
**BIOLOGY, MORPHOLOGY,
AND SYSTEMATICS OF HYDROBIONTS**

Morphofunctional Status of the Mongolian Grayling *Thymallus brevirostris* in a Mountain Lake in the South of Eastern Siberia

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Abstract—This study analyzes the histological peculiarities of the internal organs of the lake form of Mongolian grayling *Thymallus brevirostris* (Kessler, 1879) caught in the cold-water mountain Lake Hindiktig-Khol (Tuva Republic, Russia) in the summer. The maturation of the females starts at 4+ years; the peak of their spawning activity is observed at 5+. Males mature 1 year earlier than females. In summer, in the ovaries of mature females, the older generation of germ cells is represented by oocytes at the phase of the cytoplasm vacuolization; the younger generation of cells is represented by numerous previtellogenous oocytes. The peak of spermatogenesis is observed in the testes. Significant pathomorphological changes are revealed in the gill epithelium which inhibit the respiratory function. Weakly expressed liver congestion and moderate basophilia of hepatocytes both indicate normal conditions in this lake.

Keywords: histological analysis, Mongolian grayling, mountain lake, gonads, gills, liver

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INTRDUCTION

Studies of the Thymallidae family have been performed for more than two centuries (Kessler, 1879; Boulenger, 1898; Svetovidov, 1936; Berg, 1948; Tugarina and Dashidorzhi, 1972; Pivnicka and Hensel, 1978; Severin and Zinoviev, 1982; Mikheev and Maznikova, 2016). In a number of water bodies belonging to the geographical range of these fish species, graylings are an important component of the structure of the fish population of the littoral, being the dominant species of the ichthyocoenosis. The origin of this group of Salmonidae is confined to the water bodies of Altai and Mongolia, where their highest species diversity was noted (Pallas, 1776; Svetovidov, 1936; Berg, 1948; Baasanzhav et al., 1988; Travers, 1989; Koskinen et al., 2002; Weiss, 2007; Knizhin et al., 2008). However, though the European grayling *Thymallus thymallus* and Arctic grayling *Thymallus arcticus* are widespread and their biology is well-studied, the least studied representative of the family is Mongolian grayling *Thymallus brevirostris* (Kessler, 1879).

The Mongolian grayling is a common species inhabiting the inland water bodies of northwestern Mongolia, the basins of the Kobdo and Dzabkhan rivers, and a number of lakes (Gundrizer, 1966; Tugarina, Dashidorzhi, 1972); some of these water bodies are located in mountainous regions and are characterized by extreme hydrological conditions. It is currently believed (Knizhin et al., 2008; Slyn'ko et al., 2010) that the Mongolian grayling inhabiting the Kobdo

River basin is represented by large (carnivorous) and small (bottom feeding) forms. The genetic commonness of large and small forms, homogeneity of meristic characters, and similarity in the nature of color variation of the scale cover and the pattern on the dorsal fin indicate their belonging to the same species. Populations of the Mongolian grayling with a mixed type of feeding and signs of external structure, characteristic of both forms to varying degrees, also inhabit the water bodies of the Central Asian basin.

This study aims to analyze the size–age composition and histophysiological state of the gonads, gill apparatus, and liver of Mongolian grayling in Lake Hindiktig-Khol (Tuva Republic, Russia) in order to assess the state of this species at low average annual water temperatures during the period of their maximum values.

MATERIALS AND METHODS

Lake Hindiktig-Khol is a moraine-dammed lake located in the high-mountain tundra at an altitude of 2306 m above sea level. Its area is 6700 ha and it is fed by various water sources, mainly glacial. In the western part, the Mogen-Buren River flows from the lake; it is a tributary of the Kobdo River (basin of the Great Lakes Depression, Mongolia). The prevailing depths in the northern part of the lake are 20–25 m; in the eastern part, they exceed 35 m. Ice melting is observed in late June. In regards to the temperature regime, it is

considered the coldest lake among the main commercial water bodies of Tuva Republic. The surface water temperature at the end of June reaches 5.7°C; in the end of July, it is 11–12°C. The water is slightly mineralized (up to 30 mg/L) and of hydrocarbonate class, sodium group. Water transparency according to a standard Secchi disk is 16 m. The lake is characterized as an oligotrophic water body according to the dominant complex of zooplankton (Calanoida) and the biomass (0.2 g/m³). The average zooplankton abundance is 8000 ind./m³, biomass, 0.2 g/m³. The predominance of small forms of zooplankton is due to the fact that the younger age groups of grayling feed mainly on zooplankton. The average biomass of zoobenthos in the littoral zone is 2.9 g/m²; in the profundal, it is 1.9 g/m². Mollusks, chironomids, and *Gammarus* dominate by biomass in the littoral; in the profundal, chironomids dominate. Fish are presented by Mongolian grayling only in Lake Hindiktig-Khol.

Mongolian graylings were caught from July 12 to 20, 2010; they were measured and weighed and the gonads, gills, and liver were fixed in Bouin solution. Histological analysis was performed using standard techniques (Mikodina et al., 2009). Serial paraffin sections (5- μ m-thick) were prepared on an HM 335S automated rotary microtome (MICROM). The preparations were stained with Heidenhain's iron hematoxylin solution; embedded in a Bio Mount medium (Bio Optica); and analyzed under an Axio-Imager A1 microscope (Zeiss).

The diameter of oocytes and their nuclei was measured and the oocytes at different stages of development were counted on ovarian sections using AxioVision software 4.7.1 (Zeiss). Three sections were randomly selected on the preparations of the testes of each individual and seven areas of 80 μ m² each were randomly selected on each section as well; the number of A- and B-type spermatogonia and spermatocytes of I and II orders were counted for each area.

The width of the respiratory lamellae (proximal, medial, and distal areas), the number of layers of intercalated epithelial cells, and the number of mucous cells in 1 mm² were measured in the gills within the studied zone. The pathomorphological changes (cytolysis, thickening, desquamation, fusion and destruction of the respiratory lamellae, etc.) were taken into account and their areas were measured. The index of organ pathology was calculated, which was calculated from the sum of the proportions of each pathology, multiplied by the so-called significance coefficient (Bernet et al., 1999). The coefficient of significance was set to each pathology depending on its hazard to fish health and respiratory function of the gills (Shuman, 2015).

When assessing the state of the liver on histological sections of the organ, the presence of a number of adaptive deviations (hyperemia, vascularization, and basophilia of the cytoplasm of hepatocytes) and

pathological changes (fatty degeneration, destruction of liver tissue, and the appearance of cavities) were taken into account. Five liver sections in each individual were analyzed, on which the areas of hepatocytes, their nuclei, and lipid inclusions were measured in random order. The preparations were photographed with an AxioCam MRc5 camera (Zeiss).

A total of 52 specimens of Mongolian grayling were examined; 50 of them were studied using histological methods and 50 preparations of gonads were prepared, 47 of gills, and 44 of liver. All calculations were performed using MS Excel 2007 programs.

RESULTS

Fish aged 4+ to 5+ dominated in the catches (Table 1); the age of fish was determined in accordance to the published data on the size indicators (Knizhin et al., 2008). Normal development of this species may be proposed in the cold-water Lake Hindiktig-Khol. However, due to the consistently low water temperature throughout the year, the fish metabolism should be lowered and accompanied by a slowdown in maturation, low fertility, and nonannual spawning.

Gonads. The ovaries in most Mongolian grayling females in Lake Hindiktig-Khol were at maturity stage III, when vitellogenic oocytes of the cytoplasmic vacuolization phase were the oldest generation of germ cells (Fig. 1a). The next generation of germ cells was represented by previtellogenic oocytes (Fig. 2). They were also present in a large number (up to 77%) in the spawned specimens (Fig. 1b). In some fish in age groups 4+ to 7+, compared with 3- and 4-year-old specimens, the number of vitellogenic oocytes in the cytoplasmic vacuolization phase significantly increased (Fig. 1c). A significant difference in the ratio of oocytes of different phases in older age groups may indicate that Mongolian grayling matures at the age of 4+ and older in Lake Hindiktig-Khol. In females at the age of 5+ to 7+, some vitellogenic oocytes began to resorb, while others entered the period of yolk accumulation with the concurrent degeneration of post-ovulatory follicles (Fig. 1d). Consequently, such females spawned in the current year and were preparing for spawning the next year.

According to the analysis of germ cells at different stages of oogenesis, the sizes of oocytes of similar phases did not differ significantly ($p > 0.05$) or they varied slightly in females of different ages (Table 2).

Testes in most males were at maturity stage II; the germ cells were represented by spermatogonia (Fig. 3a). Cysts with spermatocytes appeared in some specimens (Fig. 3c). All types of cells were present in the gonads of most males, but the number of spermatocytes II increased with age. In fish at the ages of 2+ to 4+, spermatocytes II and type B spermatogonia prevailed in testes (Fig. 3b). Spermatocytes I and type A spermatogonia were much rarer. In the fish at the age of 5+

Table 1. Size and weight characteristics of Mongolian grayling in Lake Hindiktig-Khol

Fish age, years	Smith length, mm		Body mass, g	
	females	males	females	males
2+...3+	218.0 ± 3.4	218.4 ± 9.9	86.0 ± 5.0	88.4 ± 11.0
	208–230 (<i>n</i> = 7)	190–247 (<i>n</i> = 5)	70–110 (<i>n</i> = 7)	54–106 (<i>n</i> = 5)
4+	250.4 ± 6.5	248.8 ± 4.4	126.2 ± 8.6	128.8 ± 5.8
	215–270 (<i>n</i> = 9)	235–260 (<i>n</i> = 5)	82–160 (<i>n</i> = 9)	110–142 (<i>n</i> = 5)
5+	273.6 ± 3.3	274.1 ± 4.9	159.5 ± 5.8	156.7 ± 7.8
	256–300 (<i>n</i> = 11)	255–292 (<i>n</i> = 9)	124–196 (<i>n</i> = 11)	122–192 (<i>n</i> = 9)
6+	285.0 ± 10.2	286	190.8 ± 20.5	202
	265–323 (<i>n</i> = 5)	(<i>n</i> = 1)	142–266 (<i>n</i> = 5)	(<i>n</i> = 1)

Here and in Tables 2–4, values above the line are the mean value and its error; min–max are given below the line. The number of studied fish (*n*) is given in parentheses.

Table 2. Generative indicators in different age groups of Mongolian grayling

Gametes	Oocyte diameter, μm	Nuclei diameter, μm	Nuclear-cytoplasmic ratio, %
2+ to 3+, years			
Previtellogenic oocytes	258.2 ± 7.6 240–273	105.3 ± 1.7 101–109	68.93
Vitellogenic oocytes, cytoplasm vacuolization phase	494.9 ± 10.3 485–505	179.7 ± 13.5 166–193	57.03
6+ to 7+, years			
Previtellogenic oocytes	271.4 ± 2.1 266–275	107.3 ± 2.5 103–112	65.40
Vitellogenic oocytes, cytoplasm vacuolization phase	454.2 ± 31.6 423–486	151.0 ± 6.8 144–158	49.80
yolk accumulation phase	638.8 ± 47.1 533–745	200.4 ± 9.4 184–226	45.71

Number of examined fish of each age group *n* = 4.

and older, the largest proportion of germ cells were spermatocytes II (Fig. 4); groups of residual sperm from the last spawning were present in the seminiferous tubules (Fig. 3d).

Gills. Lake Hindiktig-Khol, located in a natural zone that excludes chemical pollution, may be considered quite acceptable for the Mongolian grayling, so we do not expect to find any serious malformation of its gill apparatus. This assumption turned out to be true for some specimens (Fig. 5a), but there were

pathologies of different natures and degrees in most of the studied fish. Anomalies in the structure of the gill apparatus of Mongolian grayling were manifested as plasmolysis and the partial (Fig. 5b) or complete fusion of the respiratory lamellae, affecting some areas of the gills (Fig. 5c), followed by the destruction of the respiratory and intercalary epithelium (Fig. 5d). The variety and frequency of occurrence of disorders increased with age, which was reflected in the index of pathology (Table 3). In the meantime, the number of

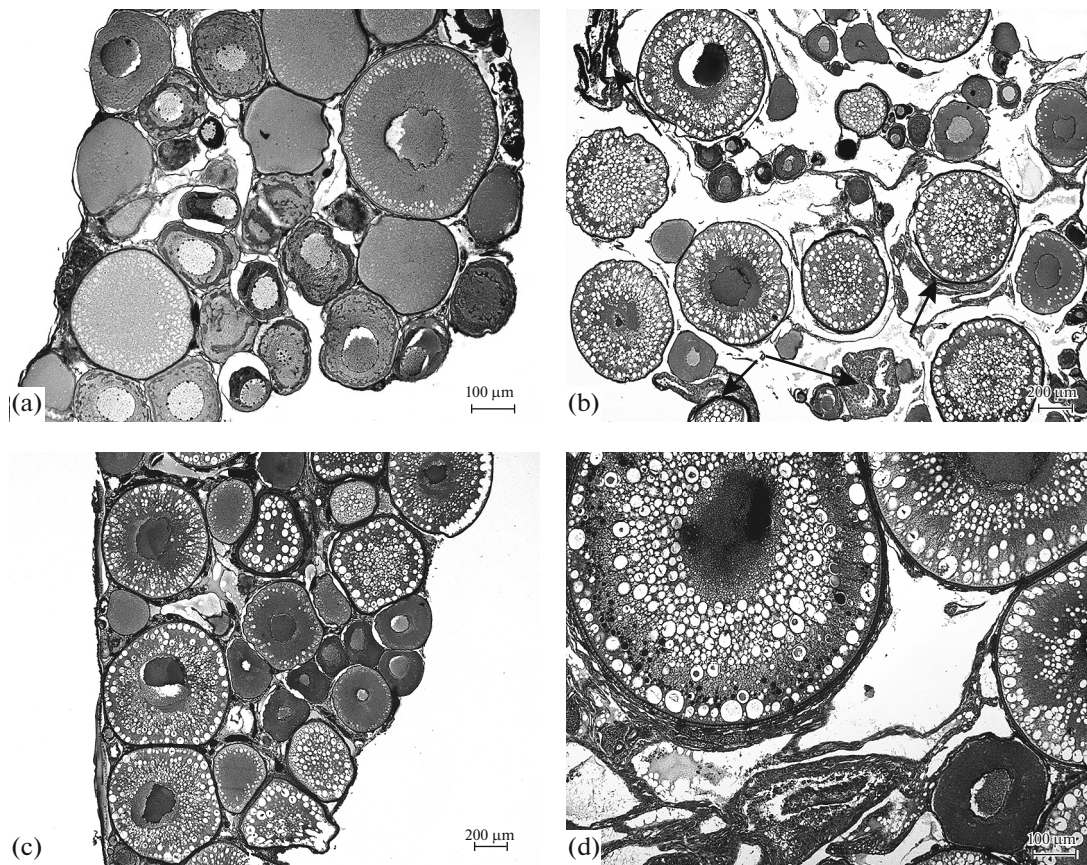


Fig. 1. Ovaries of the Mongolian grayling at different stages of maturity: (a) the phase of vacuolization of the cytoplasm begins in oocytes of the older generation ($\times 100$); (b) degenerating postovulatory follicles are visible among oocytes of the vacuolization phase of the cytoplasm ($\times 40$); (c) area of the ovary at maturity stage IIIb with a large number of oocytes at the phase of cytoplasm vacuolization ($\times 40$); and (d) beginning of the accumulation of yolk in the oocyte, with the degeneration of the postovulatory follicle visible ($\times 400$).

cell layers of the intercalary epithelium decreased slightly in sexually mature specimens. The observed high index of pathology in the gills of older fish with a significantly lower number of mucous cells and a similar number of cells of the intercalary epithelium contradicted the studies carried out on trout by Matei (Matei, 1987). According to this author, the barrier created by the gill epithelium between the external environment and the blood increased under stress or under unfavorable conditions (i.e., acidification and various types of pollution).

It can be argued that significant malformations of the gill apparatus of the Mongolian grayling in Lake Hindiktig-Khol were caused by the influence of some unfavorable factor(s).

Liver. This organ was hyperemic both in females and males of the Mongolian grayling, but no significant malformations were noted either at the macro- or microscopic level. The sizes of hepatocytes in fish of different ages and sexes (Table 4) hardly differed ($p > 0.05$). The cytoplasm of hepatocytes was moderately

basophilic. The liver cells carried few lipid droplets, the number of which varied slightly (Fig. 6a). The greatest number and variability of lipid droplets were characteristic of hepatocytes of immature specimens of both sexes at ages of 2+ to 3+ (Fig. 6b). The increased degree of basophilia of liver cells was noted in maturing specimens at gonad maturity stage III: vitellogenic oocytes in females and spermatocytes II in males.

Therefore, most of Mongolian grayling specimens in cold-water mountain Lake Hindiktig-Khol had a typical growth rate for this species, with some delay in maturing, possibly caused by a decrease in the morphofunctional state of the gill apparatus; most mature females spawn annually.

DISCUSSION

According to previous studies (Knizhin et al., 2008; Slyn'ko et al., 2010), the size indicators of the bottom-feeding form of Mongolian grayling from Lake Hind-

iktig-Khol are quite comparable with those of this species from other water bodies (Tugarina and Dashidorzhi, 1972; Shatunovsky, 1983).

According to our data, the older generation of germ cells was at the phase of vacuolization of the cytoplasm in most females during the period of active postspawning feeding. The next pool of cells in fish of all age groups was represented by previtellogenic oocytes; they were the most present in spawned specimens. The number of vitellogenic oocytes in the phase of vacuolization of the cytoplasm significantly increased in some females of the age groups 4+ to 7+ in comparison with three- and four-year-old specimens. A significant difference in the ratio of oocytes of different phases in different age groups may indicate that Mongolian grayling matures at the age of 4+ and older in this lake. In females at ages of 5+ to 7+, some vitellogenic oocytes began to resorb, but the bulk of the germ cells started to accumulate yolk. When considering the size characteristics of oocytes of the Mongolian grayling from Lake Hindiktig-Khol, no obvious differences were revealed with the oocytes of the Baikal grayling (Zaitseva et al., 2010). The absence of females omitting the forthcoming spawning season and the presence of traces of past spawning in the ovaries of Mongolian grayling (empty follicles) indicated the ecological plasticity of its reproductive system, similarly to that of the reproductive system of Coregonidae in the Ob-Irtys basin (Selyukov, 2002a, 2002b, 2012; Selyukov et al., 2012). Therefore, females of the bottom-feeding form of the Mongolian grayling mature at the age of 4+ in oligotrophic Lake Hindiktig-Khol, and the peak of spawning activity is observed at the age of 5+.

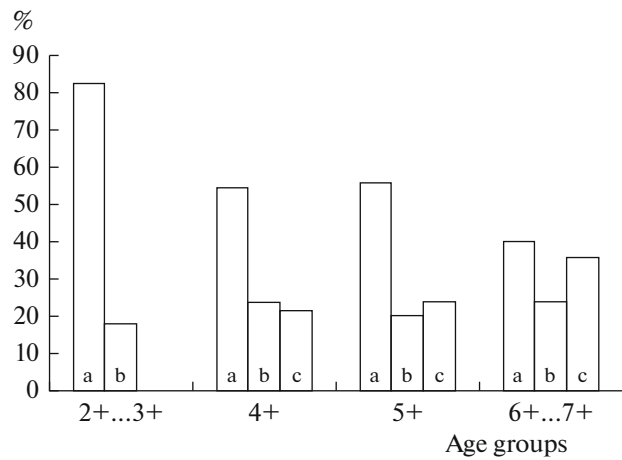


Fig. 2. Ratio of oocyte phases (%) in different age groups of the Mongolian grayling: (a) previtellogenic oocytes; (b, c) vitellogenic oocytes of the cytoplasmic vacuolation and yolk accumulation phases, respectively.

In most males, the reproductive cells were represented by spermatogonia. All types of cells were present in the testes of the other fish. In the 2+ to 3+ age group, spermatocytes II and type B spermatogonia dominated, which indicated a high probability of participation of these specimens in the next spawning season; i.e., males matured a year earlier than females. In the testes of some males of older age groups, which are at the postspawning state and preparing for the next spawning, residual sperm was observed in the lumen of the seminiferous tubules. In general, there were no significant malformations in gonad development.

Table 3. Gill epithelium characteristics in Mongolian grayling in Lake Hindiktig-Khol (July 2010)

Parameter	Fish age, years		
	3+ (n = 4)	4+ (n = 5)	5+ (n = 9)
Number of layers of intercalated epithelial cells	4.0 ± 0.4 3.3–5.0	3.5 ± 0.6 2.5–5.6	3.5 ± 0.3 2.7–5.3
Respiratory lamella width, μm	17.6 ± 0.7 16.2–19.2	19.6 ± 2.4 16.5–29.1	19.6 ± 1.5 14.5–30.1
Number of mucous cells per 1 mm ²	168.6 ± 51.8 104.4–322.0	174.4 ± 25.1 132.6–219.5	122.4 ± 15.3 65.5–199.8
Pathology index, %	1.0 ± 0.4 0.2–1.9	1.2 ± 0.4 0.6–1.9	1.3 ± 0.2 0.2–2.3

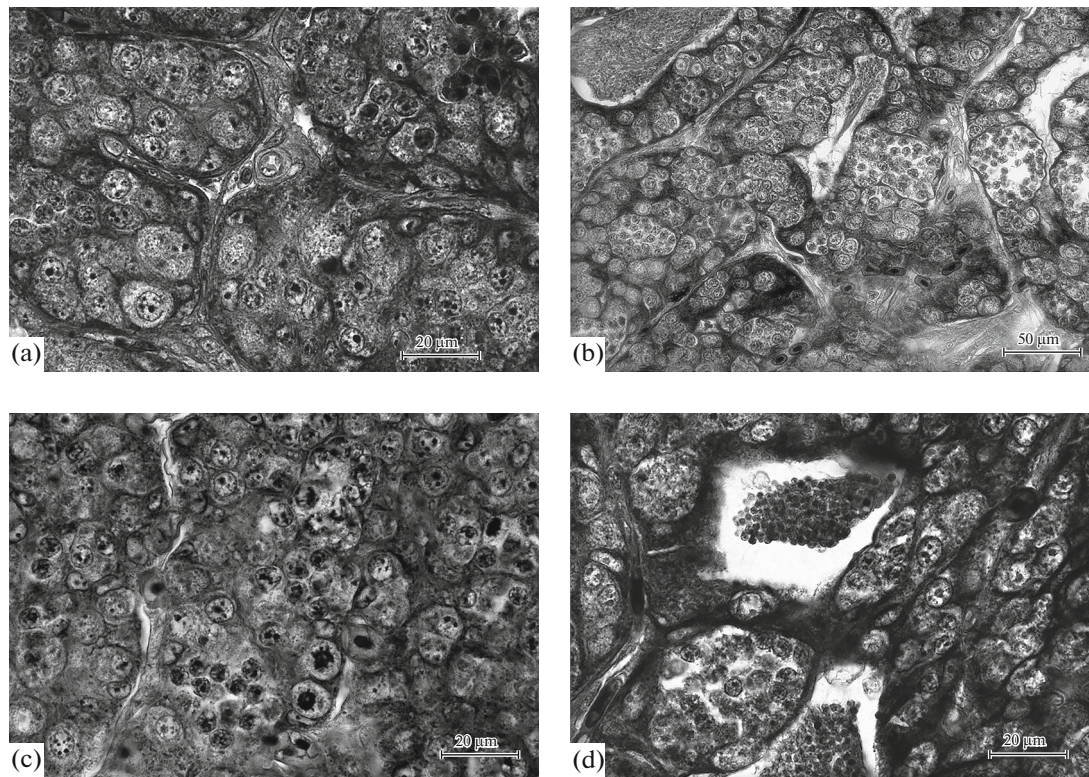


Fig. 3. State of the testes of the Mongolian grayling: (a) stage II of maturity, with sex cells represented by spermatogonia ($\times 1000$); (b) clusters of spermatocytes I and II in the testes of maturity stage III ($\times 400$); (c) predominance of type B spermatogonia in the testes of maturity stage II ($\times 1000$); (d) spermatocytes surrounded by cysts of B type spermatogonia, with resorbing residual sperm visible in the lumen of the seminiferous tubule ($\times 1000$).

An analysis of the state of the gill apparatus of fish is often used to assess their morphological and functional status (Matei, 1990); according to this parameter, the gill apparatus of the Mongolian grayling in Lake Hindiktig-Khol was at an extremely depressed state. Obviously, the hydrochemical regime caused by aerogenic transfers and/or ore-generating factors, which made up the mountain massif, was the reason for such anomalies.

Table 4. Size parameters of hepatocytes of Mongolian grayling in Lake Hindiktig-Khol

Parameter	Fish age, years		
	3+ (n = 5)	4+ (n = 4)	5+ (n = 7)
Diameter of hepatocytes, μm	6.0 ± 0.18 5.4–6.4	5.7 ± 0.07 5.5–5.8	5.8 ± 0.07 5.5–5.9
Diameter of hepatocyte nuclei, μm	2.1 ± 0.06 1.9–2.3	2.0 ± 0.07 1.8–2.1	2.0 ± 0.06 1.9–2.3
Nuclear-cytoplasmic ratio, %	54.3	53.9	52.6

No disorders in the liver state were found for the studied species, in contrast to the whitefish of the Severnaya Sos'va River (Nekrasov et al., 2014); there was a significant volume of lipid inclusions in the hepatocytes of immature specimens of both sexes (2+ to 3+) in comparison with liver cells of fish of older age groups. In the liver of maturing females, lipid inclusions disappeared, which indicated the body's energy costs for the synthesis of vitellogenin.

The state of internal organs in this population of the Mongolian grayling has well-pronounced signs of toxic stress affecting mainly the respiratory system. Considering the state of liver and gonads, similar statements are still premature; however, the disorders of the key system of vital activity inevitably leads to the suppression of other body functions.

CONCLUSIONS

The size and weight indices of the bottom-feeding form of the Mongolian grayling in Lake Hindiktig-Khol correspond to those from other water bodies given in the literature; this indicates a sufficient food supply to ensure the growth of the Mongolian grayling of both sexes even under conditions of low average

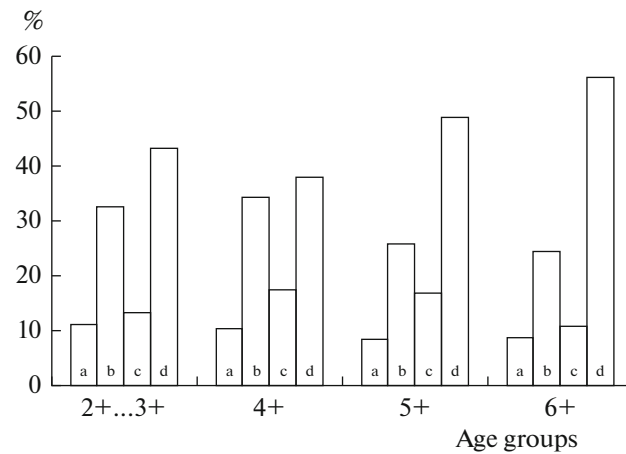


Fig. 4. Ratio of germ cells (%) in the testes of the Mongolian grayling of different age groups: (a) type A spermatogonia, (b) type B spermatogonia, (c) spermatocytes I, and (d) spermatocytes II.

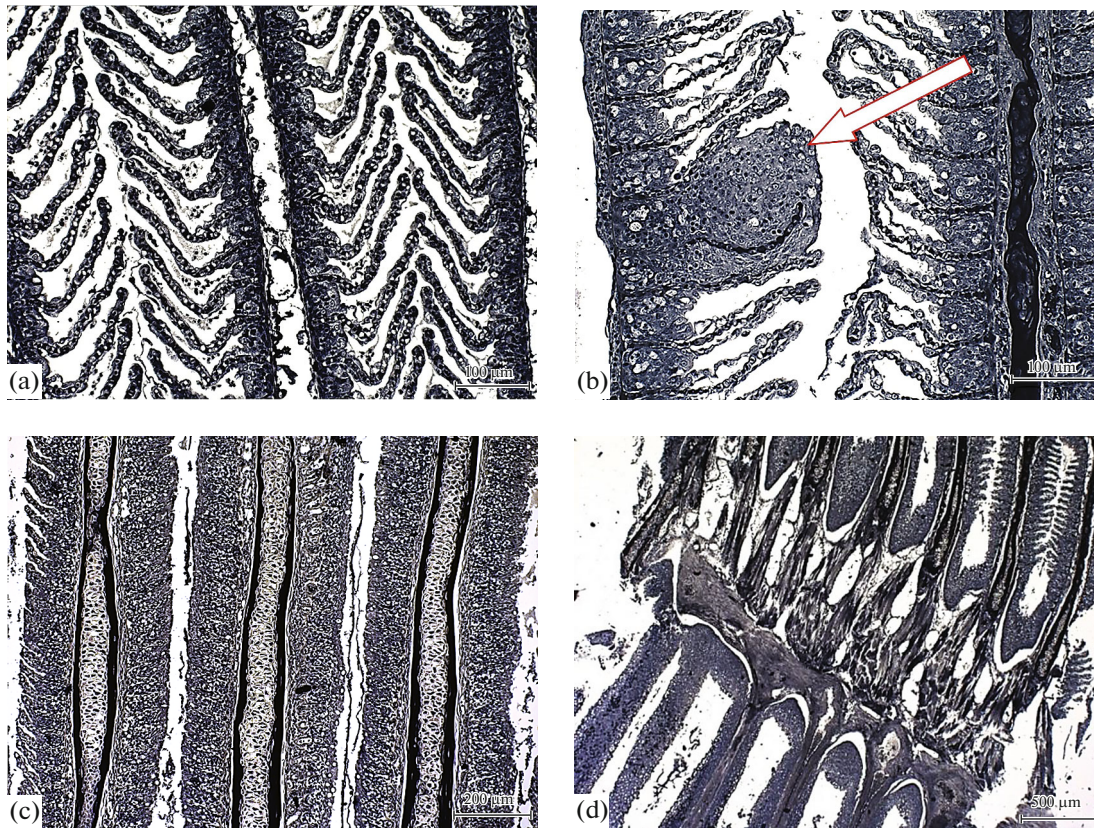


Fig. 5. Gill apparatus of the Mongolian grayling from Lake Hindiktig-Khol: (a) normal state of the gill epithelium ($\times 200$); (b) thickening (arrow) and plasmolysis of respiratory lamellae ($\times 200$); (c) fusion of respiratory lamellae ($\times 100$); (d) fusion of filaments and destruction of respiratory lamellae ($\times 40$).

annual temperatures. The females mature at the fifth year of life and males a year earlier. Degenerating empty follicles from spawning in the previous year are present in the ovaries of mature specimens; annual spawning of females and males is noted. Significant deviations in the branchial epithelium as the most

important biomarker of environmental quality indicate the presence of a certain factor(s) inhibiting the respiratory function of this species in Lake Hindiktig-Khol. None of the livers of any of the fish that were studied had anomalies; the differences in cell size and the presence of lipid inclusions reflect the sex-specific

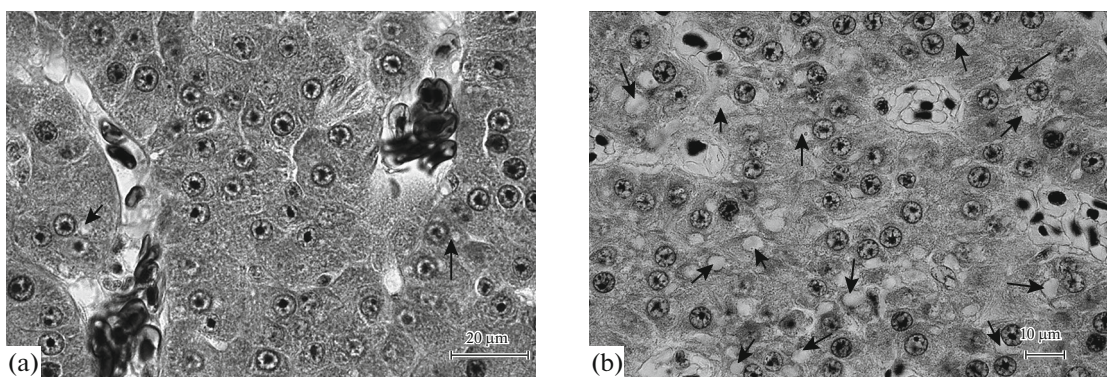


Fig. 6. Liver of the Mongolian grayling of different age groups ($\times 1000$): (a) lipid drops (arrows) are present in an insignificant amount in the cytoplasm of hepatocytes of sexually mature fish; (b) numerous lipid drops in hepatocytes of immature specimens (arrows).

features of the physiological state of specimens of different ages.

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COMPLIANCE WITH ETHICAL STANDARDS

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

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

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