

Regularities of the Life History Strategy Adoption in Masu Salmon *Oncorhynchus masou* from the Kol River (Western Kamchatka) in Regard to the Processes of Growth and Sexual Maturation

M. A. Gruzdeva^a, A. M. Malyutina^a, K. V. Kuzishchin^a, N. V. Belova^a,
S. V. P'yanova^b, and D. S. Pavlov^a

^a Moscow State University, Moscow, Russia

^b Russian Federal Research Institute of Fisheries and Oceanography (VNIRO), Moscow, Russia

e-mail: MG_office@mail.ru

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Abstract—Growth, age structure, sexual maturation, and peculiarities of the life history strategy adoption were studied for the population of masu salmon *Oncorhynchus masou* inhabiting the Kol River, Western Kamchatka. The growth rate and gametogenesis depended on the peculiarities of masu salmon generations in certain years and were the limiting factors for the juvenile differentiation and the direction of its ontogenetic development. The adoption of the resident or anadromous life history strategy in masu salmon is the epigenetic process, and the bifurcation during the life span of a single specimen is observed only once in a life, but twice in the generation, at the age of 1+ or 2+. The diversity of the life history strategy patterns was less at the northern boundary of the geographical range of masu salmon compared to the area of ecological optimum (the basin of the Sea of Japan). In the Kol River basin, nearby the northern boundary of its geographical range, the reproductive success and formation of the life history strategy diversity in the population depended strictly on the temperature regime of the water bodies, where the spawning and the freshwater period of life cycle of masu salmon take place. In Kamchatka, all the breeders were monocyclic, i.e. anadromous and resident precocious males spawned only once in a life.

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INTRODUCTION

The adoption of the anadromous or residential life history strategy is determined during the freshwater period in the populations of salmonids (Salmonidae); this event is an integral result of the morphophysiological processes of growth, metabolism, and reconstructing the osmoregulation system, and the external factors are the switching keys for the program of ontogenesis (Thorpe, 1987, 1994; Pavlov and Savvaitova, 2010). The data on the intraspecific ecological differentiation of diadromous salmonids are unequal, and it is still unclear if the mechanisms of formation of the life history strategy diversity are similar in different species. The processes of smoltification and seaward migration are studied in detail for the Atlantic salmon *Salmo salar* and brown trout *S. trutta*, but the data on the Pacific Salmon of *Oncorhynchus* genus are lacking, especially in regard to the species characterized by complex intraspecific population structure.

Masu salmon *Oncorhynchus masou* is the most associated species to the fresh water within the group of Pacific Salmon; this species along with anadromous form with seasonal races has the lacustrine, riverine,

and “dwarf” landlocked forms, presented by both males and females (Semenchenko, 1980, 1989; Ivankov et al., 1984a, 1984b; Tsygir and Ivankov, 1987; Lin and Chang, 1989; Tsygir, 1990; Kato, 1991). The ratio of these forms varies within the geographical range. Precocious males that reach maturity in the rivers are quite abundant in comparison to the other Pacific Salmon; these males are the important element of the intrapopulation structure of masu salmon together with anadromous males and females (Berg, 1937; Semenchenko, 1989). The maximal diversity of the life history strategy in masu salmon is found in the southern part of its geographical range, i.e., the basin of the Sea of Japan. In the northern part of its geographical range, in Kamchatka, only anadromous males and females were found, as well as precocious males (Semko, 1956; Malyutina et al., 2009).

The study goal was to find the regularities of the formation of the life history strategy diversity in masu salmon inhabiting the northern part of its geographical range.

MATERIALS AND METHODS

The fish were sampled in 2003–2008 in the Kol River, Western Kamchatka. The river originates in the mountains of the Sredinnyi (Middle) Ridge of Kamchatka and discharges to the Sea of Okhotsk. The length of the mainstream is 133 km, the coefficient of the river system development is 0.61 km/km², and the average discharge at the base flow is 56 m³/s (Kuzishchin et al., 2009). The riverbanks are covered by dense riparian forest; a lot of log jams are found frequently in the mainstream and back channels. Despite the relatively small size, the river refers to the well-developed floodplain braided-anastomosing riverine system with numerous tributaries of different types (piedmont and tundra) of 3–45-km length and discharge of 0.01–0.28 m³/s. The tributaries of the piedmont type predominate mostly in the upper stream; the tundra type tributaries appear in the middle and lower section of the River.

The adult specimens were sampled with beach seine, gill nets (mesh size of 30 × 30–50 × 50 mm) and hook-and-line tackle. Juveniles of different ages and precocious males were sampled by the Fish electroshocker (Smith-Root 24L) tuned for care regime (Bird and Cowx, 1993) at impulse A.C. (350–400 V, 40–60 Hz, impulse length of 2 ms). Three-pass electrofishing was performed for estimation of the population density of juveniles (Zippin, 1956); the abundance and biomass were calculated for the areas not less than 100 m² each. The sampling was performed at 26 sites of the river system, including the mainstream, tributaries, and the springbrooks in the river floodplain (so called para- and orthofluvial springbrooks according to the classification of Pavlov et al. (2009)).

The temperature regime in nine spawning tributaries was measured continuously during six years using the Vemco Minilog T8K 8-bit DataLogger automatic electronic data logger; the measurements were performed all year round with 1-h periodicity. These data were used to calculate the degree-days.

All the sampled fish were studied under overall biological analysis (Pravdin, 1966); the scales from the first to the fourth rows above the lateral line between the posterior margin of the dorsal fin and the anterior margin of the anal fin were used to determine the fish age (Pavlov et al., 2001). In total, 2733 specimens were analyzed, including mature anadromous fish, resident precocious males, and juveniles of different ages; the numbers of studied specimens referring to each group appear in the tables and figures. The sex of the young-of-the-year of masu salmon was defined according to the method of Kuznetsova (1954); the gonad status of males referred to the “cyprinoid” Scale, where the spermary of salmonids was included (Belova, 1981). The gonads were preserved in 4% formaldehyde solution.

The fish age and growth rate were assessed using only the scales with intact center. The digital photos

were taken using the image-capture hardware (Leica DMLS microscope and Canon 500D digital camera). The scale growth was measured on the digital images using ImageProPlus 4.1 image-processing software; the same approach was applied for the number of circuli. We studied several parameters: R —total radius of the scale, mm; r_1 , r_2 , and r_+ —scale width growth in the first, the second, and the current year of life, mm; S —total number of circuli; s_1 , s_2 , and s_+ —number of circuli in the first, the second, and the current year of life, respectively; R/S —average distance between the circuli during the freshwater period of life, mm; r_1/s_1 and r_2/s_2 —average distance between circuli in the first and the second years of life, mm; l_1 and l_2 —the absolute linear growth of the fork length in the first and the second years of life, mm.

The calculation of the fish fork length (mm) was performed using the formula of Li (Busaker et al., 1990): $l_i - c = r_i / R \times (L - c)$, where l_i is calculated fork length of the fish at i -age, r_i is radius of i -year annual ring on the scale, R is total radius of scale, L is observed fork length according to Smith (AC), and c is absolute term calculated under correlation analysis. The absolute term was calculated under the logarithmic equation combining the relationship of the scale radius to the fish fork length: $\ln L = c + \ln S$ when the correlation coefficient was 0.95. The condition factor was calculated under Fulton equation ($K_F = W/L^3 \times 1000 \times 100\%$), where W is body weight, g; and L is fork length according to Smith (AC), mm.

The dataset was analyzed by standard univariate statistics (Lakin, 1990). The samples were compared with principal component analysis (PCA) using Statistica 7.0 software. The PCA included preanalysis standardization of the absolute values of parameters; variation-covariation matrices were built; the length of the characteristic vector was equal to the square root of its own absolute value (Rohlf, 1993).

The gonads of different status were taken out from males and females for the histological analysis. The visual and histological description of gonad status was made under the gonad maturation scale (Persov, 1975; Murza and Khristoforov, 1991). The histological slides of gonad tissues were prepared according to standard methods (Valovaya and Kavtaradze, 1993; Mikodina et al., 2009). The histological samples were performed using the automatic machine of round-robin technique; the tissue was molded with paraffin; the slides were prepared using semiautomatic sledge microtome and stained with hematoxylin-eosin solution according to Ehrlich with additional staining with eosin. The slides were pictured under the Olympus microscope equipped with a Leica DC mounted automatic digital camera at the magnification of ×50, ×100, and ×200. The digital images were processed with the DC Viewer software.

Table 1. Relative abundance, distribution, and age structure of the freshwater population of masu salmon *Oncorhynchus masou* population in the Kol River basin (multiyear averages for the period 2003–2008)

| Sampling site | All age classes of salmonid juveniles | | | Age structure of masu salmon: parrs/precocious males, % | | | Ratio of precocious males of masu salmon, % |
|--|---|---------------|-------------------------|---|-----------|----------|---|
| | population density, ind./m ² / biomass, g/m ² | | ratio of masu salmon, % | 0+ | 1+ | 2+ | |
| | masu salmon | other species | | | | | |
| Mainstream, distances upstream off the estuary, km | | | | | | | |
| –15 | <0.01/0.06 | 4.43/33.75 | 0.11 | 16.7/– | 83.3/– | –/– | 0 |
| –25 | 0.01/0.09 | 3.24/16.13 | 0.38 | –/– | 100/– | –/– | 0 |
| –45 | 0.11/0.89 | 4.75/29.24 | 2.17 | 18.9/– | 81.1/– | –/100 | 1.0 |
| –65 | 0.24/0.96 | 3.67/17.83 | 5.24 | 14.7/– | 85.3/– | –/100 | 1.8 |
| –90 | 0.69/2.15 | 2.42/14.31 | 10.46 | 33.1/– | 66.9/44.2 | –/55.8 | 5.5 |
| Tundra tributary 1, upper stream | 1.23/7.33 | 2.64/16.17 | 36.70 | 81.5/– | 18.4/77.2 | 0.1/22.8 | 10.3 |
| Tundra tributary 2, upper stream | 1.87/7.16 | 2.32/14.39 | 45.40 | 90.4/– | 9.6/73.1 | –/26.9 | 8.8 |
| Tundra tributary 3, upper stream | 2.00/8.34 | 2.71/16.49 | 48.50 | 71.4/– | 28.6/69.5 | –/30.5 | 9.2 |
| Piedmont tributary 1, middle stream | 2.01/12.26 | 2.14/14.56 | 50.40 | 89.3/– | 10.7/63.7 | –/36.4 | 12.4 |
| Piedmont tributary 2, middle stream | 1.92/10.84 | 2.21/13.32 | 49.50 | 78.6/– | 21.4/57.1 | –/42.9 | 11.5 |
| Piedmont tributary 3, middle stream | 2.10/13.78 | 2.04/13.54 | 53.70 | 81.3/– | 18.7/68.5 | –/31.5 | 11.8 |
| Parafluvial springbrook 1 | –/– | 8.51/33.34 | 0 | – | – | – | – |
| Parafluvial springbrook 2 | 0.01/0.09 | 5.38/21.15 | 0.08 | –/– | 100/– | –/– | 0 |
| Orthofluvial springbrook 1 | –/– | 3.97/23.65 | 0 | – | – | – | – |
| Orthofluvial springbrook 2 | –/– | 9.73/37.92 | 0 | – | – | – | – |

RESULTS

Structure of the freshwater part of masu salmon population from the Kol River. The spawning of masu salmon in the Kol River basin took place in relatively small-size and low water flow tributaries of piedmont and tundra types (Kuzishchin et al., 2009). The first years of the freshwater period of life also passed here. The immature juveniles (parrs) and precocious males of masu salmon constituted more than half of the total fish population (Table 1). The juveniles of coho salmon *Oncorhynchus kisutch*, East Siberian char *Salvelinus leucomaenis*, and Dolly Varden *S. malma* also inhabit these tributaries. Most of the juveniles and precocious males of masu salmon inhabiting the tundra tributaries concentrated in the areas of the upper stream of the tributary and distribute evenly in the piedmont tributaries. In the mainstream and in the back channels of the river system, the juveniles of masu salmon were found rarely, and its rate was insignificant compared to the other salmonid species; the pre-

cocious males were presented by single specimens during the summer period only and in particular years (Table 1). The juveniles and precocious males inhabiting the tributaries represented all the age classes of masu salmon found in the Kol River, i.e., 0+, 1+, and 2+ (Malyutina et al., 2009). Most of the precocious males were specimens of 1+ age (Fig. 1). The parrs of 1+ age were the most abundant in the mainstream, the young-of-the-year juveniles were rare, only single dwarf males were found here, and all specimens of the last group were of 1+ age (Table 1). Only one specimen of 3+ age was caught for the whole period of observations (precocious male, AC = 195 mm, weight 53.6 g).

In different years, the ratio of the age classes varied within both groups of precocious males and smolts of masu salmon inhabiting the Kol River (Fig. 1). During particular years, the age structure of precocious males and smolts was similar, but there was no correlation between the age composition of smolts and the structure of smolt classes of adult anadromous fish in the

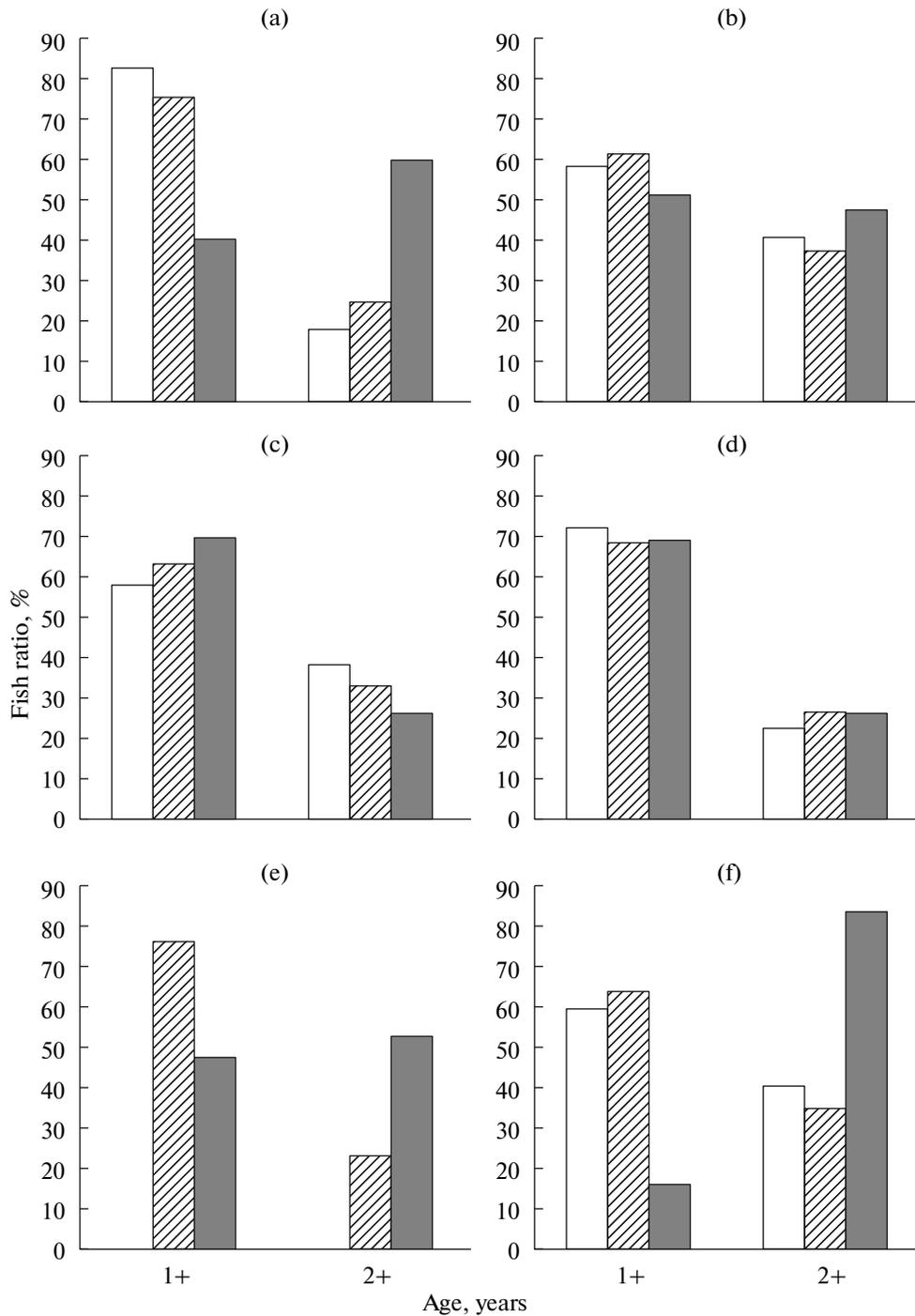


Fig. 1. Age composition of (□) smolts, (▨) precocious males, and (■) freshwater age in anadromous spawners of masu salmon *Oncorhynchus masou* of the Kol River in different years: a—2003; b—2004; c—2005; d—2006; e—2007; f—2008.

neighbor years (Fig. 1). We suppose that the water temperature was a major factor, influencing on the masu salmon growth in the spawning tributaries. Generally, the interannual variability of the temperature on the spawning grounds of masu salmon in the Kol River is insignificant: the sum of degree days for the period of May 15–October 15, i.e. the period of active feeding

and growth, varies from 1215 to 1277. Nevertheless, during the warm years, more fish of 1+ age migrated to the sea, and the number of the mature precocious males of 1+ age also increased (Fig. 2).

According to our multiyear observations, every year in June–July, the seaward migration of masu salmon juveniles takes place in all the spawning tributaries; the

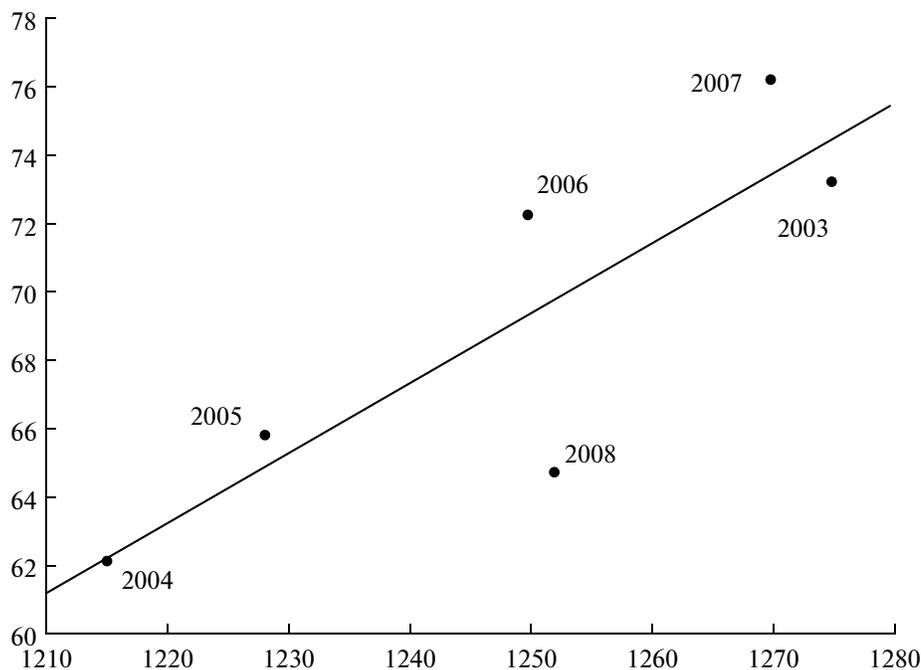


Fig. 2. Dependence of the age composition of precocious males of masu salmon *Oncorhynchus masou* in different years on the temperature regime in one spawning tributary of the Kol River ($y = -184.47 + 0.2031x$, $R^2 = 0.71$, $m = \pm 0.035$, $p < 0.01$). X-axis refers to the sum of degree-days for the period of May 15–October 15; Y-axis indicates the ratio of the precocious males (age 1+) to the total number of all precocious males (1+ and 2+), %.

fish is characterized by well-pronounced features of smolts, which evidences to the differentiation of the juveniles into the sea-run smolts and precocious males occurring in the spawning tributaries. Smolts are presented by 1+ and 2+ fish, which refers to the structure of the classes of smolts of mature anadromous fish for the period of observations (Fig. 1). The ratio of smolts and precocious males of different ages and the structure of the smolt classes in the mature anadromous fish specimens vary from year to year; however, the age structure of smolts and precocious males sampled within one year are similar (Fig. 1).

Size characteristics of the juveniles and precocious males of masu salmon. Parr males and parr females within the age class were similar by the body weight and length and by the condition factor. Smolt males and smolt females within the age class were also similar by the body weight and length and were characterized by larger body size parameters in regard to the same classes of parrs. Meantime, the condition factor in smolts was the lowest (Table 2).

Sex ratio. The sex ratio in the young-of-the-year of masu salmon varied from year to year; usually it was equal (1 : 1), but sometimes males dominated (1.25 : 1). The fish of 1+ age were characterized by the prevalence of females, 1 : 1.06–1 : 1.19. Females always dominate in smolts: in the groups of 1+ age and 2+ age, this ratio is 1 : 1.12 and 1 : 1.54, respectively.

Growth. The parameters of the scale are presented in Table 3. The growth rate was slightly higher in

females than in males within the age classes of both parrs and smolts. The scale growth and the number of circuli in the marginal scale zone in females was higher than in males of the same age group, referring both to the ages 1+ and 2+ (Table 3); however, these differences were statistically insignificant (Table 4).

The growth rate in males was the most variable. Smolt males were characterized by the highest growth rate within the age class; the width of the annual ring and the number of circuli were the highest for the year before the seaward migration (Table 3). The lowest growth rate was observed in immature parr males, the precocious males were characterized by the moderate growth rate. The differences in the growth parameters between the males of different groups were statistically significant (Table 4).

Gonad status. The histological analysis of the gonads in the parrs, smolts, and precocious males of different age groups revealed significant patchiness.

All the specimens at the age of 0+ (males and females) carried the gonads of II stage of maturation.

At the age of 1+, all the females (parrs and smolts) were also characterized by the ovaries of the stage II with the oocytes of the first stage of the cytoplasmic growth. Most of the parr males (76–82% in different years) carried the spermary of the stage II through the summer period until the end of September; the remaining parr males (18–24%) started the sexual maturation. The gonads of future precocious males were at stage II–III in June already (the start of the

Table 2. Biological characteristics of the juveniles and precocious males of masu salmon *Oncorhynchus masou* in the Kol River basin (data of 2008)

| Sex, age | Number of fish, ind. | Fork length (AC), mm | Weight, g | Condition factor, % |
|------------------|----------------------|----------------------------------|-----------------------------------|-----------------------------------|
| Parrs | | | | |
| Males, 0+ | 67 | $\frac{75.0 \pm 1.32}{55-110}$ | $\frac{7.22 \pm 0.43}{2.3-23.2}$ | $\frac{1.60 \pm 0.02}{1.24-1.99}$ |
| Females, 0+ | 85 | $\frac{74.7 \pm 1.17}{52-100}$ | $\frac{7.30 \pm 0.35}{2.4-14.9}$ | $\frac{1.64 \pm 0.02}{1.08-2.04}$ |
| Males, 1+ | 112 | $\frac{100.7 \pm 1.79}{64-154}$ | $\frac{16.94 \pm 0.92}{3.3-61.4}$ | $\frac{1.48 \pm 0.02}{0.83-2.25}$ |
| Females, 1+ | 114 | $\frac{99.7 \pm 1.66}{63-133}$ | $\frac{16.0 \pm 0.79}{2.6-34.1}$ | $\frac{1.46 \pm 0.02}{1.04-2.10}$ |
| Smolts | | | | |
| Males, 1+ | 41 | $\frac{125.7 \pm 1.10}{99-140}$ | $\frac{21.9 \pm 0.56}{10.7-32.1}$ | $\frac{1.10 \pm 0.01}{0.99-1.27}$ |
| Females, 1+ | 46 | $\frac{125.7 \pm 1.62}{92-144}$ | $\frac{22.17 \pm 0.70}{8.8-31.3}$ | $\frac{1.10 \pm 0.01}{0.95-1.41}$ |
| Males, 2+ | 22 | $\frac{148.4 \pm 2.59}{125-176}$ | $\frac{35.6 \pm 1.71}{21.5-55.5}$ | $\frac{1.08 \pm 0.02}{0.76-1.12}$ |
| Females, 2+ | 34 | $\frac{150.8 \pm 1.92}{116-170}$ | $\frac{36.1 \pm 1.60}{17.1-58.0}$ | $\frac{1.05 \pm 0.04}{0.06-1.25}$ |
| Precocious males | | | | |
| 1+ | 48 | $\frac{99.1 \pm 2.48}{73-131}$ | $\frac{16.3 \pm 1.33}{5.4-40.0}$ | $\frac{1.53 \pm 0.04}{1.11-1.90}$ |
| 2+ | 19 | $\frac{137.3 \pm 4.92}{102-181}$ | $\frac{44.4 \pm 4.71}{17.0-91.0}$ | $\frac{1.62 \pm 0.04}{1.28-1.90}$ |

The numbers above the line indicate averages and standard errors; the numbers below the line refer to variability limits.

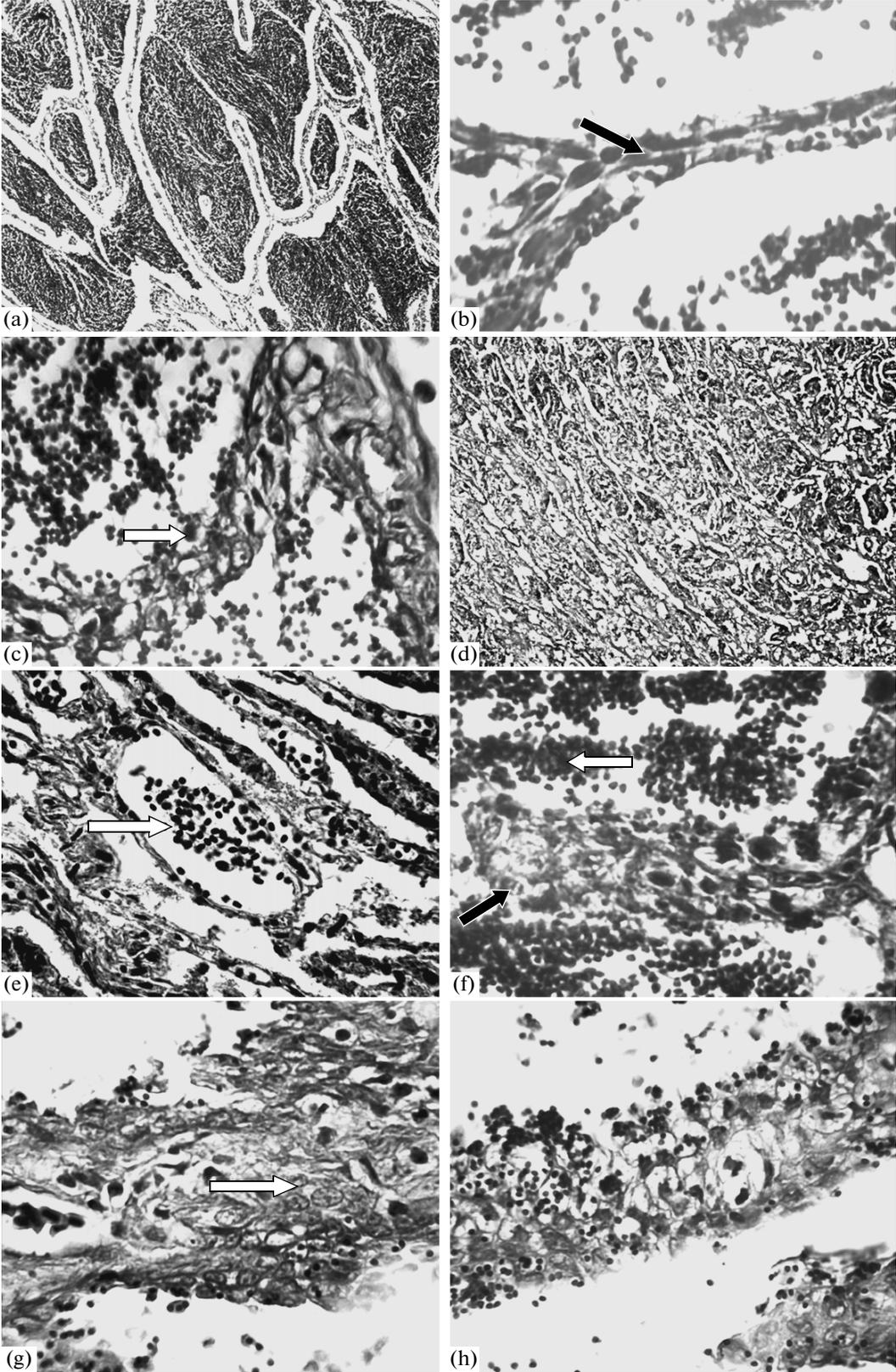
spermatogenesis en masse), and in July they were at stages III and III–IV. In August, precocious males finally matured; in the beginning of this month, they were at spawning status (stage V), and from the third week of August they were at postspawning status (VI and late VI) (Fig. 3).

The first changes in the gonads of smolt females start at the age of 2+. Small specimens of this group ($AC < 160$ mm) carry the ovaries of early II stage, and larger ones ($AC \geq 160$ mm) are characterized by the second stage of the cytoplasmatic growth of oocytes in the ovaries. The smolt males of this age usually perform seaward migration, carrying the spermary of

early II stage and late II stage. All the males of 2+-age that stay in the freshwater environment transform to precocious males; the growth rate of their gonads is similar to those observed in 1+ males, when all of them reach V stage of maturation at the end of August.

Here, we give detailed description of the status of the gonads of precocious males of masu salmon during the spawning and afterwards (Fig. 3). The spermary of stage V (Figs. 3a–3c) are characterized by the presence of seminiferous tubules filled by sperm (Fig. 3a); the tubule walls are thin (Fig. 3b) or carry the vacuolated follicle cells (Fig. 3c) that produce seminal fluid, so they look thick. At this stage (four males were

Fig. 3. Spermary of the precocious males of masu salmon *Oncorhynchus masou* of the Kol River at gonad stages (a–c) V, (d–h) VI, and late (i–l) VI: a—overall view of the spermary of gonad stage V; b—seminiferous tubules filled by sperm, the tubule walls are (→) thin; c—the tubule walls are (⇒) thick, the epithelia cells produce seminal fluid; d—overall view of the spermary of gonad stage VI; e, f—residual sperm cells appear in the (⇒) seminiferous tubules, the tubule walls carry (→) single cells that resemble degrading spermatogonia; g, h—phagocytosis of the residual sperm cells by follicle cells and histiocyte-like cells, the cell that resemble (⇒) spermatogonium locates in the tubule wall; i—overall view of spermary of late VI gonad stage; j—empty seminiferous tubules with partly degraded (→) follicle cells; k—destruction of follicle cells; l—degrading of (⇒) follicle cells with keeping the structure of seminiferous tubules; m—total degradation of seminiferous tubules, totally degraded (→) follicle cells. Magnification: a, d, i—20×; b, c, e–h, j–m—40×.



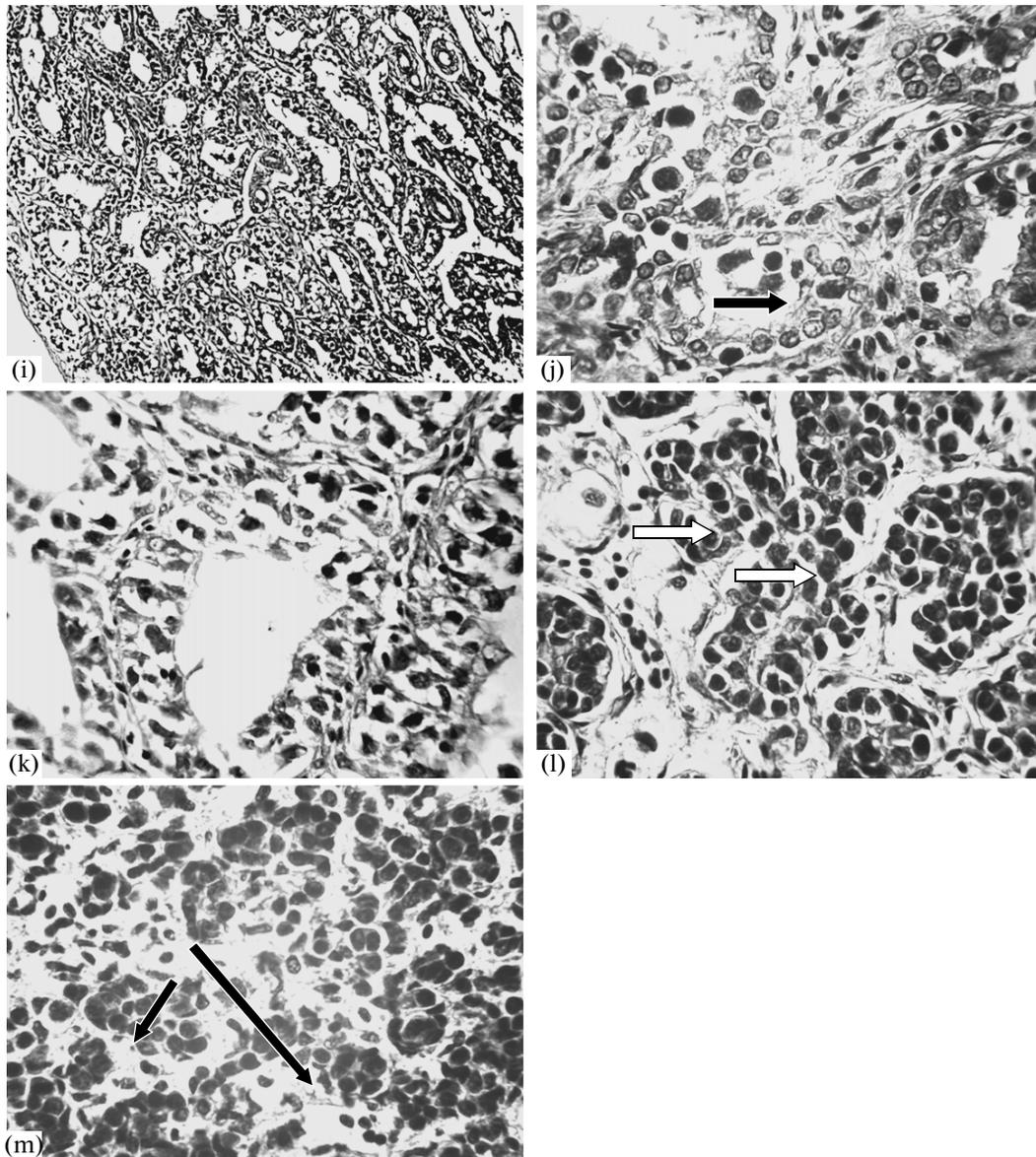


Fig. 3. Contd.

analyzed), we did not find any germ cells in the walls of the seminiferous tubules. At stage VI (Figs. 3d–3h), some residual sperm cells or a significant number of them appear in the seminiferous tubules (Figs. 3e, 3f). In many areas of spermary, active phagocytosis of the residual sperm cells takes place by follicle cells and histiocyte-like cells (Figs. 3g, 3h). Some specimens carry single cells in the walls of seminiferous tubules that resemble degrading or anomalous spermatogonia (Figs. 3f, 3g). The VI late stage of spermary development (Figs. 3i–3l) is characterized by the total absence of the residual sperm cells (Fig. 3i) and empty seminiferous tubules with partly degraded follicle cells (Fig. 3j) or totally destroyed follicle cells (Fig. 3k). The areas of the gonads of the same males and in the

other specimens carry totally degraded follicle cells and the connective tissue of the spermary stroma only (Fig. 3l). Total degradation of the walls of seminiferous tubules is found in four males (Fig. 3m). No germ cells were found in the male gonads at this stage. Therefore, precocious males in the Kol River do not have the conditions to repeat the spawning. They die after the first (and the only) spawning.

DISCUSSION

The freshwater period of the life cycle of most of juveniles and precocious males of masu salmon inhabiting the Kol River takes place in relatively small tributaries. The mainstream is a transit zone of the riverine

Table 3. Scale parameters in juveniles and precocious males of masu salmon *Oncorhynchus masou* in the Kol River

| Group | Parameters | | | | | | | |
|-------------|---|---|---|---|---|------------------------------------|------------------------------------|------------------------------------|
| | l_1 | l_2 | r_1 | r_2 | r_+ | s_1 | s_2 | s_+ |
| | Parrs | | | | | | | |
| Males, 0+ | — | — | — | — | $\frac{0.183-0.426(52)}{0.298 \pm 0.0090}$ | — | — | $\frac{7-13 (52)}{9.50 \pm 0.203}$ |
| Females, 0+ | — | — | — | — | $\frac{0.182-0.403 (79)}{0.290 \pm 0.0065}$ | — | — | $\frac{6-13 (79)}{9.27 \pm 0.179}$ |
| Males, 1+ | $\frac{48.3-77.4 (45)}{62.3 \pm 1.07}$ | — | $\frac{0.175-0.331 (45)}{0.258 \pm 0.0061}$ | — | $\frac{0.065-0.381 (45)}{0.238 \pm 0.0355}$ | $\frac{5-11 (45)}{7.71 \pm 0.192}$ | — | $\frac{3-12 (45)}{9.04 \pm 0.256}$ |
| Females, 1+ | $\frac{38.3-82.1 (44)}{63.28 \pm 1.18}$ | — | $\frac{0.163-0.373 (44)}{0.270 \pm 0.0061}$ | — | $\frac{0.153-0.41 (44)}{0.239 \pm 0.0060}$ | $\frac{6-10 (44)}{7.84 \pm 0.181}$ | — | $\frac{5-11 (44)}{8.91 \pm 0.227}$ |
| | Smolts | | | | | | | |
| Males, 1+ | $\frac{41.8-98.6 (40)}{76.30 \pm 1.60}$ | — | $\frac{0.214-0.421 (40)}{0.310 \pm 0.0098}$ | — | $\frac{0.108-0.306 (40)}{0.208 \pm 0.007}$ | $\frac{6-13 (40)}{9.48 \pm 0.226}$ | — | $\frac{3-8 (40)}{6.13 \pm 0.203}$ |
| Females, 1+ | $\frac{63.4-94.8 (46)}{79.51 \pm 1.28}$ | — | $\frac{0.228-0.435 (46)}{0.322 \pm 0.0074}$ | — | $\frac{0.059-0.325 (46)}{0.199 \pm 0.008}$ | $\frac{6-13 (46)}{9.63 \pm 0.207}$ | — | $\frac{2-8 (46)}{5.70 \pm 0.178}$ |
| Males, 2+ | $\frac{44.7-88.0 (22)}{65.80 \pm 1.98}$ | $\frac{44.3-95.3 (22)}{62.91 \pm 2.56}$ | $\frac{0.156-0.374 (22)}{0.257 \pm 0.0110}$ | $\frac{0.150-0.319 (22)}{0.234 \pm 0.0114}$ | $\frac{0.022-0.179 (22)}{0.098 \pm 0.011}$ | $\frac{4-11 (22)}{7.41 \pm 0.370}$ | $\frac{6-12 (22)}{9.45 \pm 0.360}$ | $\frac{0-6 (22)}{3.14 \pm 0.324}$ |
| Females, 2+ | $\frac{43.2-80.6 (33)}{66.29 \pm 1.40}$ | $\frac{34.7-88.4 (33)}{60.71 \pm 1.94}$ | $\frac{0.181-0.335 (33)}{0.255 \pm 0.0080}$ | $\frac{0.102-0.393 (33)}{0.244 \pm 0.0110}$ | $\frac{0.026-0.185 (33)}{0.119 \pm 0.006}$ | $\frac{4-11 (33)}{7.85 \pm 0.279}$ | $\frac{6-12 (33)}{9.77 \pm 0.276}$ | $\frac{1-6 (33)}{3.79 \pm 0.212}$ |
| | Precocious males | | | | | | | |
| Males, 1+ | $\frac{47.2-94.9 (43)}{69.04 \pm 1.49}$ | — | $\frac{0.194-0.338 (43)}{0.267 \pm 0.006}$ | — | $\frac{0.020-0.251 (43)}{0.118 \pm 0.009}$ | $\frac{6-11 (43)}{8.59 \pm 0.284}$ | — | $\frac{1-9 (43)}{4.21 \pm 0.278}$ |
| Males, 2+ | $\frac{49.8-94.4 (19)}{67.86 \pm 2.68}$ | $\frac{26.0-93.0 (19)}{54.89 \pm 3.94}$ | $\frac{0.184-0.339 (19)}{0.270 \pm 0.0105}$ | $\frac{0.087-0.415 (19)}{0.216 \pm 0.0092}$ | $\frac{0.016-0.154 (19)}{0.086 \pm 0.0084}$ | $\frac{7-11 (19)}{8.26 \pm 0.252}$ | $\frac{5-13 (19)}{8.63 \pm 0.460}$ | $\frac{1-6 (19)}{2.95 \pm 0.30}$ |

Parameters: l_1 and l_2 —absolute linear growth of the body length in the first and the second year of life, mm; r_1 , r_2 , and r_+ —scale width growth in the first, the second, and the current year of life, mm; s_1 , s_2 , and s_+ —number of circuli in the first, the second, and the current year of life, respectively. The numbers above the line outside the brackets indicate variability limits; numbers in the brackets refer to the number of observations; the numbers below the line are the averages and standard errors.

Table 4. Assessment of the statistical differences of the biological parameters in parrs, smolts, and dwarf males of masu salmon *Oncorhynchus masou* of the Kol River using Student's t-criterion

| Parameters | Groups for comparison | | | | | | | |
|----------------------|--------------------------------------|---|--|--|---------------------------------------|---------------------------------------|---|---|
| | Parr males (1+) and smolt males (1+) | Parr males (1+) and precocious males (1+) | Smolt males (1+) and precocious males (1+) | Smolt males (2+) and precocious males (2+) | Parr males (0+) and parr females (0+) | Parr males (1+) and parr females (0+) | Smolt males (1+) and smolt females (1+) | Smolt males (2+) and smolt females (2+) |
| <i>AC</i> | 11.88*** | 0.51 | 9.80*** | 2.00* | 0.21 | 0.35 | 0.04 | 0.77 |
| <i>W</i> | 4.64*** | 0.41 | 3.92*** | 1.75 | 0.14 | 0.77 | 0.26 | 0.21 |
| <i>C_f</i> | 15.46*** | 0.99 | 10.18*** | 12.75*** | 1.50 | 0.74 | 0.13 | 1.01 |
| <i>R</i> | 1.73 | 9.86*** | 14.83*** | 0.92 | 0.72 | 0.96 | 0.07 | 0.46 |
| <i>r₁</i> | 4.51*** | 1.05 | 3.74*** | 0.86 | — | 1.39 | 0.98 | 0.14 |
| <i>r₂</i> | — | — | — | 1.91 | — | — | — | 0.63 |
| <i>r₊</i> | 0.83 | 3.28** | 7.89*** | 0.86 | 0.72 | 0.03 | 0.85 | 1.62 |
| <i>S</i> | 2.75** | 8.55*** | 6.95*** | 0.69 | 0.85 | 0.07 | 0.80 | 1.01 |
| <i>s₁</i> | 5.97*** | 2.57* | 2.45** | 1.90 | — | 0.49 | 0.49 | 0.95 |
| <i>s₂</i> | — | — | — | 1.95 | — | — | — | 0.71 |
| <i>s₊</i> | 8.91*** | 12.78*** | 5.58*** | 0.43 | 0.85 | 0.38 | 1.59 | 1.68 |
| <i>l₁</i> | 7.27*** | 3.67*** | 3.32** | 0.62 | — | 0.62 | 1.57 | 0.20 |
| <i>l₂</i> | — | — | — | 1.71 | — | — | — | 0.68 |

AC—fork length according to Smith, mm; *W*—body weight, g; *C_f*—condition factor according to Fulton; *R*—total radius of the scale, mm; *S*—total number of circuli; the other abbreviations are indicated in Table 3. Significance level (*P*) is indicated as: * > 0.95; ** > 0.99; *** > 0.999.

system, where seaward run of smolts of masu salmon and anadromous migration of the adult fish to the spawning grounds occur. Particularly in these tributaries, which are the major environments for the growth of the masu salmon juveniles, the adoption of different life history strategy patterns takes place. The freshwater period of life of masu salmon in the Kol River basin takes usually one or two years, during this period, resident and anadromous specimens appear in the population.

The resident mature specimens of masu salmon inhabiting the Kol River are presented by precocious males since we did not find a single resident “dwarf” female during the period of our observations. In addition, some females mature in the rivers of Japan and Primorye, in the southern part of the geographical range, without performing seaward migration (Osanai and Otsuka, 1969; Kimura, 1972; Kubo, 1980; Ivankov et al., 1981; Kao, 1991). However, in the northern part of the geographical range of masu salmon, no maturation of females is observed for the rivers. This is supported by the histological analysis of the gonads of the juveniles of masu salmon inhabiting the Kol River, as well as by the biological analysis, when the ovaries of all females (parrs and smolts)

reach only stage II during the freshwater period of their life cycle. Therefore, the life cycle of females of masu salmon inhabiting the Kol River is strictly targeted toward the anadromous life history strategy, and the population reproduction is supported exclusively by anadromous females.

Other regularities are observed for the males of masu salmon. Their life cycle is characterized by invariant strategy, and the possibility to follow the alternative way of the life history strategy in regard to the growth rate. The most rapidly growing males within the group of the young-of-the-year after the first wintering transform to smolts. High growth rate during their first summer stimulates the process of smoltification and preconditions the launch of an anadromous type of life history strategy. It is known that smoltification in many species of salmonids is possible only if they reach minimal critical size (Chernitskii, 1993; Thorpe, 1994), which is why later this rapidly growing juveniles become anadromous foremost. Probably, the minimal body length at which masu salmon smoltify is 90 mm (Table 2), and their average body length decreases in different populations on a regular basis moving from the southernmost to the northern margin of the geographical range of this

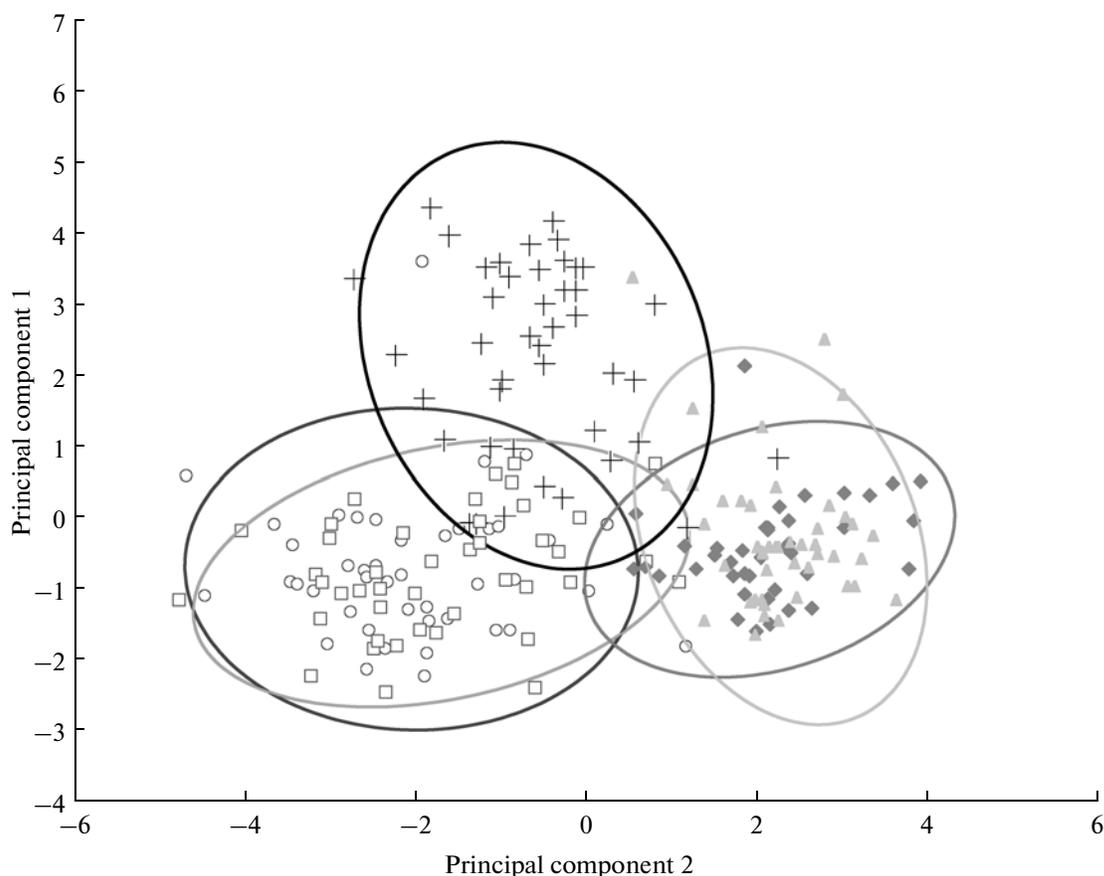


Fig. 4. Phenetic relationship between the groups of masu salmon *Oncorhynchus masou* at the age of 1+ in the Kol River, assessed by the combination of twelve parameters characterizing the fish growth. Legend: (○)—parrs, males; (□)—parrs, females; (◆)—smolts, males; (▲)—smolts, females; (+)—dwarf males.

species (Krykhtin, 1962; Sano, 1964; Kato, 1973, 1991; Churikov, 1975; Semenchenko, 1989). The males that are characterized by low growth rate during their first year of life stay one more year in the fresh waters at parr stage. The low growth rate of these males is accompanied by slow development of their gonads, since their spermary remain at stage II during the second summer of their life cycle. The males characterized by relatively high growth rate but still slower than that observed in smolts do not reach minimal critical body size to start smoltification, and these males start the process of gametogenesis that results in maturation of these specimens in the freshwater. They become precocious males at the second summer of their life cycle and realize the resident type of the life history strategy. Similar tendencies—smoltification of rapidly growing fish and continuance of the slowly growing ones in the freshwaters—were registered within the whole geographical range of masu salmon (Krykhtin, 1962; Utoh, 1976, 1977; Ivankov et al., 1977, 1984a, 1984b; Kato, 1991).

Generally, our results obtained for masu salmon refer to the data on the biology of Atlantic salmon *Salmo salar*, when a number of the authors conclude

about the growth rate as the limiting factor for the differentiation of generation into smolts and parrs. This process starts early and the absence of high-sensitive methods of analysis does not allow the registration at its very early stages (Thorpe and Morgan, 1978; Thorpe et al., 1980, 1982; Metcalfe et al., 1988; Thorpe, 1994).

The growth rate is one of the major factors affecting the differentiation of the masu salmon juveniles within the generation, as is already mentioned above. The assessment of the group variability of the growth parameters in juveniles and dwarf males of masu salmon using the principal component analysis supports this idea. The scatters that refer to the groups of parrs, smolts, and precocious males are distinct from each other, but no significant discretion is observed between them (Fig. 4; Table 5). The most pronounced differences of the growth rates are observed between smolts and precocious males of 1+ age.

The first phase of the intrapopulation differentiation (bifurcation) occurs in the masu salmon juveniles after the first wintering (Fig. 5). This phase links to the transition of the fastest growing males and females from the freshwater environment to the ocean ; their

Table 5. Factor's loading of the growth parameters in masu salmon *Oncorhynchus masou* from the Kol River that were used for the analysis of the phenetic relationships of the groups indicated in Fig. 4

| Parameters | Principal component 1 | Principal component 2 |
|------------------------------------|-----------------------|-----------------------|
| <i>AC</i> | -0.9314 | 0.0194 |
| <i>W</i> | -0.8439 | 0.2567 |
| <i>C_f</i> | 0.4487 | 0.0139 |
| <i>R</i> | -0.9148 | -0.3146 |
| <i>r₁</i> | -0.2186 | -0.7955 |
| <i>r₊</i> | 0.3647 | -0.4421 |
| <i>r₊/s₊</i> | -0.1054 | -0.7941 |
| <i>R/S</i> | -0.0647 | -0.9014 |
| <i>r₁/s₁</i> | -0.3632 | -0.7917 |
| <i>S</i> | -0.9054 | 0.2548 |
| <i>s₁</i> | 0.8812 | 0.1001 |
| <i>s₊</i> | 0.7214 | -0.1687 |

The attributes: r_1/s_1 , r_+/s_+ —the average distance (mm) between circuli correspondingly in the 1 and current year of life; R/S —the average distance between circuli (mm) in the freshwater period. The other abbreviations as in the table 3, 4. The values, highlighted in bold are statistically significant.

rapid growth promotes the launch of the smoltification process, which, in turn, blocks spermatogenesis. On the other hand, relatively slow growth of males (in regard to the growth rate of smolts) does not result in reaching the minimal size of smolts and appears to be a reason for the delayed gonad maturation or the start of their maturation, which blocks smoltification. After the second wintering, the overall pattern of the life cycle repeats in this generation, when fast-growing males and females run seaward as smolts, and the rest of males remain in the freshwater and become precocious males. The immature fish of 2+-age are quite rare in the river, and all of them are males.

Precocious males play a significant role in masu salmon reproduction in the Kol River basin. They spawn together with large anadromous males, when the ratio of anadromous females, large anadromous males, and precocious males (of different ages) is 1 : 1 : 7–15 (Kuzishchin et al., 2009). Masu salmon spawn in small streams of the Kol River, and females usually build a redd at very narrow streams that do not exceed 1-m width. In this case, precocious males play a major role in egg fertilization. After the spawning is over, anadromous males and females die quickly, but precocious males keep on the spawning grounds for a long time period and even migrate from the spawning streams to the mainstream. The survival of precocious

males of masu salmon after spawning and their active life and feeding were registered by a number of authors at the whole geographical range of species (Krykhtin, 1962; Utoh, 1976; Ivankov et al., 1977; Kato, 1991; Semenchenko et al., 2003). Moreover, it was found that repeated maturation of precocious males and even their smoltification, and, therefore, the change of the life history strategy within the ontogenesis might take place (Ivankov et al., 1977; Semenchenko et al., 2003). However, the survival of the precocious males is usually observed only in the southern areas of the species geographical range, in the zone of ecological optimum. On the northern areas of the range, in the Kol River, the precocious males after spawning have a strictly preconditioned predestination, when their gonads are affected by nonreversible degenerative changes, as was found under histological analysis (Fig. 3). The seaward run of precocious males does not occur here, since we have found only gonad stage II in smolts.

Our data evidence that the age composition of precocious males and smolts varies from year to year. Probably, this interannual variability depends on the growth peculiarities of fish during different years. The processes of intrapopulation differentiation are largely preconditioned by the environment of the early freshwater period of life and mostly by the trophic factor that supports the fish growth (Thorpe, 1987, 1994; Pavlov et al., 2007). The ecosystems of the salmonid rivers of Kamchatka are characterized by high productivity due to a large amount of the spawning Pacific salmon and, therefore, marine derived nutrients subsidy. In the Kol River basin, pink salmon *O. gorbuscha* is the major species fertilizing the riverine ecosystem (Kuzishchin et al., 2012). However, pink salmon does not spawn in the small streams where masu salmon build their redds; so there coho salmon *O. kisutch* preconditions the productivity of the ecosystem, bringing 83–88% of total marine derived nutrients. As was observed during our studies, the abundance of coho salmon that come to the streams used by masu salmon was relatively stable during the whole observation period (2003–2008) and, therefore, the level of the fertilization remained the same. That is why the variability of the environment for masu salmon growth and forming its life history strategy diversity may be preconditioned by other factors, primarily, by the water temperature.

The temperature regime of the spawning streams in the Kol River basin varies from year to year; however, masu salmon usually prefers to spawn in relatively “warm” tributaries or their parts (Kuzishchin et al., 2009). Probably, at the northern boundary of the geographical range, the parameters of the population structure of warm-water species, masu salmon, mostly depend on the abiotic environmental factors, and the water temperature regime is one of the most important for the ectotherms.

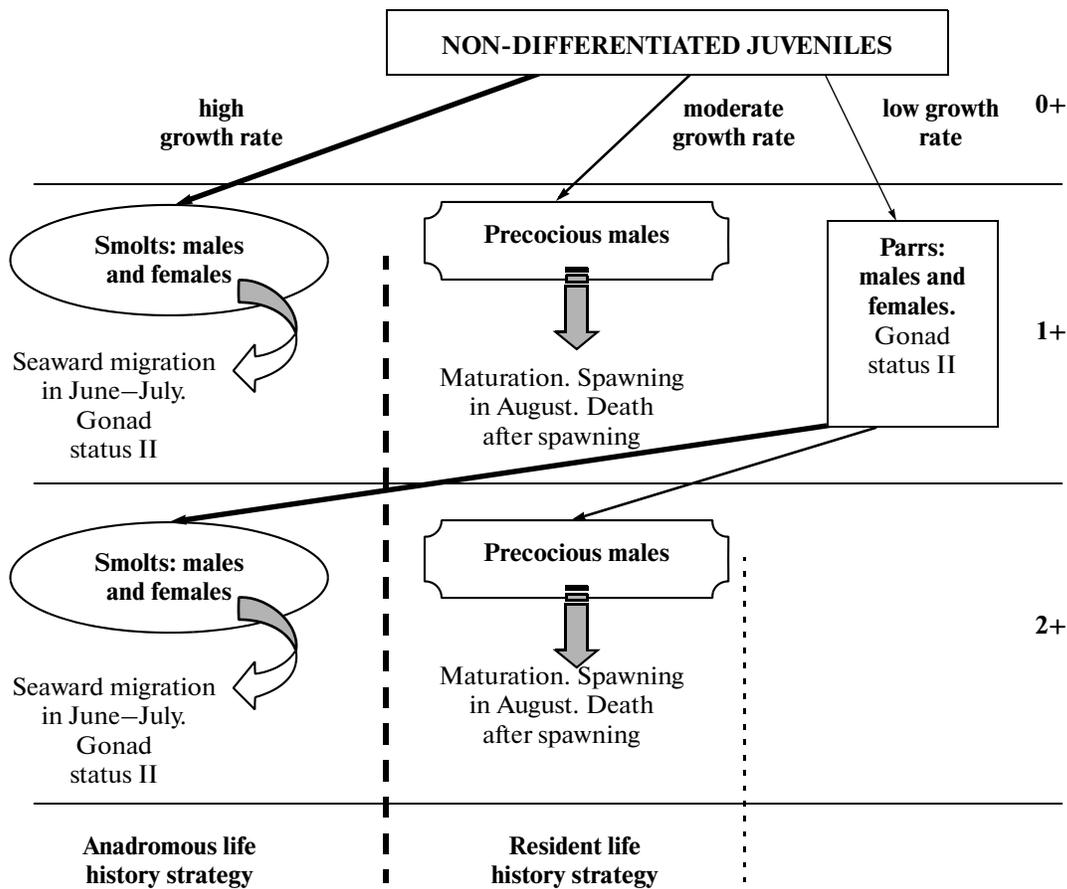


Fig. 5. Scheme of the generation differentiation of masu salmon *Oncorhynchus masou* in the Kol River basin.

The ways of the life history strategy diversity formation in masu salmon inhabiting the northern part of its geographical range differs from the specimens inhabiting the area of ecological optimum in the basin of the Sea of Japan. Only two types of the life history strategy were found for the population of masu salmon inhabiting the Kol River basin, anadromous males and females and riverine precocious males. The maturation of precocious males blocks the smoltification process and thus preconditions strictly the life cycle of the specimen through the only possibility to become the resident fish. At the same time, the populations of masu salmon inhabiting Japan are characterized by high diversity of anadromous and resident forms with both males and females (Sano, 1964; Osanai and Otsuka, 1969; Kato, 1973, 1991; Utoh, 1976, 1977; Kubo, 1980). Four forms of masu salmon males were defined for the rivers of Primorye, including the males surviving after spawning, repeatedly maturing precocious males, and the riverine precocious males that run seawards after spawning (Semenchenko et al., 2003).

In the Kol River, all the breeders, including resident precocious and anadromous males, reproduce only once a lifetime, i.e., they are strictly monocyclic.

In the southern areas of the geographical range, the males and females that mature in the fresh waters may later mature again or change the environment, i.e., they maintain the possibility to shift to the alternative life history strategy type, and the repeated spawning is registered there for at least males (Utoh, 1976, 1977; Ivankov et al., 1977, 1981; Kubo, 1980; Semenchenko, 1989; Semenchenko et al., 2003).

In the Kol River basin close to the northern boundary of the geographical range, the reproduction effectiveness and life history strategy diversity in the population are strictly preconditioned by the abiotic factors, particularly, on the thermal regime of the waterbodies where the spawning and freshwater phases of the life cycle of masu salmon take place. Probably, in the southern areas of the geographical range that are characterized by milder climate, the degree of the dependence of the population structure on the abiotic factors is less pronounced, since the age composition of anadromous breeders and riverine resident fish varies insignificantly from river to river in the basin of the Sea of Japan (Krykhtin, 1962; Sano, 1964; Osanai and Otsuka, 1969; Kimura, 1972; Kato, 1973, 1991; Churikov, 1975; Utoh, 1976, 1977; Kubo, 1980; Ivankov

et al., 1981; Semenchko, 1989; Malyutina et al., 2009).

In addition, the specificity of the biological parameters of masu salmon inhabiting Kamchatka rivers is somehow relative. Currently, the Kamchatka populations of masu salmon may be characterized by quasi-stationary status, but if the climate change at a large scale or if the anthropogenous influence will be too pronounced, their structure may change. Probably, global climate warming may affect on the populations at the northern part of the geographical range, i.e., the age composition and the ratio of the specimens of different life history strategy types of warm-water masu salmon species may change, and the repeat spawners may appear. On the other hand, it is known that the landlocked populations of masu salmon developed very quickly, in 2–3 years, in the water reservoirs, when the unsurmountable barriers appear for the migration of anadromous fish (Moiseev, 1957; Honda, 1980, 1983; Osanai, 1982). In regard to this fact, we propose the complex ecological monitoring of the salmonids on Kamchatka as an essential routine, which must include permanent observations on the species that may appear as the indicator species to track any changes in the ecosystems. We suppose that masu salmon may be included in this list of indicator species.

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REFERENCES

- Belova, N.V., Some methods of studying the pre-spawning and spawning period of fish males, in *Issledovaniya razmnozheniya i razvitiya ryb (Metodicheskoe posobie)* (Study of fish reproduction and development (Textbook)), Moscow: Nauka, 1981, pp. 58–66.
- Berg, L.S., New data on salmon (*Salmo salar*) biology, *Usp. Sovrem. Biol.*, 1937, vol. 6, no. 1, pp. 5–19.
- Bird, D.J. and Cowx, I.G., The selection of suitable pulsed currents for electric fishing in fresh waters, *Fish. Res.*, 1993, vol. 18, pp. 363–376.
- Busaker, G.P., Adelman, I.K., and Goolish, E.M., Growth, in *Methods for Fish Biology*, Schreck, C.B. and Moule, P.B. Eds., Bethesda: Amer. Fish. Soc., vol. 1, pp. 363–387.
- Chernitskii, A.G., Seaward migration and marine period of life of the juveniles of genus *Salmo* at natural and artificial reproduction, *Doct. Sci. (Biol.) Dissertation*, Moscow: VNIRO, 1993.
- Churikov, A.A., Peculiarities of seaward migration of the juveniles of *Oncorhynchus* genus in the rivers of the north-eastern coast of Sakhalin, *Vopr. Ikhtiol.*, 1975, vol. 15, no. 6 (95), pp. 1078–1085.
- Honda, N., Suzuki, K., Amita, K., et al., Studies on reproduction of landlocked masu salmon *Oncorhynchus masou* in Okutadami reservoir. I. Vertical distribution and feeding habits of fish, *Rept. Niigata Pref. Inland Water Fish. Exp. Station*, 1980, vol. 8, pp. 5–15.
- Honda, N., Kataoka, M., and Hoshino, M., Studies on reproduction of landlocked masu salmon *Oncorhynchus masou* in Okutadami reservoir. V. Studies on the growth and age of maturity of the landlocked masu salmon, *Rept. Niigata Pref. Inland Water Fish. Exp. Station*, 1983, vol. 10, pp. 13–20.
- Ivankov, V.N., Padetskii, S.N., Floryak, V.S., et al., Neotenic females of masu salmon *Oncorhynchus masou* (Brevoort) from Krivaya River (Southern Primorye), *Vopr. Ikhtiol.*, 1981, vol. 21, no. 5, pp. 938–942.
- Ivankov, V.N., Padetskii, S.N., and Chikina, V.S., About post-spawning neotenic males of masu salmon *Oncorhynchus masou* (Brevoort), *Vopr. Ikhtiol.*, 1977, vol. 17, no. 4, pp. 753–757.
- Ivankov, V.N., Padetskii, S.N., Karpenko, S.N., and Luk'yanov, P.E., Biology of the diadromous fish of Southern Primorye, in *Biologiya prokhodnykh ryb Dal'nego Vostoka* (Biology of the diadromous fish of Far East region), Vladivostok: Izd-vo DVGU, 1984a, pp. 10–22.
- Ivankov, V.N., Padetskii, S.N., and Rukhlov, F.N., Morphological variability of masu salmon and biological peculiarities of its population in different areas of its geographical range, in *Biologiya prokhodnykh ryb Dal'nego Vostoka* (Biology of the diadromous fish of Far East region), Vladivostok: Izd-vo DVGU, 1984b, pp. 95–107.
- Kato, F., Life histories of masu and amago salmon (*Oncorhynchus masou* and *Oncorhynchus rhodurus*), *Pacific salmon life histories*, Vancouver: UBC, 1991, pp. 447–520.
- Kato, F., Ecological study on the sea-run form of *Oncorhynchus rhodurus* found in Ise Bay, *Jpn. J. Ichthyol.*, 1973, vol. 20, pp. 225–234.
- Kimura, S., On the spawning behavior of the fluvial dwarf form of masu salmon *Oncorhynchus masou*, *Jpn. J. Ichthyol.*, 1972, vol. 19, pp. 111–119.
- Krykhtin, M.L., *Materialy o rechnom periode zhizni simy* (Data on the river period of masu salmon life cycle), *Trudy TINRO*, 1962, vol. 48, pp. 84–132.
- Kubo, T., Studies on the life history of masu salmon (*Oncorhynchus masou*) in Hokkaido, *Sci. Rept. Hokkaido Salmon Hatchery*, 1980, vol. 34, pp. 1–95.
- Kuzishchin, K.V., Malyutina, A.M., Gruzdeva, M.A., et al., Reproduction ecology of masu salmon *Oncorhynchus masou* in the Kol basin (Western Kamchatka), *J. Ichthyol.*, 2009, vol. 49, no. 6, pp. 441–453.
- Kuzishchin, K.V., Gruzdeva, M.A., Pavlov, D.S., et al., An attempt to apply the method of table isotopes of $\sigma^{15}\text{N}$ and $\sigma^{13}\text{C}$ to study the trophic structure and production potential of the ecosystems of salmon-inhabited rivers of Kamchatka, in *Mater. XIII Mezhdunar. nauch. konf. "Sokhranenie bioraznobraziya Kamchatki i prilegayushchikh morei"* (Proc. XIII Int. Scientific Conference on Conservation of Biodiversity of Kamchatka and Adjacent Seas), Petropavlovsk-Kamchatskii: Kamchatpress, 2012, pp. 58–60.

- Kuznetsova, A.F., Some data on the biology of juveniles of masu salmon, *Izv. Tikhook. Inst. Rybn. Khoz. Okeanogr.*, 1954, vol. 41, pp. 387–341.
- Lakin, G.F., *Biometriya* (Biometry), Moscow: Vysshaya Shkola, 1990.
- Lin, Y.-S. and Chang, K.-H., Conservation of the formosan landlocked salmon *Oncorhynchus masou formosanus* in Taiwan, a historical review, *Physiol. Ecol. Jpn. Spec.*, 1989, vol. 1, pp. 647–652.
- Malyutina, A.M., Savvaitova, K.A., Kuzishchin, K.V., et al., Population structure of the masu salmon *Oncorhynchus masou* from the Kol River (Western Kamchatka) and geographic variation in the species area, *J. Ichthyol.*, 2009, vol. 49, no. 5, pp. 390–402.
- Metcalfe, N.B., Huntingford, F.A., and Thorpe, J.E., Feeding intensity, growth rates and the establishment of life-history strategies in juvenile atlantic salmon *Salmo salar*, *J. Anim. Ecol.*, 1988, vol. 57, no. 2, pp. 463–474.
- Mikodina, E.V., Sedova, M.A., Chmylevskii, D.A., et al., *Gistologiya dlya ikhtologov. Opyt i sovety* (Hystology technique for ichthyologists. Experience and recommendations), Moscow: Izd-vo VNIRO, 2009.
- Moiseev, P.A., Evolving of landlocked form of masu salmon (*Oncorhynchus masou m. formosanus* (Jordan et Oshima)) in the basin of Sedanka River, *Dokl. Akad. Nauk SSSR*, 1957, vol. 112, no. 1, pp. 163–164.
- Murza, I.G. and Khristoforov, O.L., *Opreделение stepeni zrelosti gonad i prognozirovanie vozrasta dostizheniya polovoi zrelosti u atlanticheskogo lososya i kumzhi* (Determination of the gonad status and assessing the age of the sexual maturation in Atlantic salmon and brown trout), Leningrad: Izd-vo GosNIORKh, 1991.
- Osanaï, M., Masu salmon in lakes. Special report on freshwater fish, *Oncorhynchus masou* and *O. rhodurus*, *Sci. Rept. Hokkaido Fish Hatchery*, 1982, vol. 33, p. 79.
- Osanaï, M. and Otsuka, M., Ecological studies on the masu salmon, *Oncorhynchus masou* (Brevoort) of Hokkaido. 2. On the effect of moving upstream and spawning behavior on the sexual maturity of masu salmon, *Sci. Rept. Hokkaido Fish Hatchery*, 1969, vol. 16, p. 79.
- Pavlov, D.S., Nemova, N.N., Kirillov, P.I., et al., Lipid status and feeding habits of salmonid juveniles in the year preceding seaward migration as factors controlling their future smoltification, *J. Ichthyol.*, 2007, vol. 47, no. 3, pp. 241–245.
- Pavlov, D.S., Savvaitova, K.A., Kuzishchin, K.V., et al., *Sostoyanie i monitoring bioraznoobraziya lososevykh ryb i sredey ikh obitaniya na Kamchatke (na primere territorii zakaznika "Reka Kol")* (Status and monitoring of the biodiversity of salmonids and the environment in Kamchatka (in terms of wildlife sanctuary "River Kol")), Moscow: T-vo nauch. izd. KMK, 2009.
- Pavlov, D.S. and Savvaitova, K.A., Intraspecific structure of fish: about the problem of anadromous vs. landlocked ratio in salmonids (Salmonidae), in *Aktual'nye problemy sovremennoi ikhtologii* (Contemporary problems of ichthyology), Moscow: KMK Editorial Association, 2010, pp. 33–62.
- Pavlov, D.S., Savvaitova, K.A., Kuzishchin, K.V., et al., *Tikhookeanskije blagorodnye lososi i foreli Azii* (Salmon and trout species of Pacific origin of Asia), Moscow: Nauchnyi Mir, 2001.
- Persov, G.M., *Differentsirovka pola u ryb* (Sex differentiation in fish), Leningrad: Izd-vo LGU, 1975.
- Pravdin, I.F., *Rukovodstvo po izucheniyu ryb* (Manual on fish studies), Moscow: Pishchepromizdat, 1966.
- Rohlf, J.F., *NTSYS-pc Numerical Taxonomy and Multivariate Analysis System*, New York: Exeter Software, 1993.
- Sano, S., The ecology and protection of reproduction of genus *Oncorhynchus*, *Sci. Rept. Hokkaido Fish Hatchery*, 1964, vol. 21, pp. 1–10.
- Semenchenko, A.Yu., Krupyanko, N.I., and Gavrenkov, Yu.I., Ecological forms of males of the masu salmon *Oncorhynchus masou* from river basins of Primorye, *J. Ichthyol.*, 2003, vol. 43, no. 6, pp. 438–444.
- Semenchenko, A.Yu., Anadromous migration and biological characteristics of masu salmon *Oncorhynchus masou* (Brevoort) inhabiting Primorye, in *Populyatsionnaya biologiya i sistematika lososevykh* (Population Biology and Taxonomy of Salmonids), Vladivostok: Izd-vo DVO AN SSSR, 1980, pp. 51–57.
- Semenchenko, A.Yu., *Primorskaya sima* (Masu Salmon of Primorye), Vladivostok: Izd-vo DVO AN SSSR, 1989.
- Semko, R.S., New data on masu salmon inhabiting Western Kamchatka, *Zool. Zh.*, 1956, vol. 35, no. 7, pp. 1017–1022.
- Thorpe, J.E. and Morgan, R.I.G., Periodicity in Atlantic salmon, *Salmo salar* L. smolt migration, *J. Fish. Biol.*, 1978, vol. 12, no. 6, pp. 541–548.
- Thorpe, J.E., Reproductive strategies in Atlantic salmon, *Salmo salar* L., *J. Aquacult. Fish. Manage*, 1994, vol. 25, pp. 77–87.
- Thorpe, J.E., Morgan, R.I.G., Ottaway, E.M., and Miles, M.S., Time of divergence of growth between potential 1+ and 2+ smolts among sibling Atlantic salmon, *J. Fish. Biol.*, 1980, vol. 17, pp. 13–21.
- Thorpe, J.E., Talbot, C., and Villareal, C., Bimodality of growth and smolting in Atlantic salmon, *Aquaculture*, 1982, vol. 28, pp. 123–132.
- Thorpe, J.E., Smolting versus residency developmental conflicts in salmonids, *Amer. Fish. Soc. Symp.*, 1987, vol. 1, pp. 244–252.
- Tsygir, V.V. and Ivankov, V.N., Landlocked masu salmon inhabiting Artemovskii reservoir (Primorye), *Vopr. Ikhtiol.*, 1987, vol. 27, no. 4, pp. 576–583.
- Tsygir, V.V., Landlocked masu salmon inhabiting Sedankinskii reservoir (Southern Primorye), in *Biologiya shel'fovykh i prokhodnykh ryb* (Biology of shelf and diadromous fish), 1990, Vladivostok: Izd-vo DVO AN SSSR, pp. 47–52.
- Utoh, H., A study of mechanism of differentiation between the stream resident form and seaward migration form of masu salmon *Oncorhynchus masou* (Brevoort). II. Growth and sexual maturity of precocious masu salmon parr, *Bull. Fac. Fish. Hokkaido Univ.*, 1977, vol. 28, pp. 66–73.
- Utoh, H., A study of mechanism of differentiation between the stream resident form and seaward migration form of masu salmon *Oncorhynchus masou* (Brevoort). I. Growth and sexual maturity of precocious masu salmon parr, *Bull. Fac. Fish. Hokkaido Univ.*, 1976, vol. 26, pp. 321–326.
- Valovaya, M.A. and Kavtaradze, D.N., *Mikrotekhnika. Pravila, priemy, iskusstvo. Eksperiment* (Microtechnique. Rules, approaches, art. Experiment), Moscow: Moscow State Univ., 1993.
- Zippin, C., An evaluation of the removal method of estimation animal populations, *Biometrics*, 1956, vol. 12, no. 2, pp. 163–189.

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