded that this overlapping may occur at an older age as well. The observed overlapping indicates that some individuals of the dwarf form can be larger than individuals of the common form of the same age.

The abovementioned data attest that the so called dwarf form of *P. kaufmanni* does not appear to be as it is traditionally understood. The issue concerning the taxonomic status of this form remains open at the present time. Possibly, it would be expedient to name the forms of the shovelnose proceeding from the values of the character according to which they have chiatus, i.e., broad-snouted and narrow-snouted instead of common and dwarf forms. However, to avoid ambiguous terminology, the present paper has retained terminology adopted earlier (Sagitov, 1969b; Tleuov and Sagitov, 1973).

Females of the common form. Of the 28 females of the common form of *P. kaufmanni* examined, 8 individuals had gonads at maturity stage II and 18 individuals, at fatty stage II—in gonads, oocytes of the period of cytoplasmatic growth and earlier phases of development were recorded (Table 2, Fig. 2a). In some individuals, local degenerative processes of some oocytes and considerable aggregations of blood corpuscles were recorded. One female caught in December 1997 had gonads at an uncompleted stage of maturity IV—oocytes were filled with yolk, the nucleus was located in the center; 73.7% of oocytes were deformed, and in some oocytes, a membrane rupture was observed, which testfied to a decrease of turgor in the membranes

Table 1. The length of individuals of the common and dwarf forms of *P. kaufmanni* in different age classes

Age, years	Form					
	common			dwarf		
	lim	*M*	*n*	*lim*	*M*	*n*
1...1+	146–225	190.0	11	115–180	145.8	12
2...2+	177–283	231.9	14	135–261	189.5	30
3...3+	218–390	292.2	9	127–300	205.0	30
4...4+	242–450	358.9	7	202–300	242.0	5
5...5+	380–440	405.0	3	203–285	249.0	3
6	410	410.0	1	185–258	221.5	2
7	430	430.0	1			
8				244	244	1
Total			46			83

(Fig. 2b). Its fecundity comprised 19980 eggs with a diameter of 1.7–1.9 mm. In another female caught in April 1999, gonads were at the completed stage of maturity IV; all its ovicells were deformed; in 47.8% of oocytes, the delamination of membranes was recorded; in 87% of oocytes, membranes had an uneven coloration.

Females of the dwarf form. Of 51 examined females of the dwarf form of *P. kaufmanni*, 18 individuals had gonads at maturity stage II. Similar to the common form, sexual cells were represented by oocytes of cytoplasmatic growth and earlier phases of development. In some individuals, gonads contained clots of the basal membrane and pigment aggregations indicating that spawning had occurred earlier. Gonads of 17 females were at fatty stage II; their microstructure was similar to the abovementioned one; it differed only in a rarer oocyte arrangement due to a large amount of deposited fat. The GSI and C_{mat} in females at this stage were considerably higher (Table 2). In two individuals caught in September and December, the start of fat deposition in oocytes (II–III stage of gonad maturity) was observed—the first yolk granules had formed in the center of the ooplasm around the nucleus in one to two rows, and then under the membrane also (Fig. 3). Gonads of three females were at maturity stage III—an active process of nutrient accumulation had taken place in the oocytes; they were completely filled with yolk. In October–December, three females with gonads at an uncompleted maturity stage IV were caught (Table 2). Their oocytes had definitive sizes with a central location of the nucleus; of them, 69.2–83.3% were deformed; the membranes were completely formed, but in 34.6–44.4% of ovicells, their local delamination and rupture were observed and in 11.5–27.8%, their uneven staining were observed. From February 19 to April 7 in different years, five females with mature genital products were caught. In three of them, gonads were at a completed maturity stage IV; in two, ovicells had partially ovulated (stage V); their diameter was 1.5–2.0 mm. The thickness of the jelly-like membrane of mature ovicells comprised one-fourth of the total thickness of all membranes; the inner yolk membrane had a similar thickness; the outer yolk membrane was two times as thick as the inner membrane. Some anomalies in the structure of mature ovicells were observed: their complete or partial deformation (63–100% of oocytes) in different individuals; local rupture and delamination of membranes (4.5–50.0% of oocytes), and an uneven staining of membranes (29.4–100% of oocytes). The fecundity of these individuals was 2750–4365 (on average, 3759) eggs. At the end of April 1998 and the end of May 1999, three spent females (VI–II maturity stages of gonads) were caught; this was evidenced by empty follicles and single mature oocytes subjected to resorption.

Of 56 examined females of *P. kaufmanni*, six individuals caught in 1997–1999 had gonad microstructure characteristic of the postspawning period. Noteworthy for mature individuals of this species, were the unusually small length, low weight, and young age of these females: the length of five individuals varied from 115 to 152 mm; the weight, from 8.5 to 22 g; the age, from 1+…2+; and GSI and C_{mat}, from 0.3 to 0.5% (on average, 0.4%). The sixth female (its relation to this or another form was not determined) caught in October 1999 was even smaller and younger (L, 81 mm; Q, 3.05 g; age, 0+; and GSI, 0.4%). Its gonads contained a great amount of pigment, which is observed after mass resorption of mature ovicells (Fig. 4a). The

Table 2. Main biological indices of female *P. kaufmanni* at different stages of gonad maturity

Stage of gonad maturity	L, mm	Q, g	Age, years	GSI, %	C_{mat}, %	*n*	Data source
Common form							
II	146.0–275.0 / 199.5	19.0–130.0 / 58.6	1+–3+	0.3–0.7 / 0.5	0.2–0.6 / 0.4	8	Our data
II fatty	175.0–440.0 / 277.1	38.5–689.0 / 181.8	1+–7	0.4–11.8 / 2.7	0.4–10.4 / 2.5	18	″
IV uncompleted	450.0	580.0	4+	11.9	9.8	1	″
IV completed	285.0	159.0	5	17.3	14.2	1	″
II	180.0–410.0	–	–	–	0.1–0.45	–	Makeeva and Sagitov, 1979
II fatty	–	–	–	–	0.55–1.38	–	″
Dwarf form							
II	115.0–201.0 / 162.4	8.5–46.0 / 28.5	1+–6	0.3–3.8 / 1.0	0.3–3.3 / 0.9	18	Our data
II fatty	134.0–269.0 / 199.2	15.5–132.0 / 54.4	1+–4	0.7–7.0 / 3.3	0.6–6.1 / 2.9	17	″
II–III	193.0–231.0 / 212.0	45.0–69.0 / 57.0	2+–3+	2.5–2.7 / 2.6	2.2–2.5 / 2.4	2	″
III	202.0–246.0 / 217.7	50.0–96.5 / 66.2	2+–3+	4.6–6.5 / 5.4	4.2–5.7 / 4.8	3	″
IV uncompleted	221.0–244.0 / 229.0	67.5–105.0 / 82.2	3+–4+	17.6–20.9 / 19.6	14.2–15.9 / 15.2	3	″
IV completed; V	202.0–262.0 / 230.0	43.0–98.0 / 75.4	4–5	20.0–28.1 / 24.7	15.5–20.1 / 17.9	5	″
VI; VI–II	223.0–258.0 / 241.7	66.5–101.0 / 85.5	2–8	1.3–1.7 / 1.6	1.1–1.4 / 1.3	3	″
III and IV	217.0–232.0 / 225.8	43.5–54.2 / 47.8	6–8	7.7–22.5 / 15.7	6.0–15.8 / 11.5	5	Makeeva and Sagitov, 1979
IV	230.0–315.0	40.9–70.5	7–8(6)	–	5.3–17.6 / 11.8	29	Tleuov and Sagitov, 1973
The form not determined							
Juv.	76.0–102.0 / 89.0	2.45	0+	0.5	0.4	2	Our data
I; II	81.0–132.0 / 98.0	3.05–14.0 / 6.3	0+–1+	0.3–1.8 / 0.8	0.3–1.5 / 0.7	5	″
I; I–II	132.0–176.0	–	1–2+	–	–	–	Makeeva and Sagitov, 1979

Note. In tables 2, 3 and 5, above the line—range of variation of a parameter, below—its mean value.

minimal length and weight of females of the dwarf form with mature genital products (uncompleted maturity stage IV) in our material were 195 mm, 43 g, and four years, respectively.

Males of the common form of the big shovelnose *P. kaufmanni*. Gonads of all examined males of this form were at maturity and fatty maturity stages II—an active reproduction of spermatogonia had taken place

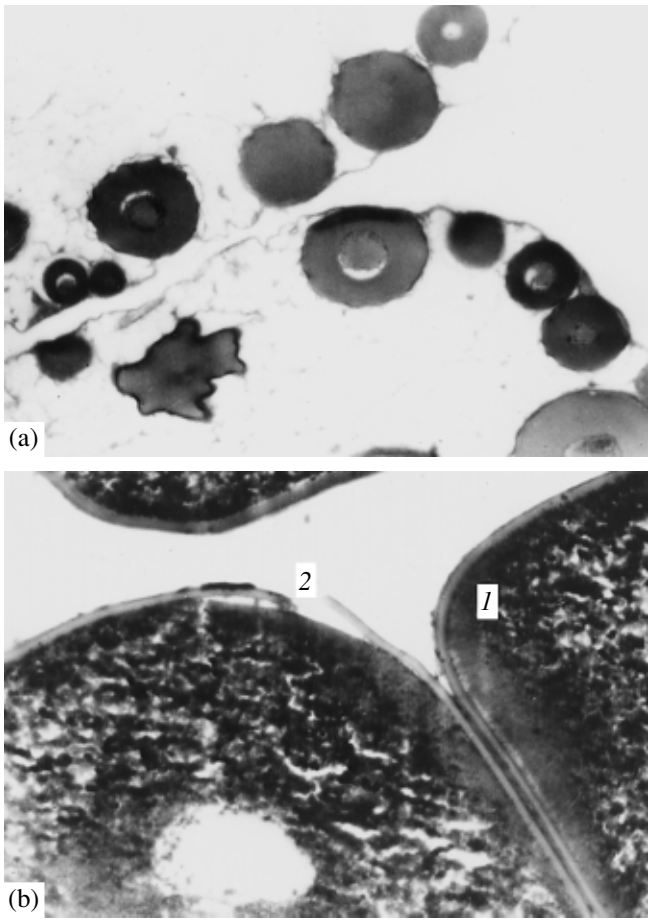

Fig. 2. Microstructure of female gonads of the common form of *Pseudoscaphirhynchus kaufmanni*. (a) II fatty stage of gonad maturity—oocytes of the period of cytoplasmatic growth are located in one row along the borders of egg-bearing plates (♀ L 390 mm, Q 390 g, age 4+; December 3, 1997); (b) IV uncompleted stage of gonad maturity—fragments of mature ovicells, the nucleus is located in the center of oocytes (♀ L 450 mm, Q 580 g, age 4+; December 3, 1997). (*1*) oocyte deformation; (*2*) membrane rupture. Magn. 23×.

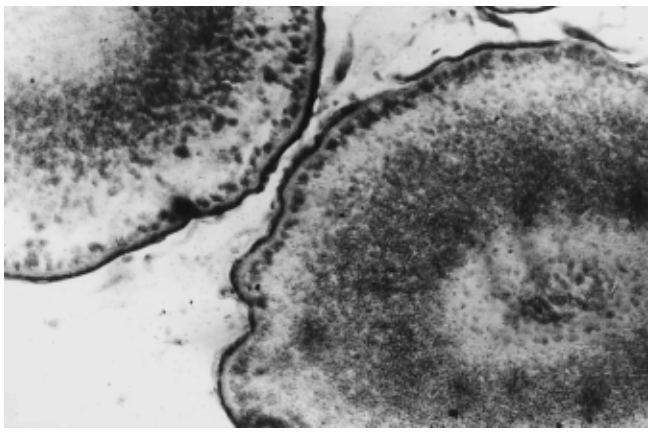

Fig. 3. Microstructure of gonads at maturity stages II–III in a female of the dwarf form of *Pseudoscaphirhynchus kaufmanni*. Fragments of two oocytes; formation of yolk in them (♀ L 231 mm, Q 69 g, age 3+, December 1, 1997). Magn. 58.5×.

in them (Table 3). These individuals exhibited some deviations from the normal development of gonads (Table 4): small cavities among seminiferous tubules, a local lobed structure of the testes, aggregations of blood corpuscles, the presence among seminiferous tubules of oocytes of the period of cytoplasmatic growth (Fig. 4b), as well as fatty tissue deposition in the generative part of the gonads) (normally, fatty tissue is deposited only on the gonad surface without affecting its generative part).

Males of the dwarf form. Of 38 examined males of this form of *P. kaufmanni*, 28 individuals had gonads at maturity and fatty maturity stages II and II. Their microstructure was similar to that in males of the common form at these stages of maturity (Table 3). In seven males of the dwarf form caught in September and October, an active wave of spermatogenesis (stage III) had proceeded. Three males with gonads at maturity stage IV

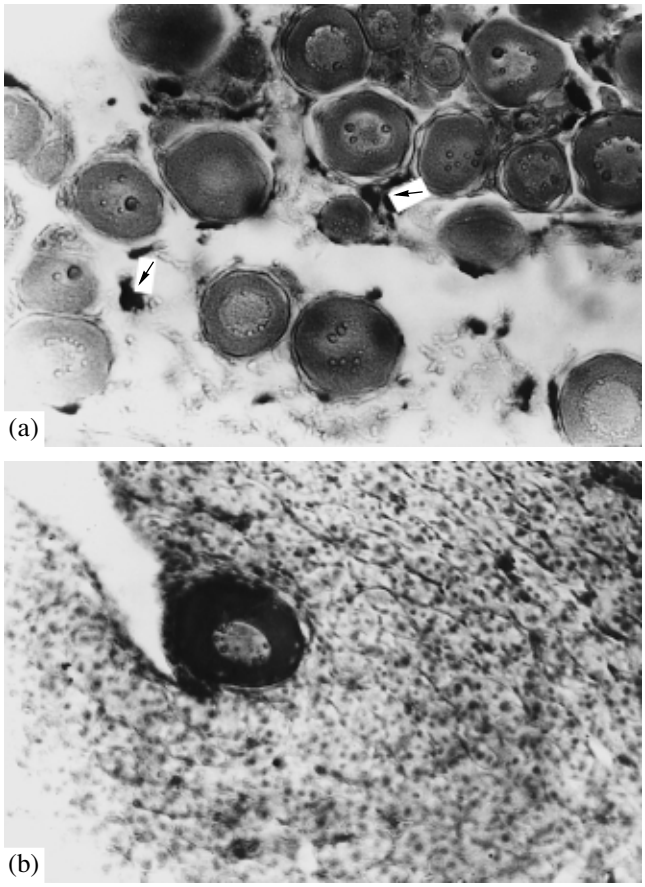

Fig. 4. Microstructure of gonads of *Pseudoscaphirhynchus kaufmanni*. (a) female, form not determined (L 81 mm, Q 3.05 g, age 0+; October 26, 1999), VI–II stages of gonad maturity—aggregations of pigment granules among oocytes of the period of cytoplasmatic growth (designated by arrows). (b) male of a common form (L 260 mm, Q 107 g, age 2+; October 1, 1998, II stage of gonad maturity—oocyte of the period of cytoplasmatic growth among seminiferous tubules. Magn. 58.5×.

Table 3. Main biological indices of male *P. kaufmanni* at different stages of gonad maturity

Stage of gonad maturity	L, mm	Q, g	Age, years	GSI, %	C_{mat}, %	*n*	Data source
Common form							
II	198.0–420.0 / 266.6	53.0–380.0 / 137.9	1+–4+	0.2–0.6 / 0.3	0.2–0.5 / 0.3	5	Our data
II fatty	205.0–420.0 / 318.0	61.5–522.0 / 248.9	1–6	0.2–3.8 / 1.6	0.2–3.4 / 1.4	13	″
Dwarf form							
II	127.0–261.0 / 171.1	13.3–104.0 / 36.1	0+–3	0.2–1.9 / 0.6	0.2–1.8 / 0.5	15	Our data
II fatty	135.0–300.0 / 194.4	19.0–178.0 / 56.7	0+–4	0.3–3.4 / 1.6	0.3–3.0 / 1.4	13	″
III	196.0–250.0 / 217.9	54.5–109.0 / 77.2	2+–3+	2.9–15.3 / 9.0	2.7–12.7 / 7.7	7	″
III–IV	221.0	75.0	3+	5.2	4.7	1	″
IV	220.0–240.0 / 230.0	80.0–81.0 / 80.5	3+	3.4–5.3 / 4.4	3.1–4.6 / 3.9	2	″
I; I–II; II	110.0–296.0	–	2–5	–	0.24–0.34	–	Makeeva and Sagitov, 1979
II fatty	–	–	–	–	1.0	–	″
III–IV	219.0	–	6		7.39	1	″
IV	233.0–240.0	–	7–9	–	3.0	2	″
IV	240.0–303.0 / 265.0	39.3–78.7 / 56.2	6–7(5)	–	0.23–7.39 / 2.73	24	Tleuov and Sagitov, 1973
VI	242.0	–	5	–	2.26	1	Makeeva and Sagitov, 1979
The form not determined							
I; II	72.0–152.0 / 110.8	2.15–20.0 / 9.4	0+–1	0.2–0.5 / 0.4	0.2–0.5 / 0.4	4	Our data

were caught in December; their seminiferous tubules contained spermatozoids. In gonads of some individuals, the same anomalies as in males of the common form of *P. kaufmanni* were recorded (Table 4).

Big shovelnose of an unidentified form. In addition to the abovementioned forms of *P. kaufmanni*, our materials contained 11 individuals of small size at ages of 0+ and 1+; their relation to this or another form was not elucidated. Of them, two individuals were juvenile; sex differentiation had not yet occurred; and sexual cells were represented by gonia only. Five individuals were females; in their gonads, egg-bearing plates had been formed that contained oocytes of the early phases of development and the start of cytoplasmatic growth (maturity stages I and II) (Table 2). Another four individuals proved to be females with gonads at maturity stages I and II—in the former, sexual cells were represented by primary spermatogonia; in the latter, spermatogonia reproduced and the seminiferous tubules had been formed (Table 3).

Little Amu-Dar shovelnose *P. hermanni*

The gametogenesis of *P. hermanni* has not been described up to the present time. Our studies showed that the main processes of development of its sexual cells and gonads in females and males are similar to those described for *P. kaufmanni* (Makeeva and Sagitov, 1979). Therefore, the present paper cites only some specific features of gametogenesis characteristic of the little shovelnose.

Females of the little shovelnose—three of 14 individuals available to us were immature with gonads at maturity stage II. In seven individuals with gonads at

Table 4. Male proportion (%) of *P. kaufmanni* and *P. hermanni* with anomalies in macro- and microstructure of gonads

Stage of gonad maturity	Number of males with anomalies in the macro- and microstructure of gonads, %					*n*
	lobed structure of the testes and outgrowths on them	cavities among seminiferous tubules	aggregations of blood corpuscles in the testes	fatty cells in the generative part of the testes	oocytes of the period of cytoplasmatic growth in the testes	
P. kaufmanni (common form)						
II	40.0	60.0	40.0	–	20.0	5
II fatty	–	16.7	–	33.3	25.0	12
P. kaufmanni (dwarf form)						
II	21.4	57.1	14.3	–	14.3	14
II fatty	7.1	14.3	35.7	28.6	21.4	14
III	–	85.7	–	–	14.3	7
III–IV	–	100.0	–	–	–	1
IV	2	–	–	–	–	2
P. hermanni						
I	–	–	–	–	–	2
II	33.3	33.3	–	–	33.3	3
II fatty	25.0	–	–	25.0	–	4
III–IV	100.0	100.0	–	–	–	1
Hybrid of *P. kaufmanni* and *P. hermanni*						
III–IV	–	100.0	–	–	–	1

Table 5. Main biological indices of *P. hermanni* at different stages of gonad maturity

Stage of gonad maturity	L, mm	Q, g	Age, years	GSI, %	C_{mat}, %	*n*
Females						
II	128.0–140.0 / 136.0	10.2–19.0 / 14.7	1–1+	0.9	0.5–0.9 / 0.7	3
II fatty	159.0–178.0 / 169.1	18.0–28.0 / 23.1	2–3+	3.5–6.5 / 5.2	3.2–5.6 / 4.7	7
IV completed	193.0–203.0 / 198.0	35.0–41.0 / 38.0	4	27.3	12.9–20.0 / 16.5	2
VI	188.0–233.0 / 210.5	33.0–50.5 / 41.8	4–5	–	–	2
Males						
I	90.0–117.0 / 103.5	3.7–8.8 / 6.3	1	0.1	0.1	2
II	160.0–225.0 / 185.0	20.0–48.0 / 32.7	1+–5+	0.4	0.4	3
II fatty	131.0–180.0 / 159.0	11.2–30.0 / 21.3	1–3	0.6–3.6 / 2.0	0.5–3.1 / 1.6	4
III–IV	202.0	39.8	4	3.4	3.0	1
Hermaphrodytes						
II fatty	196.0	32.2	3	4.9	4.3	1

fatty maturity stage II, similar to females of the big shovelnose, the GSI and C_{mat} were increased due to the accumulation of great amounts of fat in the gonads (Table 5). Two females caught on February 19, 2000 and on February 25, 2002 at the age of four years had mature oocytes (completed maturity stage IV). The nucleus in all oocytes had shifted toward the animal pole, and the disintegration of the nuclear membrane had begun. Single oocytes were smaller by a factor of 1.5 than the basic group of sexual cells. Some oocytes had resorbed. From 42.1 to 100% of oocytes were deformed. The ratio of the thickness of membranes of mature oocytes in the big and little shovelnoses was equal: jelly-like and inner yolk membranes were of equal thickness, and the outer yolk membrane had a thickness two times greater. The membranes of all mature oocytes upon histological treatment were stained unevenly. In 28.6–68.4% of oocytes, a local delamination of the jelly-like and yolk membranes was observed (Fig. 5a). In a female caught in February 2002, 50% of the examined oocytes contained vacuoles in the outer yolk membrane, and in 21.4% of sexual cells, among yolk of the vegetative pole, a substance of unknown nature was revealed. The absolute fecundity of this female was 958 eggs.

On April 25, 1996, two spent females of the little shovelnose, 188 and 233 mm long, at the ages of five and four years, respectively, were caught. Their gonads contained numerous empty follicles and pigment granules from the resorption of residual mature oocytes (Fig. 5b).

Males of *P. hermanni* had gonads at maturity and fatty maturity stages II (Table 5). The microstructure of their gonads was similar to that of males of the big shovelnose. One male caught in November 2000 had gonads at maturity stages III–IV. Gonads of males of the little shovelnose exhibited the same anomalies as the males of the big shovelnose (Table 4).

In one hermaphrodyte individual of the little shovelnose, one gonad contained oocytes of cytoplasmatic growth and earlier stages of development located in one row along the margin of egg-bearing plates (fatty stage II); nearly two-thirds of the cells degenerated. In another gonad, reproducing spermatogonia were observed, which is typical for males with gonads at fatty stage II. In one section of the testis, big aggregations of blood corpuscles were recorded.

A male presumably a hybrid between the big and little shovelnoses (L, 215 mm; Q, 62 g; GSI, 4.7; C_{mat}, 4.4%; maturity stage III–IV) was caught in October 2002. In its gonads, an active wave of spermatogenesis was observed; about half the seminiferous tubules contained spermatozoids; and small cavities were found among the seminiferous tubules.

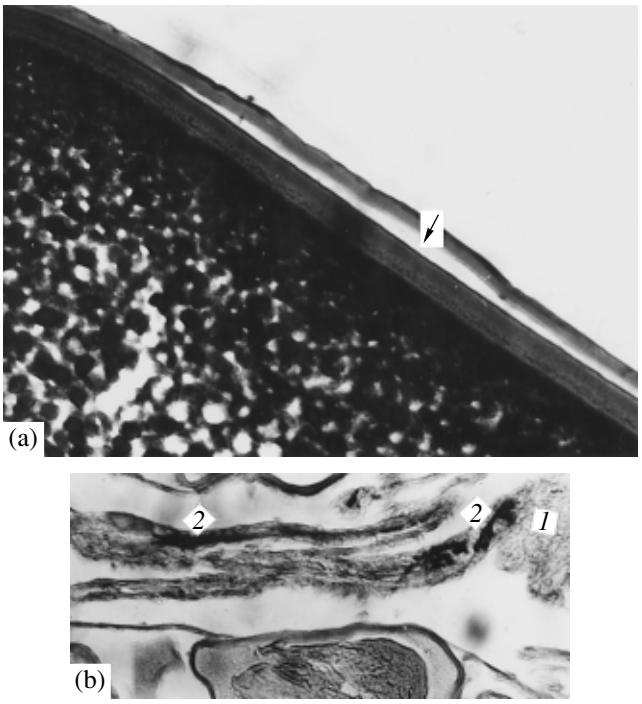

Fig. 5. Microstructure of gonads of female *Pseudoscaphirhunchus hermanni*. (a) IV completed stage of gonad maturity—fragment of mature ovicell; a local exfoliation (designated by an arrow) of the jelly membrane from the yolk membrane (♀ L 203 mm, Q 41 g, age 4+; February 19, 2000). (b) stage of gonad maturity VI (♀ L 233 mm, Q 50.5 g, age 4+; April 25, 1996). (*1*) empty follicles, (*2*) pigment granules that remained after the resorption of single unspawned mature ovicells among oocytes of the period of cytoplasmatic growth (the structure of the latter is disturbed due to an accidental sample freezing prior to fixation). Magn. 58.5×.

DISCUSSION

The spawning of *P. kaufmanni* according to several authors (Nikolsky, 1938; Teuov and Sagitov, 1973; Makeeva and Sagitov, 1979) proceeds from mid-March to April inclusively, and according to our data, it occurs mainly in April. Thus, three spent females of the dwarf form available in our material were caught in the period from late-April to late-May. Their gonads contained few resorbing residual ovicells, which attested to successful spawning by these individuals. The spawning of *P. hermanni* proceeds within the same period. Previously (Tleuov and Sagitov, 1973; Makeeva and Sagitov, 1979), it was shown that females of the dwarf form of *P. kaufmanni* reach sexual maturity at the age of six–eight years at a body length of over 200 mm. Their coefficient of maturity reaches 14–18%. According to our data, females and males of this form at the present time reach sexual maturity at the age of four–five and three–four years, respectively, at similar sizes and coefficients of maturity (Tables 2 and 3). Female *P. hermanni* reach sexual maturity at the same age as females

of the dwarf form of *P. kaufmanni* (four–five years) at similar sizes and GSI values (Tables 2 and 5).

In females and males of the big and little shovelnoses, the GSI in the process of development of their gonads is similar. In females of the dwarf form of *P. kaufmanni*, with gonads of maturity and fatty maturity stages II, the average values of GSI are slightly higher than in females of the common form, although maximum values of this index (up to 11.8%) were recorded for individuals of the common form (Table 2). The same differences are also characteristic of males with gonads at maturity stage II, but they were not observed at fatty stage II (Table 3). Our material attests to an increase in recent years in the values of C_{mat} in females with gonads in fatty maturity stage II (Table 2) in comparison with the 1960s (Makeeva and Sagitov, 1979), although, the sizes and weights of the fish bodies did not undergo particular changes. In our samples, there were only two females of the common form of *P. kaufmanni* with mature genital products (stage IV) caught in December 1997 and April 1999. This indicates a low reproductive capacity for this form of the big shovelnose. An analogous conclusion was arrived at by former researchers (Tleuov and Sagitov, 1973; Makeeva and Sagitov, 1979) whose materials contained no form of this female with mature genital products.

The start of vitellogenesis was traced in females of the dwarf form of *P. kaufmanni*. From September to December, in oocytes, yolk begins to deposit, first in one to two rows in the center of ooplasm around the nucleus and then filling the entire ovicell. At this time, the GSI is low (2.5–2.7%). Mature females and males of the dwarf form of the big shovelnose occur in catches occasionally. As in most acipenserids, in females of both forms of *P. kaufmanni*, the uncompleted stage IV of gonad maturity continues until December; towards the spawning period (April), oocytes mature completely and the nucleus shifts to the animal pole (completed stage IV). The ratio of the thickness of membranes of mature oocytes of the big and little Amu-Dar shovelnoses is similar, which agrees with the data of other authors—the thickness of the jelly-like membrane in the dwarf form of the big shovelnose is 6 μm; the summary thickness of yolk membranes is 16.4–18.45 μm (Makeeva and Sagitov, 1979; Vorob'eva and Markov, 1999). The fecundity of females of the dwarf form, according to our data, has considerably increased in recent years from 990–1910 (Tleuov and Sagitov, 1973) to 2750–4365 eggs (on average, 3759 eggs).

In males of the dwarf form of *P. kaufmanni*, the active wave of spermatogenesis (maturity stage III) begins in September. In December, almost all seminiferous tubules are filled with spermatozoids (maturity stage IV). Males of the common form of *P. kaufmanni* with mature genital products were lacking in our materials.

The accumulation of material on the pathologies of gameto- and gonadogenesis permits comparative assessment of the state of reproduction of fish populations. Formerly (Makeeva and Sagitov, 1979) only the natural process of resorption of mature ovicells in one female of the dwarf form of *P. kaufmanni* was mentioned. Our collections did not contain females of this kind; however, individuals of this form with anomalies in the structure of mature oocytes were found—their deformation (63–100%), local rupture and delamination of membranes (4.5–50% of oocytes) indicates turgor disturbance in the membranes and their strength; the uneven staining of membranes (in 29.4–100% of cells) is an index of changes in the biochemical processes in the oocytes. Our materials contained only two females of the common form of *P. kaufmanni* and *P. hermanni* each with mature oocytes where the same anomalies were revealed as in the dwarf form of *P. kaufmanni*.

In males of the big and little shovelnoses, anomalies in the micro- and macrostructure of gonads were revealed (Table 4) that were not found in these species previously. In one individual, there can be several anomalies simultaneously. The greatest number of males with disturbances in gonad development was revealed in the big shovelnose; the range of its anomalies is the widest at the early stages of gonad development. In individuals with gonads at maturity stage IV, no anomalies were observed. It is not excluded that this is related to a small number of mature fish in our samples. Despite the fact that in males of the little shovelnose, the frequency of occurrence of anomalies is smaller and their range is narrower, they have a pattern of more profound changes. Single oocytes of cytoplasmatic growth found in gonads of ten males of the big shovelnose (16.7% of the total number of males of both forms), possibly, did not develop further and were resorbed. The presence of oocytes in the testes, the lobed gonad structure, and outgrowths on their external side indicated the initial moments in the disturbance of the hormonal control of the reproductive function in these individuals and their inclination to hermaphroditism. The revealed case of hermaphrodytism in the small shovelnose indicated more profound disturbances in the given individual. The penetration of the fatty tissue into the generative part of the gonad at fatty stage II in males testified to a disturbance of lipid metabolism in these fish. The emergence of cavities among seminiferous tubules and the aggregations of blood corpuscles indicated destructive processes in the gonads. Similar anomalies in the structure of sexual cells and gonads were recorded in acipenserids of the Volga–Caspian basin and rivers of Siberia (Romanov *et al.*, 1990; Shagaeva *et al.*, 1993; Akimova and Ruban, 1996; Ruban and Akimova, 2001*; et al.)* and were related to water body pollution. Possibly, in female and male shovelnoses, these anomalies were also caused by unfavorable environmental conditions (Zholdasova, 1997).

The abovementioned disturbances in gonad microstructure in four females of the dwarf form of *P. kauf-*

manni and in two females of an unelucidated form (Fig. 4a) that had short length, low weight, young age, and gonads at maturity stage II do not allow us to be quite confident that they had already reproduced since there were no mature females with such parameters in our materials. However, there is much evidence on dwarf forms of various fish species from different water bodies that reproduce at small sizes and young ages (Aliev, 1953; Dmitrieva, 1957; Mosksal'kova, 1960; Kuliev, 1965; Shikhshabekov, 1969; Khaberman, 1978; Koshelev, 1984; Kuznetsov, 1986; Travkina, 1997; Ustarbekov, 2000; Savvaitova *et al.*, 2001; Alekseev and Kirillov, 2001; *et al.*). One of the main factors causing the emergence of small individuals in the populations and their early maturation is a decreased food supply, which enables populations to maintain high numbers even under unfavorable conditions (Makeeva and Nikolsky, 1965; Nikolsky, 1969). Possibly, the emergence in *P. kaufmanni* of mature individuals of unusually small size is also determined by this factor. Previously, it was shown (Makeeva and Sagitov, 1979) that the minimal time interval between the spawnings of females of the dwarf form of *P. kaufmanni* comprises three to four years. Our data support this conclusion. However, there is evidence that when shovelnoses were kept under artificial conditions (in special units at the Moscow Zoo) and were given plenty of food, this period decreased to one year; increased absolute fecundity during their artificial rearing was also recorded (Goncharov *et al.*, 1991).

CONCLUSIONS

The processes of gameto- and gonadogenesis of *P. kaufmanni* and *P. hermanni* are similar and proceed according to a scheme common for all acipenserids. In years, females and males of the dwarf form of *P. kaufmanni* have begun to reach sexual maturity at an earlier age (at four–five and three–four years). Their length and the relative weight of their gonads are close to those in individuals described previously (Tleuov and Sagitov, 1973; Makeeva and Sagitov, 1979). Female *P. hermanni* also mature at an age of four to five years at a body length and weight similar to these indices in the dwarf form of *P. kaufmanni*. According to our data, *P. kaufmanni* and *P. hermanni* spawn mainly in April, at a water temperature of 13–20°C. In September, the nutrient accumulation in female oocytes (vitellogenesis) and a wave of spermatogenesis in males (gonad maturity stage III) begin. The thickness of membranes of mature oocytes has not changed in recent decades. The ratio of the thickness of the jelly-like, inner yolk and the outer yolk membranes is 1 : 1 : 2. In recent years, different anomalies have emerged in the micro- and macrostructure of gonads of the big and little shovelnoses that were not recorded previously. Anomalies of this kind in females involve: the deformation of some mature oocytes, local delamination and rupture of membranes, and their uneven staining; in males: a lobed structure of the testes and the formation of outgrowths on their outer surfaces, cavities among seminiferous tubules, aggregations of blood corpuscles between seminiferous tubules, the development of single oocytes of the period of cytoplasmatic growth in the tissue of the testis, and the presence of one hermaphrodyte individual in the little shovelnose. In the big shovelnose, the range of anomalies is wider than in the small shovelnose, but in the latter, the anomalies are more clearly pronounced. The revealed disturbances in the structure of sexual cells and gonads of shovelnoses are, possibly, related to the deterioration of the ecological situation in the Amu Darya (Zholdasova, 1997).

Among female *P. kaufmanni*, for the first time individuals were found with gonad microstructure suggesting their unusually early sexual maturation at small sizes and low body weight. They account for 7.0% of the total number of females of this form; their age is 0+…2+; length, 81–152 mm; weight, 3.05–22.0 g. The population of the dwarf form of *P. kaufmanni* is in the most favorable state. Catches of mature individuals of this population with gonads at maturity stages III, IV, V, and VI are common. However, the revealed anomalies in the micro- and macrostructure of gonads attest to a decrease of the quality of their genital products. In *P. hermanni* and the common form of *P. kaufmanni*, the reproductive capacity of populations is, possibly, lower due to a small number of females and males with mature genital products.

ACKNOWLEDGMENTS

The study was supported by the Russian Foundation for Basic Research, grant no. 02-04-48229; U.S. National Science Foundation, grant no. DEB-9527938; Civilian Research and Development Foundation for Independent States of Former Soviet Union, grant no. TBI-2045.

REFERENCES

Akimova, N.V. and Ruban, G.I., Systematization of Disturbances in the Reproduction of Acipenserids (Acipenseridae) at Anthropogenic Impacts, *Vopr. Ikhtiol.*, 1996, vol. 36, no. 1, pp. 65–80.

Alekseev, S.S. and Kirillov, A.F., The First Finding of the Arctic Char *Salvelinus alpinus* Complex in the Aldan Basin and Its Significance for the Understanding of the History of Char Dispersal in Eastern Siberia, *Vopr. Ikhtiol.*, 2001, vol. 41, no. 4, pp. 465–480.

Aliev, D.S., Ichthyofauna of Freshwater Lakes of Western Uzboi, *Tr. Murgab. Gidrobiol. St., Akad. Nauk Turkmen. SSR*, Ashkhabad, 1953, vyp. 2, pp. 7–75.

Dmitrieva, E.N., Morphoecological Analysis of Two Species of the Crucian Carp *Carassius carassius*, *Tr. Inst. Morfol. Zhivotn. Akad. Nauk SSSR*, 1957, vyp. 16, pp. 102–170.

Dragomirov, N.I. and Shmal'gauzen, O.I., Ecologo-Morphological Features of Larval Shovelnose, *Dokl. Akad. Nauk SSSR, Nov. Ser.*, 1952, vol. 85, no. 6, pp. 1399–1402.

Goncharov, B.F., Shubravyi, O.I., and Uteshev, V.K., Reproduction and Early Development of the Big Amu-Dar Shovelnose (*Pseudoscaphirhynchus kaufmanni* Bogd.), *Ontogenez*, 1991, vol. 22, no. 5, pp. 485–492.

Khaberman, Kh.Kh., Peculiar Form of the Bream *Abramis brama* from Lake Yaskhan of Turkmen SSR, in *Biologicheskie osnovy rybnogo khozyaistva vodoemov Srednei Azii i Kazakhstana* (Biological Basis of Fish Management of Water Bodies of Central Asia and Kazakhstan), Conf. Proc., Frunze: Ilim, 1978, pp. 431–433.

Kozhin, N.I., Rare Acipenserids, *Tr. Tsentr. Nauchno-Issled. Inst. Osetr. Rybn. Khoz.*, 1970, vol. 2, pp. 34–36.

Koshelev, B.V., *Ekologiya razmnozheniya ryb* (Ecology of Fish Reproduction), Moscow: Nauka, 1984.

Kuhajda, B.R., Mayden, R.L., Salnikov, V.B., and Birstein, V.J., Examination of Intraspecific Variation and Life History Characteristics of *Pseudoscaphirhynchus kaufmanni* and *P. hermanni* (Actinopterygii, Acipenseridae), Central Asian Sturgeon Endemic to the Amu Darya River, *Program Book and Abstracts of Joint Meeting of the American Society of Ichthyologists and Herpetologists*, 80th Annual Meeting, 2000, pp. 223–224.

Kuliev, Z.M., On the Morphology and Biology of the Dwarf Roach *Rutilus rutilus* of Kizylagach Bay, *Izv. Akad. Nauk Az. SSR, Ser. Biol. Nauk*, 1965, no. 2, pp. 42–47.

Kuznetsov, Yu.K., Study of Ovarian Functions in Connection with the Emergence of Dwarfism in Fish and Cyclostomata with Reference to Representatives of the Genera *Osmerus* Lacépede and *Lampetra* Grey, *Cand. Sci. (Biol.) Dissertation*, Leningrad: Leningr. Gos. Univ., 1986.

Makeeva, A.P. and Nikolsky, G.V., Sexual Structure of the Spawning Population of Fish, Its Adaptive Value, and Methods of Control, in *Teoreticheskie osnovy rybovodstva* (Theoretical Foundations of Fish Culture), Moscow: Nauka, 1965, pp. 53–72.

Makeeva, A.P. and Sagitov, N.I., Materials on Gametogenesis and Reproduction of the Big Amu-Dar Shovelnose (*Pseudoscaphirhynchus kaufmanni* Bogd.), in *Biologicheskie osnovy razvitiya osetrovogo khozyaistva v vodoemakh SSSR* (Biological Basis of Sturgeon Fish Management in Water Bodies of the USSR), Moscow: Nauka, 1979, pp. 155–169.

Maksunov, V.A., *Promyslovye ryby Tadzhikistana* (Commercial Fish of Tadzhikistan), Dushanbe: Donish, 1968.

Moskal'kova, K.I., Some Features of the Growth and Reproduction of *Knipowitscha* Iljin in Taganrog Bay, *Tr. Azov. Nauchno-Issled. Inst. Rybn. Khoz. (AzNIIRKh)*, 1960, vol. 1, no. 1, pp. 441–446.

Nedoshivin, A.Ya., Materials on the Study of the Don Fishery, *Tr. Azov.-Chernomor. Nauchno-Promysl. Eksped.*,1928, no. 4, pp. 1–175.

Nikol'skaya, M.P., The Development of the System of Ampullary Organs in the Big Amu-Dar Shovelnose *Pseudoscaphirhynchus kaufmanni* (Bogd.), in *Morfologiya, ekologiya i povedenie osetrovykh* (Morphology, Ecology, and Behavior of Acipenserids), *Sb. nauch. tr.* (Collection of Scient. Papers), Moscow: Nauka, 1989, pp. 71–89.

Nikolsky, G.V., *Ryby Tadzhikistana* (Fish of Tadzhikistan), Moscow: Akad. Nauk SSSR, 1938.

Nikolsky, G.V., On Parallel Intraspecific Variation in Fish, *Vopr. Ikhtiol.*, 1969, vol. 9, no. 1, pp. 7–13.

Nikolsky, G.V., *Chastnaya ikhtiologiya* (Descriptive Ichthyology), Moscow: Vysshaya Shkola, 1971.

Romanov, A.A., Sheveleva, N.N., and Altuf'ev, Yu.V., Disturbance of Gonado-Gametogenesis of Acipenserids of the Caspian Sea, in *Fiziologo-biokhimicheskii status volgo-kaspiiskilh osetrovykh v norme i pri rassloenii myshechnoi tkani (kumulyativnyi politoksikozis)* (Physiological and Biochemical Status of the Volga–Caspian Acipenserids in the Norm and at the Delamination of the Muscular Tissue (Cumulative Polytoxicosis)), Rybinsk: IBVV Akad. Nauk SSSR, 1990, pp. 92–100.

Roskin, G.I. and Levinson, L.B., *Mikroskopicheskaya tekhnika* (Microscopical Devices), Moscow: Sov. Nauka, 1957.

Ruban, G.I. and Akimova, N.V., The State of the Reproductive System and Causes of the Population Decline of the Siberian Sturgeon *Acipenser baerii* of the Ob River, *Vopr. Ikhtiol.*, 2001, vol. 41, no. 2, pp. 278–282.

Sagitov, N.I., On the Morphobiological Inhomogeneity of the Population of the Big Amu-Dar Shovelnose (*Pseudoscaphirhynchus kaufmanni* Bogd.), *Vestn. Karakal. Fil. Akad. Nauk Uzb. SSR*, 1968a, no. 2, pp. 30–34.

Sagitov, N.I., On the Morphology of the Big Amu-Dar Shovelnose (*Pseudoscaphirhynchus kaufmanni* Bogd.), *Vopr. Ikhtiol.*, 1968b, vol. 8, no. 5, pp. 807–816.

Sagitov, N.I., On the Maturation and Fecundity of the Big Amu-Dar Shovelnose *Pseudoscaphirhynchus kaufmanni* Bogd.,*Vestn. Karakal. Fil. Akad. Nauk Uzb. SSR*, 1968c, no. 1, pp. 13–24.

Sagitov, N.I., On the Growth of the Big Amu-Dar Shovelnose *Pseudoscaphirhynchus kaufmanni Bogd., Vestn. Karakal. Fil. Akad. Nauk Uz. SSR*, 1969a, no. 1, pp. 39–44.

Sagitov, N.I., On the Dwarf Form of the Big Amu-Dar Shovelnose *Pseudoscaphirhynchus kaufmanni* Bogd., *Nauchn. Dokl. Vyssh. Shk., Ser. Biol. Nauk*, 1969b, no. 6, pp. 12–15.

Salikhov, T.V., Kamilov, B.G. and Atadzhanov, A.K., *Ryby Uzbekistana (opredelitel')* (Fishes of Uzbekistan (Key)), Tashkent: FAN, 2001.

Salnikov, V.B., Kuhajda, B.R., and Mayden, R.L., Conservation Studies and Life History Characteristics of *Pseudoscaphirhynchus kaufmanni* and *P. hermanni* (Actinopterygii, Acipenserdae), Shovelnose Sturgeon Endemic to the Amu Darya River in Central Asia, *4th Int. Symp. on Sturgeons*, Oshkosh, Wisconsin, USA, 8–13 July 2001, Extended Abstr., 2001, pp. 88–89.

Savvaitova, K.A., Gruzdeva, M.A., Kuzishchin, K.V., and Stygar, V.M., Lake Chars of the Genus *Salvelinus* (Salmonidae) of Paramushir Island, the Kuril Islands, *Vopr. Ikhtiol.*, 2001, vol. 41, no. 1, pp. 5–18.

Serebryakova, E.V., Study of Gonads of Spawners of the Sturgeon of the Volgograd Reservoir, *Tr. Vses. Nauchno-Issled. Inst. Morsk. Rybn. Khoz. Okeanogr.*, 1964, vol. 56, sb. 3, pp. 117–130.

Shagaeva, V.G., Nikol'skaya, M.P., and Akimova, N.V., Study of the Early Ontogenesis of the Volga Acipenserids (Acipenseridae) in Connection with the Anthropogenic Impact, *Vopr. Ikhtiol.*, 1993, vol. 33, no. 2, pp. 230–240.

Shikhshabekov, M.M., The Presence of Different Forms of the Roach *Rutilus rutilus*, Bream *Abramis brama*, and Carp *Cyprinus carpio* in Arakum Water Bodies of Dagestan, *Vopr, Ikhtiol.*, 1969, vol. 9, no. 1, pp. 46–50.

Shmal'gauzen, O.I., The Development of Larval Big Amu-Dar Shovelnose *Pseudoscaphirhynchus kaufmanni* Bogd., *Ontogenez*, 1991, vol. 22, no., pp. 493–513.

Tleuov, R.T., Allamuratov, B., and Konstantinova, L.G., The Aral Problem and Ways for Its Solution, *Rybn. Khoz.*, 1989, no. 6, pp. 47–52.

Tleuov, R.T. and Sagitov, N.I., *Osetrovye ryby Amudar'i* (Sturgeon Fish of the Amu Darya), Tashkent: FAN UzSSR, 1973.

Travkina, G.L., Specific Features of Oogenesis and Dynamics of Oocyte Development in the Amur Sleeper *Percottus glehni* Dybowski, *Tr. Biol. Nauchno-Issled. Inst. S.-Peterb. Gos. Univ.*, 1997, issue 44, pp. 29–38.

Trusov, V.Z., Some Specific Features of Maturation and the Maturity Scale of Gonads of the Russian Sturgeon *Acipenser gueldenstaedti*, *Tr. Vses. Nauchno-Issled. Inst. Morsk. Rybn. Khoz. Okeanogr.*, 1964, vol. 56, sb. 3, pp. 69–78.

Ustarbekov, A.K., Morphological Variability of the Main Commercial Species of Cyprinids of the Caspian Basin, *Abstract of Doctor (Biol.) Dissertation*, Moscow: IPEE RAN, 2000.

Vorob'eva, E.I. and Markov, K.P., Ultrastructural Specific Features of the Eggs in Representatives of Acipenseridae in Connection with the Biology of Reproduction and Physiology, *Vopr. Ikhtiol.*, 1999, vol. 39, no. 2, pp. 197–209.

Zholdasova, I., Sturgeons and the Aral Sea Ecological Catastrophe, *Environ. Biol. Fish.*, 1997, vol. 48, pp. 373–380.

Translated by I.A. Pogosyants