

Ovarian development and cycles in cultured Siberian sturgeon, *Acipenser baeri*

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Abstract – Sturgeon lack external sexual dimorphism and have longer-than-annual ovarian cycles. Using gonadal biopsy of marked fish, we identified sex and monitored ovarian development in one cohort of cultured Siberian sturgeon over the age interval 8.5-12.5 year. Sex ratio in the population did not differ from 1:1 (268 females and 286 males). Each November, the females were separated into two groups: one with ovarian follicle diameter ≥ 2.8 mm (Group 2, spawnable) and another with smaller follicles in previtellogenic or vitellogenic growth (Group 1). During the 5 year period of observations, 11.2 % of the initial 268 females were lost. The oocytes of Group 2 exhibited migratory germinal vesicle but its position in animal hemisphere was not peripheral in November. The annual changes in proportions of Group 2 females, from 34.6 to 63.3 %, reflected ovarian cycles of different duration. Majority of 196 females, matured two or more times during a period of study, exhibited biennial ovarian cycle or recurring cycles of 1 and 2 years in the same individual. Annual and triennial cycles were also observed. Some abnormalities in oocyte pigmentation are described. © Ifremer-Elsevier, Paris

***Acipenser baeri* / broodstock management / ovarian development / ovarian cycle**

Résumé – Développement des ovaires et cycles ovariens chez l'esturgeon sibérien (*Acipenser baeri*) en élevage. Les esturgeons ne présentent pas de dimorphisme sexuel et ont des durées de cycles ovariens supérieures à 1 an. En pratiquant des biopsies sur des animaux marqués, nous avons identifié le sexe et suivi le développement ovarien d'une cohorte d'esturgeons sibériens mis 5 ans en élevage, de 8,5 à 12,5 ans. Le sex-ratio dans la population ne diffère pas du rapport 1:1 (268 femelles et 286 mâles). Chaque année en novembre, les femelles étaient séparées en deux groupes : l'un dont le diamètre des follicules ovariens était $\geq 2,8$ mm (Groupe 2), potentiellement capable de pondre dans un délai bref) et l'autre avec des plus petits follicules ovariens en prévitellogenèse ou en vitellogenèse (Groupe 1). Durant les 5 années d'observation, 11,2 % des 268 femelles initiales ont été perdues. Les ovocytes du Groupe 2 montrent une migration de la vésicule germinale mais pas en périphérie en novembre. La proportion annuelle de femelles du Groupe 2 varie entre 34,6 et 63,3 %, traduisant des cycles ovariens de durée variable. La majorité des 196 femelles a eu deux maturations sexuelles ou plus, durant la période expérimentale et a présenté des cycles bisannuels ou des cycles récurrents de 1 et 2 ans chez les mêmes individus. Des cycles annuels et triannuels ont également été observés. Quelques pigmentations anormales des ovocytes sont décrites. © Ifremer-Elsevier, Paris

***Acipenser baeri* / développement ovarien / cycle ovarien**

1. INTRODUCTION

Depending on the objective of sturgeon production (restocking or human consumption), broodfish are either obtained from the wild or farmed [4]. In most parts of the world, wild sturgeon populations are decreasing [5, 16]. Moreover, some disturbances in the reproductive development have been observed [2]. Therefore, the use of captive broodstock may be advisable for commercial culture and stock enhancement

programmes to avoid any additional impact on the wild population and to provide, in some cases, more healthy reproductive conditions. Due to the late age of the first sexual maturity, long gonadal cycles, and non-yearly spawning of sturgeon (see [9] for a review), the management of sturgeon broodstock is more complex and costly than for most other fish species. Recent studies were focused on domestication and reproductive management of Siberian sturgeon [1, 17], white sturgeon

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[8] and fertile hybrid *Huso huso* × *Acipenser ruthenus* [3, 6].

In order to establish more effective broodstocks of Siberian sturgeon management, we carried out selection of gravid females from the same cohort for five consecutive years. Females were separated into two groups: Group 1 with the ovarian follicle diameter < 2.8 mm, called 'rejected' (previtellogenic, early and mid-vitellogenic), and Group 2, called 'preselected' (late vitellogenesis, and migratory germinal vesicle). We know by experience that the Group 2 females are potentially spawnable within a few months while Group 1 needs at least one more year to fully mature. This practice has proved to be efficient in selecting females suitable for spawning, but the ovarian cycles were observed in only a few fish belonging to different age cohorts [17]. The objectives of this study conducted with marked fish of the same cohort were (i) to improve identification of the ripe females, and (ii) to examine the duration of ovarian cycles.

2. MATERIAL AND METHODS

2.1. Fish culture and maintenance

The experimental fish were the second generation of Siberian sturgeon born in 1984 as a result of reproduction carried out according to methods described [17]. Their parents arrived in France in 1975 as juveniles, originated from hatchery spawning of wild sturgeon from the Lena River. From 1991, fish were reared in 100 m² concrete raceways (25 × 4 m and 0.8-1.2 m depth) supplied with running aerated river water at stocking density from 12.5 to 18 kg·m⁻². The raceways were shaded though the water was generally turbid allowing the fish to spread all over the bottom of the raceway. The water temperature ranged from 5 to 8 °C in winter to 25 to 28 °C in summer. Fish were fed an artificial trout diet at a daily rate of 0.1-0.7 % of body weight depending on the water temperature, even when they were close to spawning, as this species is known to continue feeding during reproductive migration [15]. Before the high summer water temperatures, the fish were fed for one week with an antibiotic-supplemented food and the following week with a special food (Hepalim from Biomar Comp.) to protect liver and kidney against various disorders. From the time of sampling in November to the end of the reproductive period the fish were fed a trout broodstock diet supplemented with vitamin E.

2.2. Tagging of fish

Fish were tagged with three tags. One was a Petersen disc with a small coloured electric wire casing placed at the base of the dorsal fin using a piece of nylon thread and a small metallic sleeve. Two other tags were ovine Tip tags of two different colours placed on each of the pectoral fins using pliers. Each of

the three tags had an individual fish number. The multiple marking prevented loss of information and allowed quick visual identification of sexes by tag colour. In the following years of sampling (1993-1996), the tags were checked and replaced if necessary, and a metal probe was used to sample fragments of gonadal tissue.

2.3. Sampling

All fish in cohort (N = 575) were sampled once a year, in November, during the years 1992-1996. At a time of sampling, fish were brought from outside raceways into hatchery tanks, were weighed to the nearest 0.1 kg, then placed on an adapted table and supplied with continuous flow of aerated water in the mouth without anaesthetic [7].

Sturgeon exhibit no sexual dimorphism. In 1992, we determined the sex of the fish by observing under a stereomicroscope a small piece of gonad obtained via a small abdominal incision placed between the 3rd and 4th ventral scute (from the vent) slightly lateral to the ventral mid-line. The incision was closed with cross-stitches. In case when germ cells which were not identifiable, a smear of the gonadal tissue was observed under a compound microscope (× 400). This allowed us to distinguish the presence of spermatozoa.

2.4. Ovarian follicles and assessment of ovarian cycle

The following observations were noted on the fresh ovarian follicles: diameter, shape, colour and the presence of atretic follicles. Diameter was calculated as the mean of minimum and maximum diameters measured to the nearest 0.1 mm in 15-20 eggs from each female. In Group 2 females, we determined the polarization index (PI, the ratio of distance between germinal vesicle and the animal pole to the oocyte's diameter, egg envelopes excluded) of the oocytes after fixation by boiling according to Kasanskij et al. [10]. These measurements were made under stereomicroscope with eye-piece micrometer (× 16) on fifteen follicles. We also recorded morphological abnormalities of ovarian follicles, such as marbled coloration and pigmentation of cortex and ooplasm of the intact and bisected (after boiling) eggs. The photographs of follicles and oocytes were taken under a stereomicroscope.

The dividing line between Group 1 and Group 2 females was 2.8 mm follicle diameter which was a minimum size of ovarian eggs to allow spawning in the following months [17]. The Group 2 females were firstly assayed for in vitro oocyte maturation (in presence of 1 µg·mL⁻¹ progesterone) and females with germinal vesicle breakdown (GVBD) response > 90 % were induced to spawn by hormonal injection [17]. Although not all Group 2 females spawned, we observed that all fish with follicle diameter > 2.8 mm will develop larger follicles in spring with migrated germinal vesicle (Williot, unpublished). Therefore, the

duration of ovarian cycles in population was estimated by the time (years) separating two successive observations on the ovaries of individual fish with the minimum follicle diameter 2.8 mm or larger.

2.5. Statistical analysis

The χ^2 test was used to examine the sex ratio in population (H_0 1:1) and the student *t*-test to compare mean body weight of groups 1 and 2 females. In the latter case, the homogeneity of variances (*F*-test) was examined before carrying out *t*-test.

3. RESULTS

3.1. Number of females

The results of initial sex determination and continuing inventory of male and female broodstock are shown in *table I*. At 8.5 year old, the sex was determined for 96.4 % of the 575 fish. The sex-ratio (female: male) was 48.4 %: 51.6 %, not significantly different from the equality ($\chi^2 = 0.23$; $P = 0.63$). During the four year experimental period, the total number of fish and of females decreased by 9 % and 11 % respectively. This decrease was due to mortality, observed during or after high summer temperatures, or culling some animals exhibiting irreversible signs of starvation, deformation of the vertebral column, or skin-damage due to their inability to swim normally. In different sampling years, the proportions of Group 2 females varied, from 35 to 63 % of total female population (*table I*). The mean body weight of Group 2 females was significantly greater than that of Group 1 females and increased from 7.4 to 8.8 kg during a period of observation. Moreover, the mean weight of Group 2 females increased continuously from year to year (*table II*).

Table I. Composition (number) of the 1984 Siberian sturgeon cohort during 5 year observation period (sampled each year in November).

	1992	1993	1994	1995	1996
Age (years)	8.5	9.5	10.5	11.5	12.5
Animals in the cohort	575	575	552	530	523
Males	286	286	279	279	274
Females	268	268	257	240	238
Lost females			11	17	2
Unknown sex	21	21	14	11	11
Group 2 females	129	158	89	152	108
n and (%) of the females	(48.1)	(58.9)	(34.6)	(63.3)	(45.4)

3.2. Gonads and ovarian follicles

Different stages of the ovarian development are shown in *plate I*. Two main types of follicles size distribution can be noted. In some females the size of vitellogenic follicles is very heterogeneous [1, 4, 5]; in

Table II. Body weight (mean \pm sd) of Siberian sturgeon females (Groupe 1 - 'rejected', Groupe 2 - 'selected'). Mean in each row are significantly different (*t*-test, $P < 0.05$).

Year of sampling	Group 1		Group 2	
	Weight (kg)	n	Weight (kg)	n
1992	6.48 \pm 2.23	139	7.41 \pm 2.56	129
1993	6.69 \pm 2.44	110	7.73 \pm 2.74	158
1994	6.47 \pm 2.43	166	7.94 \pm 2.70	89
1995	6.94 \pm 2.18	88	8.21 \pm 2.9	152
1996	7.01 \pm 2.66	130	8.83 \pm 2.67	108

others it seems to be fairly uniform [2, 3]. Smaller follicles have white colour [1, 2] and pigmentation starts when they reach diameters between 1 200 and 1 600 μ m, becoming darker with further growth [3]. The follicle shape is spherical, up to a size of around 3 mm. It is mainly during this intensive growth period that the residues of non-resorbed atretic follicles [2] may be seen. The fully grown follicles [6] vary in colour from greenish or brownish to black and exhibit different pigmentation patterns around the animal pole. They are usually ovoid [6] or pear-shaped. Along with these large follicles, there are small (200-300 μ m) and sometimes medium-size (400 to 500 μ m) follicle clutches present in the ovaries [7]. In the advanced stage of oocyte development, the germinal vesicle migrates from a central position to the periphery, when the follicle diameter is ≥ 2.8 mm [8]. It is possible to illustrate two extreme stages of gonadal development from two accidental mortalities. One is an underdeveloped ovary (*plate II*, 9) with large amount of fat tissue and very small follicles of 200 μ m (*plate I*, 1), and the other is a fully mature ovary (*plate II*, 10) with large black follicles. We can also distinguish clearly the ostium through which ova enter during oviposition to pass to the oviduct, the length of which is around one third of that of the abdominal cavity. In a denuded fully grown follicle, the multiple micropyles can be seen (*plate II*, 11).

Aside from these common patterns, three abnormalities were observed. Though it very seldom occurs in November, some females had fully grown atretic follicles, with a marble appearance (*plate II*, 12). Depending on the progress of atresia, few atretic follicles may be present in a sample or all oocytes in advanced clutch undergo degeneration, the last step of which is the appearance of small black atretic bodies containing black pigments (*plate I*, 2). The second abnormality was the presence of small irregularly distributed whitish spots (*plate II*, 13). These spots appear to arise due to formation of small pits at the plasma membrane. The third abnormality is a dark pigmentation of the yolk and cytoplasm surrounding the germinal vesicle (*plate II*, 14). This pigmentation is always observed along with the changes in pigmentation of the animal cortex of the oocyte. This observation has been carefully investigated from 1993 onward. The number of females exhibited this abnormality during the four years represented 15-25 % of Group 2 females. As the

most common duration of the ovarian cycles was two years, we also calculated the number of females which successively exhibited this abnormality between 1993 and 1995 and between 1994 and 1996. In both cases one third of these females exhibited similar abnormality during the second cycle. All these females were spawnable as a result of induced ovulation success.

The distribution of mean follicle diameter of females is shown (figure 1). The distributions are bimodal and

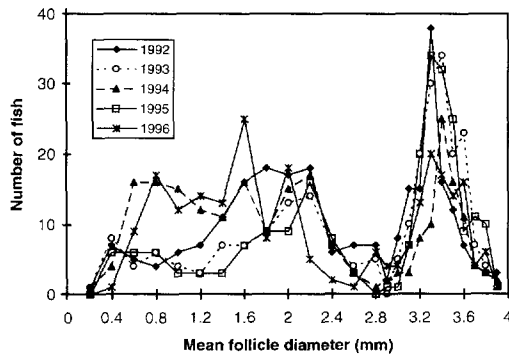


Figure 1. *Acipenser baeri*: Distribution of the mean follicle diameter of all females sampled during 5 years.

quite similar for each sampling year, especially for the right part of the plot (Group 2 females) with the follicle diameter greater than 2.8 mm and the mode at 3.3-3.4 mm. The threshold value of 2.8 mm allowed the separation of sampled population into two distinct groups each year. The left-hand parts of the distributions (Group 1 females) are more heterogeneous in shape, suggesting the presence of fish in different stages of ovarian vitellogenesis.

The distributions of the polarization index (PI) values are very similar from year to year, with mode corresponding to a PI value of 10% (figure 2). It is also noteworthy that for all the years, with the exception of 1993, the number of females with the PI values below 7.5% is very low. No oocytes with peripheral germinal vesicle (PI < 5%) were observed. In more advanced stage of migration, the germinal vesicle enlarges and changes its shape from spherical to ellipsoid. In the bisected eggs fixed by boiling the normal colour of the ooplasm is pale yellow with sometimes a clearer area close to animal pole.

3.3. Duration of ovarian cycles

To estimate proportions of iteroparous females with different duration of ovarian cycles, all mortalities (11.2%) and fish that never reached maturity (1.9%) or matured only once (8.2%) were omitted from the initial pool of 268 females (table I). The remaining 196 iteroparous females, the majority of which were in Group 2 in either 1992 or 1993, were analysed for the

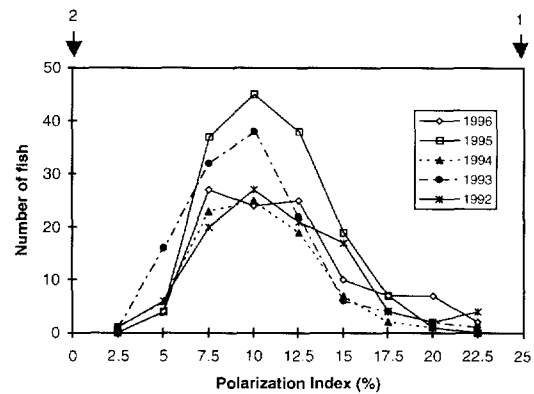


Figure 2. *Acipenser baeri*: Distribution of the oocyte polarization index in Group 2 - females for which ovarian follicle diameter ≥ 2.8 mm; females sampled each year in November, during 5 consecutive years. Arrows 1 and 2 on the top indicate central and peripheral germinal vesicle position, respectively.

duration of ovarian cycles (table III). Small proportions of fish exhibited either ovarian single or recurring annual ovarian cycles. The predominant ovarian cycles were biennial or recurring biennial and annual cycles observed in the same fish. Triennial cycle was observed in 11% of population (table III).

4. DISCUSSION

From an initial cohort of 575 animals, with our rapid method of sexing, we correctly characterised the sex in 96.4% of the 8.5 year old fish and determined 1:1 sex ratio in cultured population.

The threshold of the ovarian egg diameter 2.8 mm was used to discriminate, once a year in November, the potentially spawnable females, allowing for separation of fish into two groups. The Group 2, pre-selected or potentially spawnable females, exhibited homogenous distribution of follicle diameter with a mode 3.3-3.4 mm, compared to Group 1 ('rejected') which had smaller follicle with more scattered size distribution, varied between the years. This heterogeneity in the size of follicles from rejected females may reflect variation in rates of vitellogenic growth of the oocytes. The threshold follicle diameter 2.8 mm appears to correspond with the end of stage 4 of vitellogenic oocyte in Siberian sturgeon [12]. Previtellogenic follicles were always present in fully developed gonads of Siberian sturgeon as in cultured *Acipenser transmontanus* [8].

The distributions of oocyte polarization index values from Group 2 females were similar each sampling year and the migration of germinal vesicle to the animal pole of the oocyte was not completed in most of the fish sampled in November. In practice, we used the oocyte PI for choosing the most advanced females for

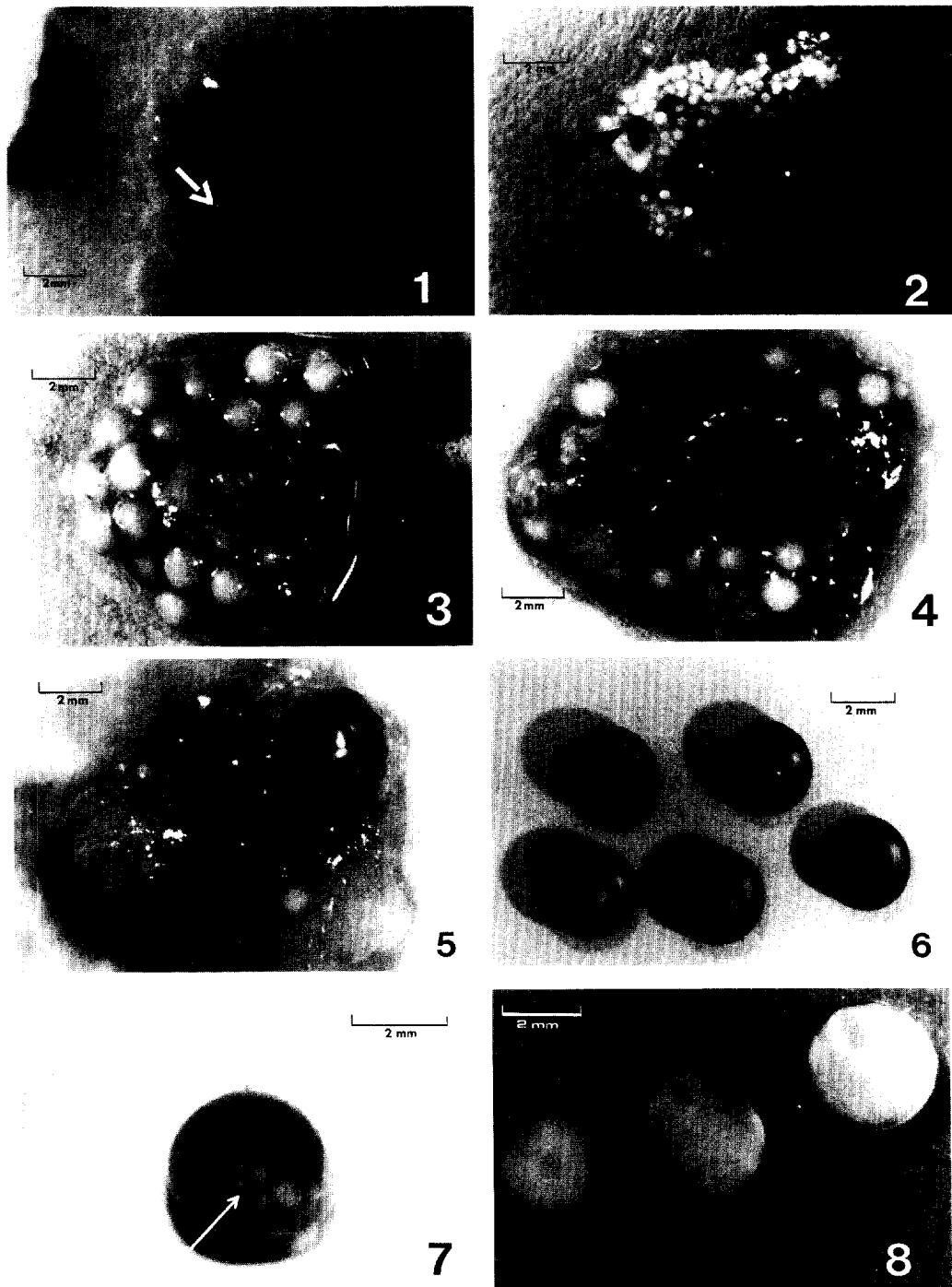


Plate I. Gonadal development in Siberian sturgeon females (biopsy samples).

- 1 - Small follicle embedded in a fatty gonadal tissue (arrow).
- 2 - Early stage of development, with small white follicles and darkly pigmented residual bodies (arrows).
- 3 - Advanced vitellogenic stage with homogenous slightly pigmented follicles.
- 4 - Heterogenous population of the ovarian in early vitellogenic stage.
- 5 - Heterogenous population of the follicles in a more advanced stage.
- 6 - Fully grown ovarian follicles.
- 7 - Fully grown follicle with attached small white follicles (arrow).
- 8 - Bisected (after boiling) follicles in different advanced stages of germinal vesicle migration.

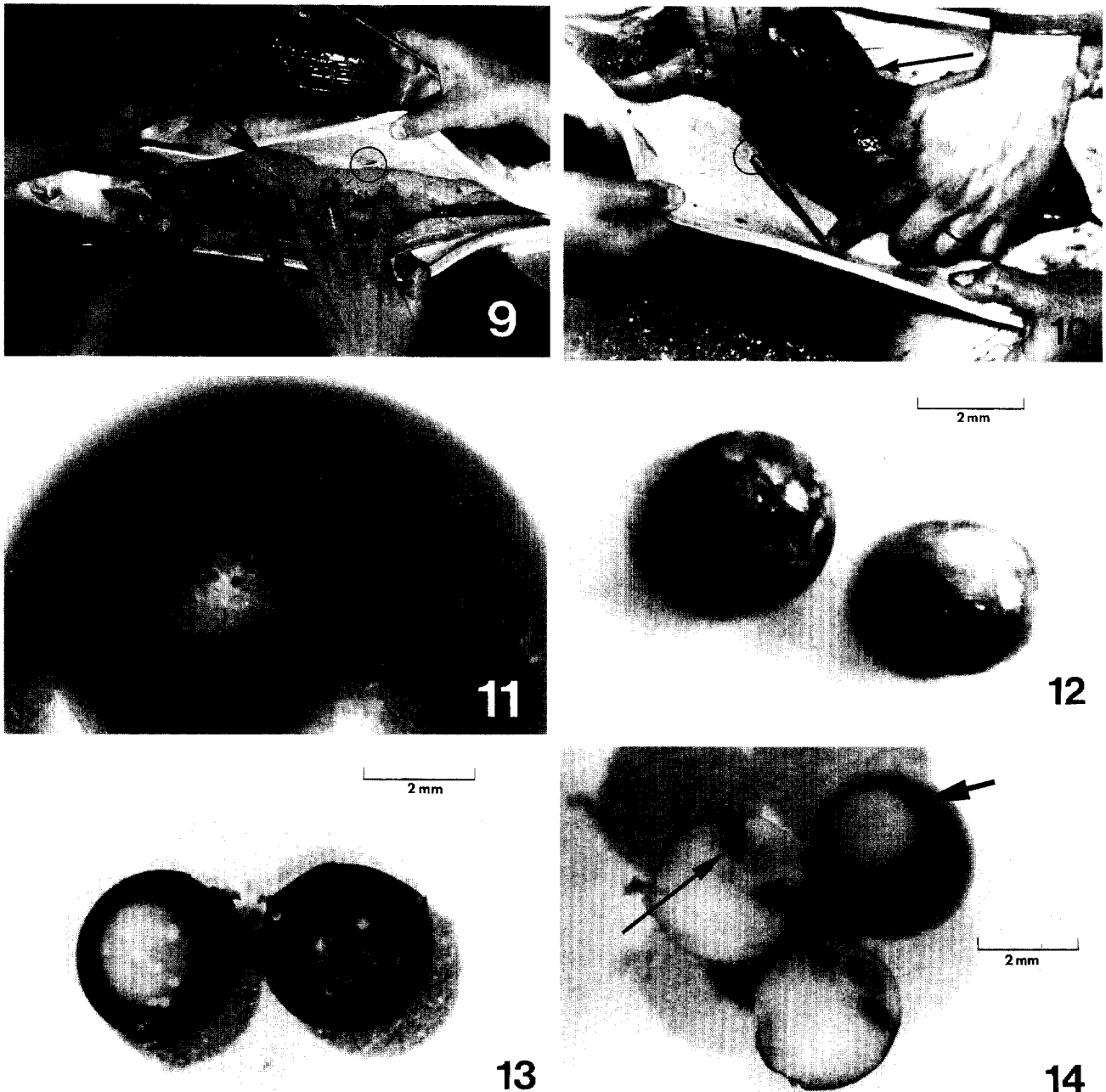


Plate II. Gonadal development (continued).

- 9 - Fatty gonad (arrow) of immature female and ostium of Müllerian duct (circle).
 10 - Fully grown darkly pigmented gonad (arrow) and the ostium pointed by a surgical tool (circle).
 11 - Denuded fully grown follicle with micropyles seen as small darkly spots around the animal pole area (arrow).
 12 - Atretic follicles showing a typical marbled coloration.
 13 - Irregularly distributed whitish spots in the animal pole area of fully grown denuded follicle.
 14 - Dark pigmentation of the yolk (bisected egg, left arrow) associated with discoloration of the animal pole area (right arrow).

the first hatchery reproduction, after determining their readiness to ovulate by the *in vitro* germinal vesicle breakdown assay.

The analysis of female body weight revealed that the mean weight of Group 2 females was consistently

higher than that of Group 1 females, reflecting increased mass of their gonads.

The marbled appearance of ovarian follicles was described as a typical indication of the ovarian atresia in *Acipenser stellatus* [11]. The fact that such follicles

were rarely observed in our November samples suggest that cultured Siberian sturgeon do not undergo ovarian regression before completion of vitellogenesis. However, the more advanced stages of atretic follicles were often present in fish with fully developed gonads as described in *Acipenser transmontanus* [8]. This suggests that the ovarian atresia may occur in the post-vitellogenic phase of development and full resorption of atretic follicles in sturgeon may require significant time.

During the five years experimental period we observed that the most common type of ovarian cycle was biennial, including single and recurring with regular (2 years) and irregular intervals (1 + 2 and 2 + 1 years). The recurring or single annual cycles were rare (table III), usually they preceded or followed a

Table III. Estimated duration of the individual ovarian cycles in sampled population of Siberian sturgeon females.

Cycle (year)	Females	
	n	%
Recurring		
1	7	3.6
2	39	19.9
1 & 2	62	31.6
1 & 3	3	1.5
Single		
1	1	0.5
2	63	32.2
3	21	10.7
Total	196	100

two year cycle. From the total number of ovarian cycles observed in this study (all females pooled), the annual cycle was 25 %, biennial 64 %, and triennial 11 % of all cases. The frequencies of the annual and biennial ovarian cycles in domestic Siberian sturgeon correspond well with the data on cultured *Acipenser*

transmontanus [8, 13] and are somewhat higher than our previous observations on Siberian sturgeon females from different age cohorts [17]. The variation in number of Group 2 fish over a period of 5 years (from 34.6 % to 63.3 %, annual average of 50 %, table I) may be explained by the existence of these irregular recurring ovarian cycles influenced by husbandry and environmental factors.

The most common (50 % of the fish) breeding interval of wild Siberian sturgeon female in the Lena River was shown to be 4 years [1, 14]. The latter author also reported that this interval was reduced to 1 or 2 years under rearing conditions which is in good agreement with our data.

Half of the males within the cohort matured each year.

As it has been reported for wild fish [15], the domestic Siberian sturgeon exhibit great variability in the pigmentation of full grown oocytes. Besides the normal variability, two unusual cases were observed in this study. One was a presence of small white spots (pits) on the plasma membrane of the oocyte. The other was a dark pigmentation of yolk and cytoplasm around the germinal vesicle which may involve movement of the pigment granules from the egg cortex, although it was not verified by histology. Korniyenko [11] described a movement of black pigment into the cytoplasm as a thin layer in the eggs of *Acipenser stellatus* and suggested that this movement might be responsible for the marbled appearance of follicles and signifies the onset of ovarian atresia. In the present study, the distribution of black pigment in the egg yolk appeared to be different from that reported by Korniyenko [11], as well as the external appearance of the follicles which exhibited regular dark pigmentation except for the animal pole area. Further investigation is needed to examine if this apparently abnormal pigmentation pattern relates to deterioration of egg quality.

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