

Morphophysiological Patterns of Life History Strategy Adoption in Dolly Varden *Salvelinus malma* in Kamchatka

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Abstract—Growth, age composition, gonad maturity and patterns of life history strategy adoption in the population of Dolly Varden from the Kol River (West Kamchatka) are studied. Major factors controlling differentiation of juveniles and trajectories of ontogenetic developments, growth rate and gametogenesis in generations in particular years. The differentiation in a generation into anadromous and resident groupings is completed mainly at the age of 4 years. The process of formation of resident and migratory life history strategy in Dolly Varden is epigenetic. Bifurcation in the life of one specimen is observed once in life, and that in a generation is observed four times: at the first, the second, the third, or the fourth year. The life cycle of females from the Kol River is invariant until they reach the age of 1 year, and that in males is during the 4 years of the freshwater phase. In Kamchatka, all spawners, including precocious males, may reproduce several times during life.

Keywords: Dolly Varden *Salvelinus malma*, growth, age, gonads, life cycle, life strategy, anadromy, residence, precocious males, intrapopulation differentiation

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Diversity of life strategies in populations of salmonid fishes (Salmonidae) in the freshwater phase of their life cycle depends on specific traits of their growth, metabolism, gonad maturation, and transformation of their osmoregulatory system. Morphophysiological processes depending on environmental parameters channel the program of individual development (Thorpe, 1994; Hendry and Stearns, 2004; Pavlov and Savvaitova, 2008). Information on intraspecific ecological differentiation on salmonid species is different. In detail, it is known in Atlantic salmon *Salmo salar*, brown trout *S. trutta*, and masu salmon *Oncorhynchus masou* (Thorpe, 1987, 1994; Chernitskiy, 1993; Elliott, 1994; Thorpe et al., 1998; Bohlin et al., 2001; Gruzdeva et al., 2013). On the contrary, in chars of the genus *Salvelinus*—a major fish component of the community of salmonid rivers of high latitudes and of the boreal zone of the Pacific basin, fish with a very complex intraspecies organization—many patterns of formation of intraspecies diversity remain little unknown (Savvaitova, 1989; Tiller, 2007; Pavlov et al., 2013). One of such species in whose populations there are coexisting specimens with different level of anadromy and residence is Dolly Varden *Salvelinus malma*.

It is obvious that the intricate structure of fish may be elucidated by a complex of parameters characterizing the individual physiological state. Assessment of such parameters elucidates the individual reaction of fish to changes of particular environmental factors leading for adoption of a certain life history strategy (Hutchings and Jones, 1998; Debat and David, 2001; Hutchings, 2004). Demonstrative indicators of selection of life history strategy are specific traits of fish growth (Mina, 1986; Myers et al., 1986) and of formation of their gonads (Gruzdeva et al., 2013, 2015).

The present study is aimed at elucidation of patterns of life history strategy adoption in Dolly Varden with reference of the population from the Kol River (western coast of Kamchatka).

MATERIALS AND METHODS

The data was obtained in the Kol River (western Kamchatka (Fig. 1). The river origins in the spurs of the Sredinnyi (Middle) Kamchatka Ridge and discharges to the Sea of Okhotsk. Its length along the main channel is 133 km, the density of the riverine network in the catchment area is 0.61 km/km², and mean water discharge at the baseflow is 56 m³/s. The river is a complex, braided-anastomosis system with a

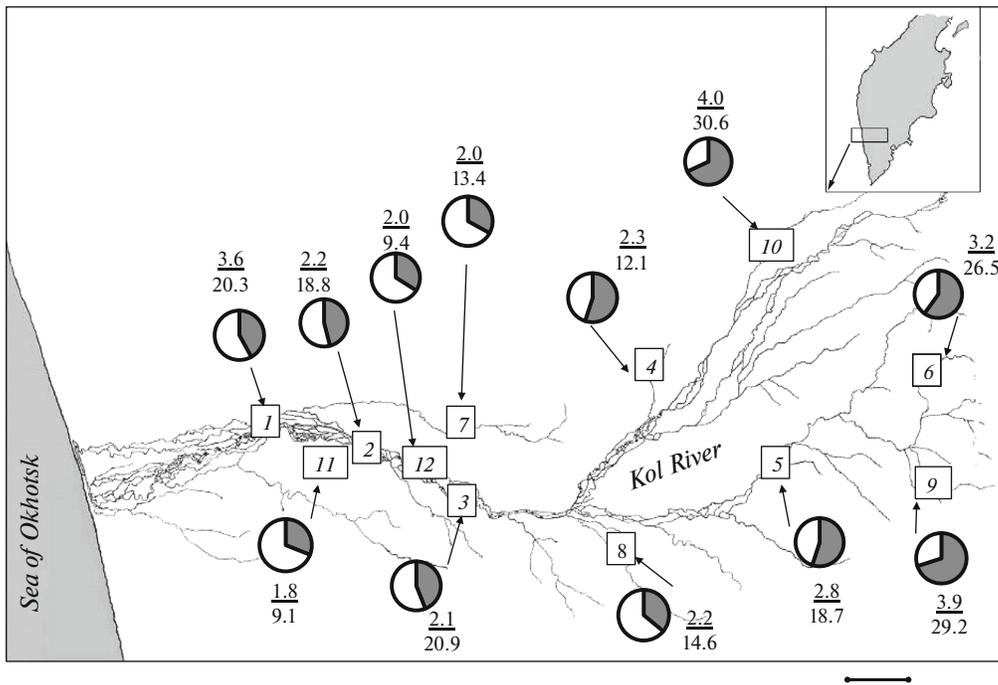


Fig. 1. Schematic map of the Kol River basin and distribution in it of juveniles of Dolly Varden *Salvelinus malma* of all age classes. Designation of sites: 1–6—main stream of the river, distance from the mouth 15, 25, 30, 55, 65, and 90 km, respectively; 7—tundra tributary, the Krasnaya River; 8—tundra tributary, the Sqweechik Creek; 9—mountain tributary, Uvalnyi Creek; 10—mountain tributary, Tsepkiy Creek; 11—springbrook 1; 12—springbrook 2. Juveniles of Dolly Varden (■), juveniles of all other species of Salmonidae (□); digits above the line—density of Dolly Varden juveniles, specimens/m²; under the line—biomass, g/m². Scale bar: 4 km.

developed system of floodplain water bodies and numerous tributaries of various types (mountain and tundra) from 3 to 45 km in length and water discharge from 0.01 to 2.08 m³/s (Pavlov et al., 2009; Kuzishchin et al., 2010).

Mature fish were caught with a beach seine, gill nets, and hook-and-line tackle; juveniles and mature male parr – precocious males were caught using electrofishing unit Smith-Root 24L turned for care regime (Bird and Cowx, 1993) at impulse A.C. (350–400 V, 40–60 Hz, impulse length of 2 ms). After capture, all specimens were immobilized with solutions MS-222 or clove oil (Kouřil et al., 2009; Mikodina et al., 2011). Three-pass electrofishing were performed for estimation of the population density of juveniles (Zippin, 1956); the abundance and biomass were calculated for the areas not less that 100 m² each. The sampling was performed at 26 sites of the river system, including the mainstream, tributaries, and the floodplain springbrooks. Behavior of fish during spawning was studied by underwater observations by means of a GoPro chamber and by visual observations using snorkeling devices.

All the sampled fish were studied under overall biological analysis (Pravdin, 1966). In total, 2733 specimens were analyzed. Sex and maturity stage of gonads were determined (Sakun and Butskaya, 1968; Persov,

1975; Murza and Khristoforov, 1991; Makeeva, 1992; Chmylevskiy, 2003). For histology, gonad fragments were fixed in 4% formaldehyde.

Fish age was determined by the biggest otolith—sagitta. For back calculation of fish growth, the radius of otoliths (R) and increments of the otolith were determined. On the basis of these data $l_1, l_2, l_3 \dots l_4$ were calculated—increments of the body length in the first, second, third, etc. and in the current year of life. Back calculation of fish body length at different age was made by Lea equation (Busaker et al., 1990): $l_i - c = r_i/R(FL - c)$, where l_i is the determined body length of a specimen at the i th age, r_i is radius of the i th annual ring on the otolith, R is complete radius of the otolith, FL is the observed fork length, c is constant term calculated by the equation of relationship of otolith radius with fish length: $\ln FL = c + \ln R$, correlation of correlation making over 0.95.

The dataset was analyzed by standard univariate statistics (Lakin, 1990). The samples were compared with principal component analysis (PCA) (James and McCulluch, 1990). 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). Back deciphering of the life cycle of fish is based on microchem-

ical analysis of otoliths, ratio of ions of strontium and calcium on longitudinal sections along the transect of the history (Kalish and 1990; Radtke et al., 1997; Zimmerman et al., 2003). Mass fraction of ions Sr and Ca was determined by X-ray fluorescent analysis (Z-RayFA) on a Tornado M4 spectrometer (Bruker AXS, Germany) (Pavlov et al., 2013, 2016).

Histological mounts were prepared in a standard way (Romeis, 1968) using semiautomated equipment (Medite, Germany): TPC-15 histoprocessor, TES-99 embedding station, a Meditome M530 microme. Gonad sections 3–5 μm thick were consecutively stained with Ehrlich hematoxylin and eosin. Photographs of gonad sections were made by means of a Keyence Biorevo BZ-9000 motorized microscope (Japan).

Development level of oocytes of maturity stage II of gonads was estimated by the nuclear-plasmatic ratio (NPR) calculated as the ratio of nucleus area to cytoplasm area on a section near its central part. Smaller NPR corresponds to more intensive cell growth (Pavlov et al., 2014). Measurements of annual increments of otoliths and determinations of NPR were made by means of Image J ver. 1.50i software. Significance of NPR differences was determined by Student's test.

RESULTS

Intrapopulation structure in Dolly Varden from the Kol River. On the basis of size, age composition, sex composition, abundance, and distribution of fish in the riverine system, we found that the local population of Dolly Varden is complex and consists of nondifferentiated juveniles and of intraspecific groupings differing in life history strategies (resident and anadromous) and in biological parameters (Fig. 2).

Determination of anadromous or resident life strategy is made on the basis of the ratio of ions in otoliths. In parr ($n = 11$), precocious males ($n = 12$), and resident specimens ($n = 4$), the transects of life history are characterized by low values of Sr/Ca ratio during all individual life and vary from 4.10×10^{-3} to 5.58×10^{-3} on average in different specimens. In anadromous fish, the transects of life history are characterized by low values of Sr/Ca ratio: from 3.11×10^{-3} to 5.44×10^{-3} in the otolith zone corresponding to the freshwater phase followed by a series of consecutive peaks with high values, from 5.53×10^{-3} to 10.31×10^{-3} in the otolith zone that corresponds to the marine phase. On average, this ratio is 6.01×10^{-3} – 6.61×10^{-3} . A high level of Sr/Ca ratio in the otolith during the marine phase is retained in the period of returning to the river.

The freshwater component of the population of Kol River Dolly Varden is represented by juveniles—parr and smolts that migrate to the sea and by fish attained maturity in the river—precocious males (mature male parr) retaining juvenile shape (body proportions and coloration) and rare resident specimens

having different body proportions and coloration than in juveniles (high body, 22–24% FL, dark olive with contrasting red or pink spots, without parr marks on sides, belly is bright orange even between spawning periods).

In parr of Dolly Varden the sex ratio among yearlings, two-year-old fish, and four-year-old fish is approximately equal, while there are two times more females than males among 3-year-old fish. Among smolts, females always prevail: 2+—3.0 : 1; 3+—1.6 : 1; 4+—2.0 : 1. On the contrary, males prevail among residents (Fig. 2).

In the Kol River basin, Dolly Varden parr are present everywhere from headwaters to the mouth in all kinds of locations and biotopes: mainstream, secondary channels, tributaries, spring brooks. They keep a dominant place by abundance and biomass among the salmonid juveniles with a prolonged freshwater period (Fig. 1, Table 1). In the river, downstream migrants (smolts) occur from the mid-May until mid-July. The change in coloration of smolts (silvering) occurs in the last week of May to the first week of June. The outmigration in Dolly Varden smolts begins in mid-June after water is warmed above 10°C, and the peak of downstream migration is recorded in the third to fourth week of June. The outmigration mainly ends to the end of the first week of July.

Precocious males of Dolly Varden are distributed all over the river system but are rare in the mainstream and small water bodies of the accessory system. They make a noticeable part of all fish in assemblages of the upper reaches of the river, of spawning tributaries (of tundra and mountain type), and in large spring brooks (Fig. 1, Table 1). The precocious males seem not to make intra-river migrations and are located in spawning-foraging sites of the river system. In summer, they keep among juveniles. In autumn, beginning from early September, they concentrate in the spawning grounds (Gruzdeva et al., 2011a, 2011b, 2014a, 2014b). By the distribution and foraging behaviour, the precocious males are almost indistinguishable from juveniles (Kuzishchin et al., 2015).

The resident specimens occur principally in the Kol River mainstream; however, they migrate from the mainstream to spawning tributaries in September. Thus, in contrast to precocious males, the riverine resident fish are rheodromous (term according to Pavlov and Starobogatov, 2014) and made periodic movements within the river system.

The migratory (anadromous) component of the Dolly Varden population consists of two groupings (Fig. 2). The first one consists of relatively small in length and weight immature fish returning to the river for wintering after a short (3–4 months) period of coastal migration in the sea; they are so-called “thunders” (term according to Savvaitova, 1989; Tiller, 2007). The second one is represented by large mature fish that made several consecutive visits to the

Table 1. Relative abundance, distribution, and age composition of the freshwater part of the population of Dolly Varden *Salvelinus malma* in the Kol River basin (mean data for 2003–2008)

| Stretch of river system | Age composition, parr/precocious males, % | | | | | | Part of precocious males, % |
|-------------------------|---|--------|-----------|----------|--------|-------|-----------------------------|
| | 0+ | 1+ | 2+ | 3+ | 4+ | 5+ | |
| 1 | 77.5/– | 11.6/– | 9.3/– | 1.6/100 | –/– | –/– | 0.1 |
| 2 | 78.8/– | 14.9/– | 5.5/– | 0.8/– | –/– | –/– | 0.0 |
| 3 | 76.7/– | 15.7/– | 5.9/– | 1.7/100 | –/– | –/– | 0.1 |
| 4 | 86.1/– | 11.2/– | 1.7/– | 1.0/100 | –/– | –/– | 1.2 |
| 5 | 82.4/– | 14.2/– | 3.4/4.4 | –/81.2 | –/14.4 | – | 7.9 |
| 6 | 85.3/– | 12.6/– | 2.1/5.2 | –/78.8 | –/13.1 | –/2.9 | 8.1 |
| 7 | 76.8/– | 15.3/– | 6.2/16.5 | 1.7/61.7 | –/20.3 | –/1.5 | 9.2 |
| 8 | 80.2/– | 14.8/– | 3.6/8.8 | 1.4/74.7 | –/16.5 | –/– | 10.9 |
| 9 | 73.5/– | 15.1/– | 9.6/23.2 | 1.8/48.8 | –/25.4 | –/2.6 | 14.4 |
| 10 | 71.2/– | 16.3/– | 10.3/11.4 | 2.2/32.5 | –/40.6 | –/3.3 | 12.1 |
| 11 | 83.6/– | 9.2/– | 4.8/– | 0.5/80.4 | –/19.6 | –/– | 4.3 |
| 12 | 81.4/– | 8.8/– | 6.2/– | 3.6/68.4 | –/31.6 | –/– | 3.7 |

Main river channel (1–6); distance from mouth: 1–15 km; 2–25 km; 3–30 km; 4–55 km; 5–65 km; 6–90 km; 7—tundra tributary, the Krasnaya River; 8—tundra tributary, the Sqweechik River; 9—tundra tributary, the Uvalnyi Creek; 10—tundra tributary, Chepkki Creek; 11—spring brook 1; 12—spring brook 2.

variations, at the spawning act, most precocious males are at the distance of 1–3 m from the redd and the eggs are actually fertilized by a migratory male, more rarely by resident and by two to three of the largest precocious males. According to our observations, small precocious males do not make a significant contribution to reproduction of the population.

Size-weight characteristic of juveniles, precocious males, and resident riverine fish. Males and females of parr of one age are, as a rule, similar in body size and weight. Their comparative analysis did not reveal noticeable differences (Table 2). In comparison with parr of the same age, the smolts are characterized by greater size and weight of the body. Precocious males possess significantly ($p > 0.999$) greater length ($2+ - t = 5.87$ and 5.62 , $3+ - t = 3.99$ and 3.56) and weight ($2+ - t = 6.44$ and 5.60 , $3+ - t = 4.38$ and 5.34) of the body in comparison with smolts and parr. In comparison with juveniles and precocious males of the same age, the resident mature specimens are characterized by maximum length and weight of body. Immature thunders are represented mostly by females and male at the age $3+ - 4+$ (life history age groups of $3.0+$ and $4.0+$). In our samples, the mature migratory specimens of Dolly Varden were of the age $4+ - 8+$; most of them visited the sea two or three times. In classes of the same age, they are characterized by the largest length weight of the body in comparison with thunders and all representatives of the freshwater component.

Growth. Males and females of parr of the same age are similar in back calculated body increments (Table 3). In comparison with parr of the same age, the smolts of the same age ($2+$) are characterized by significantly

greater increment of body length ($t = 2.83$, $p > 0.999$) in the year preceding migration to the sea. At the age $3+$, precocious males, in comparison with parr and smolts, have significantly greater back-calculated increments ($t = 3.19$, $p > 0.999$) of the body length in the year preceding maturation. The riverine mature specimens are characterized by the highest, in comparison with parr, smolts, and precocious males, increments of the body length beginning with the first year of life.

Assessment of growth parameters of parr, smolt, and precocious males of the Kol River Dolly Varden by principal component analysis revealed the presence of group variation: factor areas corresponding to parr, smolts, and precocious males occupy somewhat separate positions, up to appearance of discontinuity between parr and two other groups (Fig. 3).

Maturity stages of gonads. Determination of maturity stages of gonads of Dolly Varden revealed mosaic pattern within each group (Figs. 4, 5).

Females. All parr at the age $1+$ had ovaries of maturity stage II (Fig. 4a). At the age $2+$ and $3+$, the fraction of parr with ovaries at maturity stage III did not exceed 33%.

Smolts at the age $2+$ and $3+$ also had the ovaries at the maturity stage II or III. The part of fish with gonads at stage III was somewhat higher than that in parr of the same age: 38% at the age $2+$, reaching 75% at the age $3+$. The ovaries of all smolts and residents at the age $4+$ and of thunders ($3+$ and $4+$) were at the maturity stage III.

Table 2. Biological characteristics of the river and migratory component of the population of Dolly Varden *Salvelinus malma* in the Kol River basin

| Sex, age | <i>n</i> | Length (<i>FL</i>), mm | Weight, g |
|--------------------------------|----------|--------------------------|------------------------------|
| Parr | | | |
| Males, 0+ | 18 | 63.4 ± 1.36 (54–74) | 2.64 ± 0.21 (1.4–4.2) |
| Females, 0+ | 17 | 61.6 ± 1.17 (55–70) | 2.47 ± 0.21 (1.7–4.5) |
| Males, 1+ | 92 | 98.4 ± 1.61 (67–137) | 13.01 ± 0.80 (3.0–38.6) |
| Females, 1+ | 91 | 95.9 ± 1.61 (62–137) | 12.02 ± 0.77 (2.1–35.9) |
| Males, 2+ | 65 | 124.2 ± 2.44 (91–173) | 25.04 ± 2.03 (8.5–79.1) |
| Females, 2+ | 130 | 125.9 ± 1.46 (87–188) | 26.26 ± 1.30 (8.1–74.3) |
| Males, 3+ | 10 | 139.9 ± 4.51 (131–175) | 28.97 ± 4.47 (19.3–67.6) |
| Females, 3+ | 10 | 139.8 ± 5.47 (121–172) | 31.38 ± 7.16 (15.8–83.0) |
| Smolts | | | |
| Males, 2+ | 5 | 134.4 ± 4.68 (118–146) | 25.00 ± 2.57 (15.6–30.7) |
| Females, 2+ | 14 | 133.8 ± 2.69 (119–151) | 24.15 ± 1.51 (16.4–36.8) |
| Males, 3+ | 10 | 142.5 ± 4.52 (120–167) | 29.19 ± 2.61 (19.1–48.3) |
| Females, 3+ | 16 | 145.5 ± 2.25 (132–163) | 30.37 ± 1.56 (20.9–44.5) |
| Males, 4+ | 1 | 139 | 29.6 |
| Females, 4+ | 2 | 144.0 ± 4.00 (140–148) | 29.55 ± 0.75 (28.8–30.3) |
| Precocious males | | | |
| 2+ | 84 | 142.8 ± 2.01 (94–179) | 42.87 ± 1.86 (9.3–82.8) |
| 3+ | 34 | 164.1 ± 4.04 (101–209) | 56.38 ± 4.38 (9.5–135.7) |
| 4+ | 12 | 189.2 ± 5.03 (164–225) | 73.38 ± 6.50 (49.9–127.6) |
| 5+ | 2 | 201.0 ± 1.00 (200–202) | 88.45 ± 0.75 (87.7–89.2) |
| Resident fish | | | |
| Males, 3+ | 3 | 214.3 ± 11.70 (198–237) | 124.93 ± 22.39 (102.0–169.7) |
| Males, 4+ | 4 | 227.0 ± 3.19 (218–233) | 158.30 ± 8.45 (135.2–174.6) |
| Females, 4+ | 1 | 228 | 149.7 |
| Thounders* | | | |
| Females, 3+ | 15 | 250.4 ± 3.53 (241–262) | 208.8 ± 6.42 (191–229) |
| Males, 3+ | 16 | 257.2 ± 3.77 (240–268) | 213.4 ± 7.15 (171–244) |
| Females, 4+ | 19 | 267.3 ± 3.90 (260–277) | 262.6 ± 7.47 (241–275) |
| Males, 4+ | 18 | 263.2 ± 9.46 (243–292) | 249.8 ± 26.52 (177–326) |
| Typically anadromous migrants* | | | |
| Males, 4+ | 7 | 326.9 ± 13.00 (292–395) | 397.1 ± 53.19 (279–667) |
| Females, 4+ | 11 | 325.9 ± 3.45 (311–350) | 388.7 ± 14.9 (303–463) |
| Males, 5+ | 25 | 363.6 ± 7.65 (311–481) | 547.0 ± 34.57 (321–1064) |
| Females, 5+ | 49 | 377.7 ± 4.70 (314–432) | 617.9 ± 20.49 (343–852) |
| Males, 6+ | 28 | 458.4 ± 8.73 (385–540) | 1060.8 ± 60.87 (642–1598) |
| Females, 6+ | 27 | 422.6 ± 5.09 (379–478) | 832.9 ± 26.61 (592–1093) |
| Males, 7+ | 14 | 519.9 ± 9.42 (465–585) | 1504.6 ± 72.23 (1190–2169) |
| Females, 7+ | 5 | 462.6 ± 21.58 (398–532) | 1066.0 ± 166.10 (567–1610) |
| Males, 8+ | 2 | 573.5 ± 13.50 (560–587) | 1743.0 ± 83.50 (1660–1827) |

Outside of parentheses—mean of parameter and its error; within parentheses—variation limits; * combined (river + sea) age is indicated.

In June, migratory females—spawners of age classes 4+, 5+, 6+, and 7+ had gonads at maturity state III or IV (in equal proportion). Transition of gonads or migratory females to stage V continued from early August up to spawning. In September, one spent female was caught with ovaries at stage VI–II. Only two adult migratory specimens missing spawning were

caught in the year of collection of the material (one in mid-August, another in mid-September), both at the age 5+; their gonads were at maturity stage III.

Males. The testes of parr of the age 1+ were at maturity stage II (Fig. 4b). At the age 2+, the part of specimens with gonads at maturity stage III was 17%, and it reached 40% at 3+.

Table 3. Calculated increments of body length of parrs, precocious males, and resident specimens of Dolly Varden *Salvelinus malma* from the Kol River.

| Sex, age, years | n | Length increment, mm | | | |
|------------------|----|-----------------------------------|--------------------------------------|--------------------------------------|--------------------------------------|
| | | l_1 | l_2 | l_3 | l_4 |
| Parr | | | | | |
| Males, 1+ | 11 | $\frac{67.1 \pm 2.59}{51.5-78.4}$ | — | — | — |
| Females, 1+ | 13 | $\frac{75.2 \pm 3.16}{58.5-93.6}$ | — | — | — |
| Males, 2+ | 20 | $\frac{69.7 \pm 2.23}{53.0-95.1}$ | $\frac{115.2 \pm 2.29}{89.3-134.2}$ | — | — |
| Females, 2+ | 28 | $\frac{67.8 \pm 1.34}{53.5-81.1}$ | $\frac{116.2 \pm 1.74}{96.3-130.8}$ | — | — |
| Males, 3+ | 8 | $\frac{61.7 \pm 3.13}{53.4-74.7}$ | $\frac{98.2 \pm 5.39}{85.2-125.2}$ | $\frac{132.9 \pm 4.76}{117.2-158.3}$ | — |
| Females, 3+ | 8 | $\frac{61.8 \pm 4.47}{40.5-75.3}$ | $\frac{100.1 \pm 6.88}{60.8-122.5}$ | $\frac{131.7 \pm 5.76}{113.1-145.0}$ | — |
| Smolts | | | | | |
| Males, 2+ | 5 | $\frac{74.4 \pm 4.97}{63.7-89.5}$ | $\frac{130.4 \pm 3.88}{116.3-138.1}$ | — | — |
| Females, 2+ | 13 | $\frac{75.5 \pm 2.82}{59.9-94.4}$ | $\frac{128.9 \pm 2.24}{116.5-139.4}$ | — | — |
| Males, 3+ | 10 | $\frac{68.7 \pm 3.39}{53.9-81.1}$ | $\frac{107.4 \pm 4.12}{87.5-129.8}$ | $\frac{138.2 \pm 4.43}{118.7-164.3}$ | — |
| Females, 3+ | 16 | $\frac{67.1 \pm 2.51}{50.2-89.5}$ | $\frac{111.9 \pm 3.01}{95.9-136.9}$ | $\frac{141.5 \pm 2.32}{127.7-158.9}$ | — |
| Males, 4+ | 1 | 47.8 | 96.8 | 114.1 | 134.8 |
| Females, 4+ | 2 | $\frac{56.1 \pm 2.06}{54.0-58.2}$ | $\frac{81.2 \pm 3.19}{78.1-84.4}$ | $\frac{112.5 \pm 2.01}{110.5-114.5}$ | $\frac{138.8 \pm 4.56}{134.3-143.4}$ |
| Precocious males | | | | | |
| 2+ | 20 | $\frac{69.2 \pm 1.30}{57.9-79.9}$ | $\frac{115.1 \pm 3.66}{88.6-139.9}$ | — | — |
| 3+ | 19 | $\frac{65.3 \pm 2.53}{45.1-87.6}$ | $\frac{118.5 \pm 4.21}{79.9-139.7}$ | $\frac{150.7 \pm 5.31}{94.5-174.6}$ | — |
| 4+ | 11 | $\frac{69.3 \pm 3.25}{50.5-83.3}$ | $\frac{120.4 \pm 4.99}{82.9-142.2}$ | $\frac{157.6 \pm 4.71}{129.1-183.6}$ | $\frac{186.5 \pm 5.21}{161.4-219.2}$ |
| 5+ | 2 | $\frac{68.1 \pm 0.19}{67.9-68.2}$ | $\frac{110.8 \pm 18.55}{91.9-129.6}$ | $\frac{140.5 \pm 7.43}{133.1-147.9}$ | $\frac{169.7 \pm 0.81}{168.8-170.4}$ |
| 6+ | 1 | 68.6 | 105.6 | 146 | 168.7 |
| River residents | | | | | |
| Males, 3+ | 1 | 83.7 | 129.8 | 169.0 | — |
| Males, 4+ | 4 | $\frac{82.1 \pm 4.72}{72.3-94.5}$ | $\frac{141.4 \pm 7.83}{123.6-156.5}$ | $\frac{179.6 \pm 8.29}{166.6-204.0}$ | $\frac{206.7 \pm 6.67}{192.8-222.9}$ |
| Females, 4+ | 1 | 84.8 | 137.4 | 183.7 | 221.3 |

Here and in Table 4: above the line—mean value of a parameter and its error; under the line—variation limits. l_1 , l_2 , l_3 , l_4 —body length increments in the first, second, third, and fourth year of life, respectively.

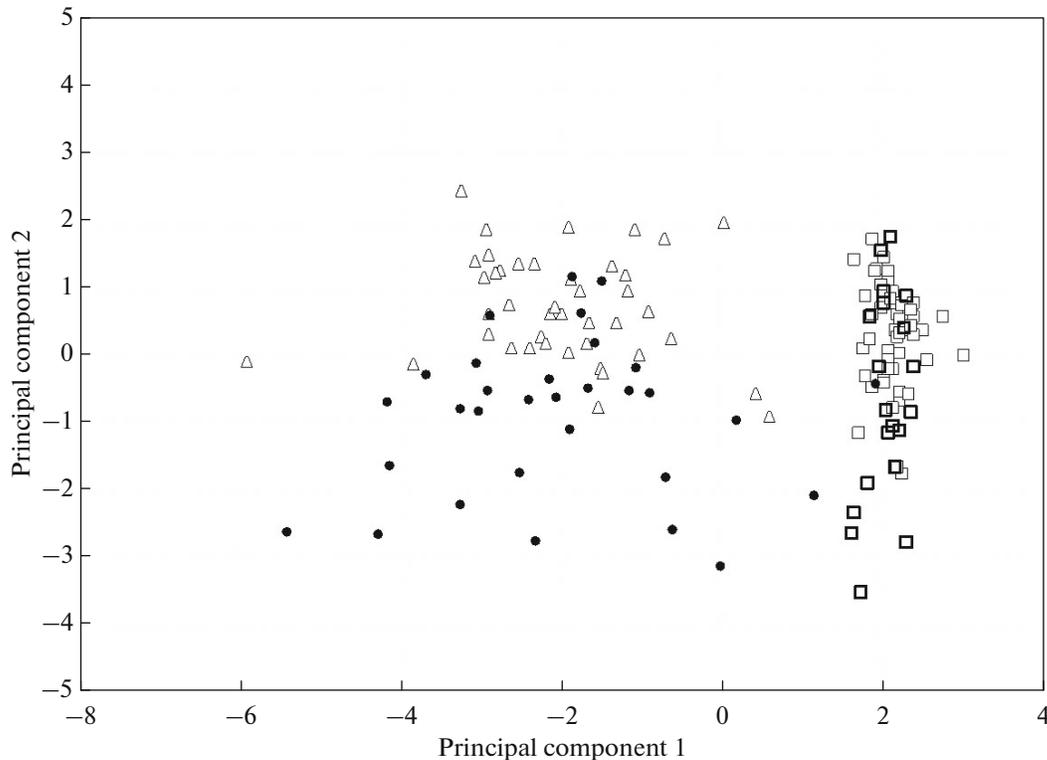


Fig. 3. Fenetic relationship of intrapopulation groups of Dolly Varden *Salvelinus malma* from the Kol River estimated by 11 characters of fish growth (body length and weight, radius of otolith, width of the first, second, third annual zones and of the increment zone of the current year, calculated body length at the age 1, 2, 3 years, and that in the current year), age 3+: (□) parr, (●) smolts, (△) precocious males.

Smolts at the age 2+ had testes at maturity stage II. Up to the age 3+, the gonads in 18% of specimens reaches maturity stage III.

Riverine resident males at the age 3+ and 4+ were caught on the spawning ground in September; their gonads were at maturity stage V. The testes of thunders caught in September at the age 4+ and 5+ were at the maturity stage III. Typically anadromous specimens (spawners) of all age classes (4+–8+) in June had gonads at maturity stage III and IV, 42 and 58% of specimens, respectively. In September, all anadromous males had testes at maturity stage V, except two specimens of age 6+ whose gonads were at maturity stage II (these fish were missing spawning).

In precocious males, the cytological state of gonads differed depending on sampling time (Fig. 5). In June, the gonads of precocious males of age 3+ and 4+ were at maturity stage III and IV (Fig. 5). Gonads of all specimens caught in July (age 3+ and 5+) attained early maturity stage IV. In August, precocious males (age 3+) had testes at maturity stages IV and IV–V in equal ratios.

The testes of anadromous males of age 5+ and 6+ arriving to the river in July were at maturity stages III and IV in equal ratios. In the beginning of September, most anadromous males (97%) had gonads at maturity

stage V; others (3%) missed the spawning, and their gonads were at maturity stage II.

Cytological condition of gonads of juveniles. In all female parr at the age 1+, gonads are represented by oocytes of the period of previtellogenesis that are characterized by a large nucleus and homogeneous cytoplasm. On sections along the periphery of cell nuclei, the nucleoles are seen. On average, there are 6 psc per section. At the age 2+, the value of NCR is lower than at the age 1+, and the diameter of cells of the previtellogenesis period, on the contrary, is higher (Table 4). The ovaries at maturity stage III contain the oocytes of the period of beginning of vitellogenesis whose diameters (261–368 μm) noticeably surpass those in previtellogenous oocytes. In the periphery of cytoplasm of vitellogenic oocytes, vacuoles are formed; the nucleus forms extensions to cytoplasm and the number of nucleoli increases, on average, to 12 pcs per section. At age 3+, the values of NCR and diameters of oocytes generally are similar to those at the age 2+. The ovaries at maturity stage III contain vitellogenic oocytes 183–440 μm in diameter. The obtained results mean that the female parr at the age 1+–3+ are not yet ready for spawning.

In gonads of female smolts at the age 2+, previtellogenic oocytes (Stage II) are characterized by some-

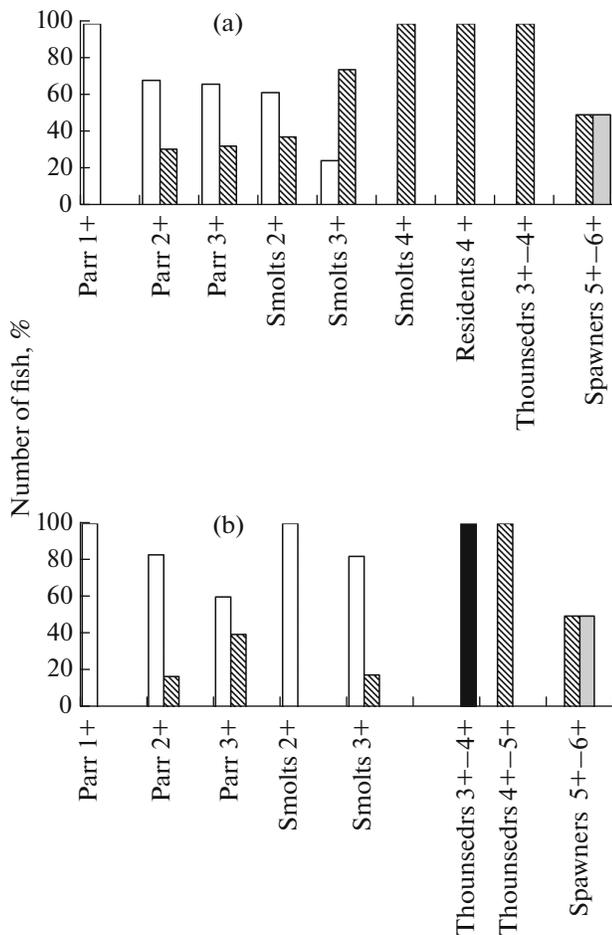


Fig. 4. Frequency of occurrence of specimens with gonads at various maturation stages in intrapopulation groups of Dolly Varden *Salvelinus malma* from the Kol River: (a) females, (b) males; maturation stages: (□) II, (▨) III, (■) IV, (■) V.

what greater values of NVR and diameter than the sex cells in the ovaries of female parr of the same age (Table 4). Sometimes, dark circular zones are seen in the cytoplasmic material intensively absorb in hematoxylin lac—RNA zones (Fig. 6a). In gonads of maturity stage III, the diameter of vitellogenic oocytes (276–419 μm) exceeds that in the sex cells in the gonads of female parr of the same age. These traits indicate to rapid development of only a minor part of cells, while the majority of the cells available in gonads of female smolts are less developed than those in the ovaries of parr of the same age. At the age 3+ in female parr, the cytological state of previtellogenic oocytes and their state parameters (NCR and diameter) hardly differ from those at the age 2+ (Table 4), while the diameters of vitellogenic oocytes increase noticeably (326–683 μm). Vacuolization level of such oocytes is various: from two to three rows of vacuoles over periphery of

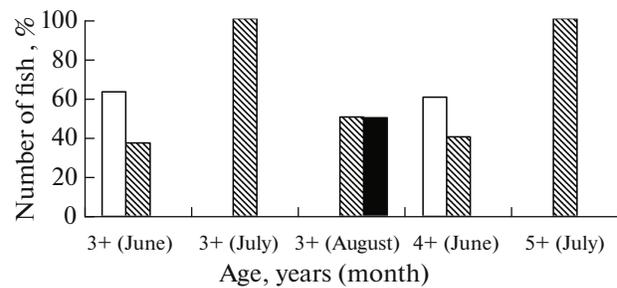


Fig. 5. Frequency of occurrence of precocious males of Dolly Varden *Salvelinus malma* in the Kol River with gonads at various maturation stages in relation to capture month; designations as in Fig. 4.

cytoplasm in gonads of most specimens to almost complete vacuolization of cytoplasm in some gonads. At the age 4+, the gonads are at maturity stage III, whose diameters of vitellogenic oocytes, possessing already vacuolized cytoplasm (Fig. 6b), is 200–560 μm .

The gonads of male parr at the age 1+ contain spermatogonia still in the process of mitotic division. Up to the age 2+ and 3+ in the testis at maturity stage II, the spermatocytes of order II appear; in testes of maturity stage II, spermatocytes of order I appear starting prophase I of meiosis. In the testes at maturity stage III, spermatocytes of order II appear, which are almost two times smaller than spermatocytes of order I.

All testes of smolts at the age 2+ contain only spermatogonia. The cytological state of gonad in male smolts at the age 3+ (Fig. 7a) corresponds to that in parr at the age 2+. This indicates to a considerable retardation of spermatogenesis rate in the fish selecting the anadromous type of life history strategy.

State of gonads of precocious males and of riverine resident specimens. Cytological state of gonads in precocious males correlates with their age (3+, 4+, 5+) only in structure of seminal canalicules, but it differs depending on capture month (June, July, August). In gonad maturity stage III of the specimens reaching maturity for the first time, the lumens of seminal canalicules hardly differ (Fig. 7b). In polycyclic spawning, they are well expressed (Fig. 7c). Presence of wide lumens is a significant character of the fact the precocious males in the Kol River basin are characterized by polycyclic spawning in their life cycle. In the beginning of maturity stage IV, the gonads contain spermatids in addition to spermatocytes indicating to the beginning of spermatogenesis. Spermatids are still smaller than spermatocytes of order II; they absorb in hematoxylin lac more intensively and are stained darkly. To the end of maturity stage IV, in testes, few spermatozooids located in lumens of seminal canalicules (Fig. 7d) formed between cysts with earlier sex cells (spermatocytes and spermatids). The spermatozooids differ from other sex cells in smaller size, elongated form, and presence of a flagellum. At maturity

Table 4. Oocyte diameter and nuclear-cytoplasmic ratio (NCR) in gonads of maturity stage II in parr and smolts of Dolly Varden *Salvelinus malma* from the Kol River

| Group | Diameter, μm | NCR |
|----------|--------------------------------------|-------------------------------------|
| Parr 1+ | 100.8 ± 3.15 (123) 33.6–186.1 | 0.50 ± 0.015 (130) 0.17–1.33 |
| Parr 2+ | 131.7 ± 5.27 (136) 31.6–258.4 | 0.36 ± 0.008 (334) 0.13–0.88 |
| Parr 3+ | 137.4 ± 6.79 (83) 28.1–248.1 | 0.37 ± 0.017 (155) 0.12–2.05 |
| Smolt 2+ | 136.9 ± 7.64 (99) 24.8–317.4 | 0.40 ± 0.008 (418) 0.13–1.44 |
| Smolt 3+ | 126.6 ± 7.08 (120) 30.1–331.1 | 0.42 ± 0.013 (201) 0.17–1.26 |

In parentheses—number of measured oocytes; other designations as in Table 3.

stage V, the greater part of generative tissue of testes contain seminal canaliculi with spermatozoids and a few earlier sex cells such as spermatids and spermato-cytes.

A sole resident female was at the age 4+ with gonads at maturity stage III (June). Diameters of

oocytes of vitellogenesis period (379–725 μm) indicate to a rapid transition of ovaries to the beginning of maturity stage IV. By all evidence, the gonads of this female would not reach maturity up to autumn and it's spawning would be possible only the next year (at reaching age 5+).

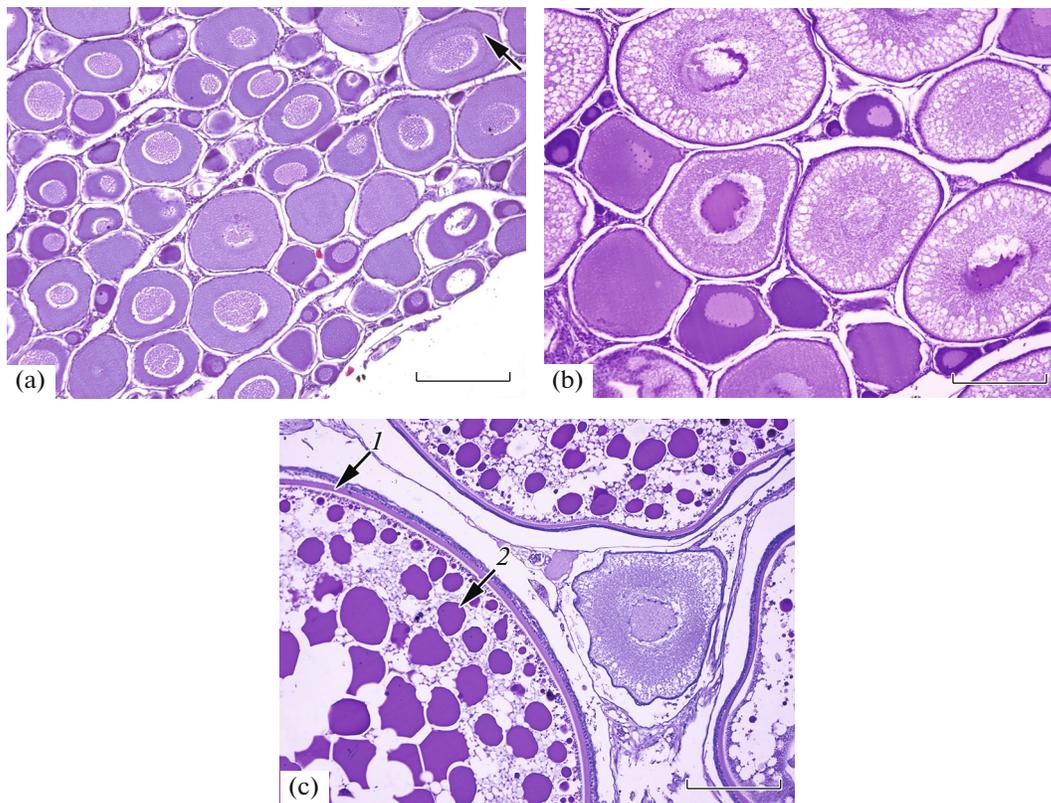


Fig. 6. Ovaries of Dolly Varden *Salvelinus malma* from the Kol River: (a) smolt 2+, previtellogenic oocytes, RNA zone in oocyte cytoplasm (\rightarrow); (b) smolt 4+, beginning of vacuolization of oocyte cytoplasm; (c) anadromous female 5+, accumulation of yolk granules in oocytes; 1—zona radiata; 2—yolk granule. Scale: 300 μm .

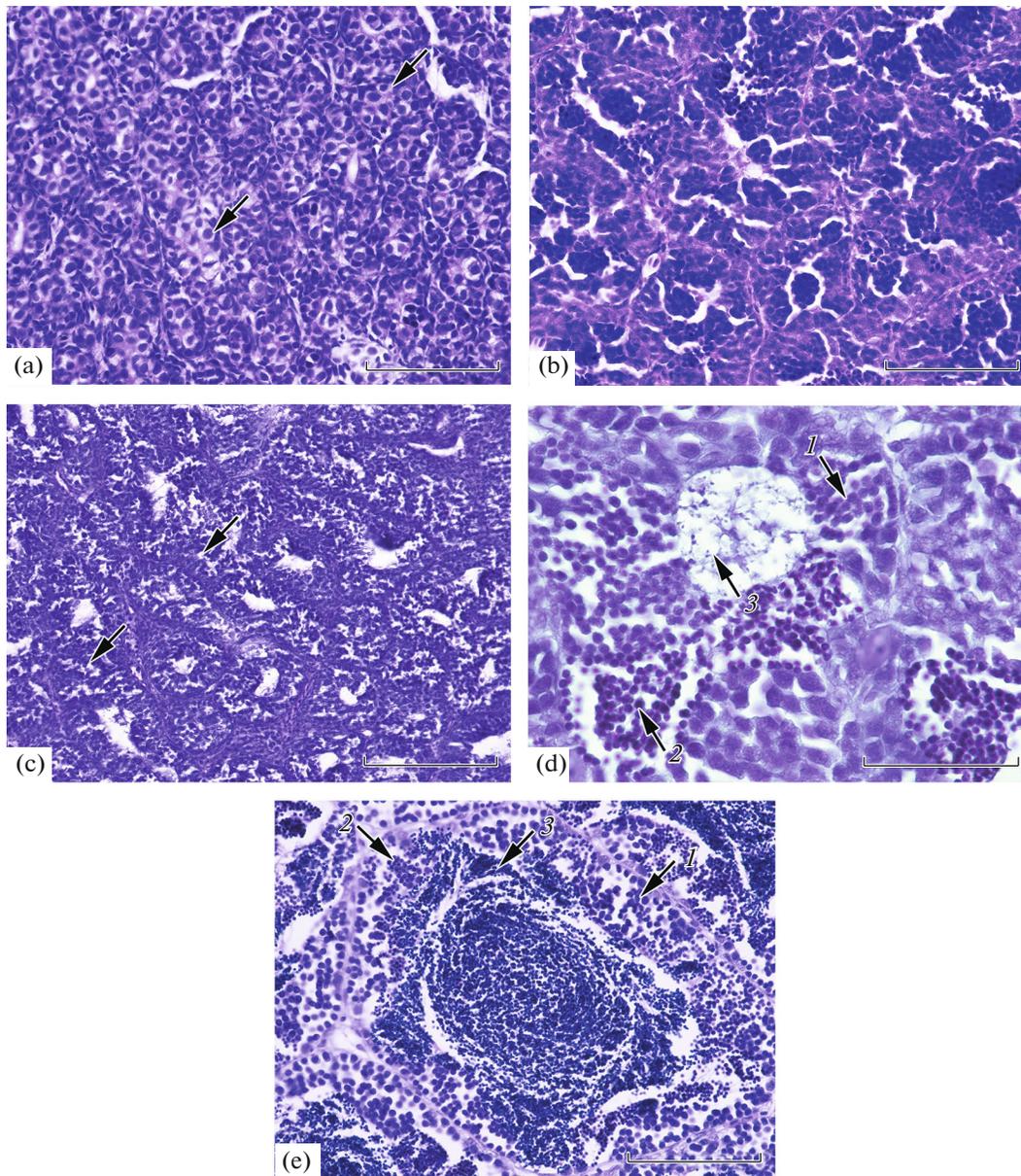


Fig 7. Testes of Dolly Varden *Salvelinus malma* from the Kol River; (a) smolt 3+, maturity stage II, spermatogonia (→); (b) precocious male 3+, stage III; (c) precocious male 4+, early maturity stage III, lumina of seminal canaliculi (→); (d) precocious male 5+, stage IV; (e) resident male 4+, stage V, seminal canalicule; 1—spermocytes; 2—spermatids; 3—spermatozooids. Scale: (a, b, c, d) 100, (e) 50 μm .

Resident males of age classes 3+ and 4+ are captured in September at the spawning period; their testes were at maturity stage V (Fig. 7e) and they were cytologically analogous to gonads of precocious males. In walls of canaliculi with spermatozooids, the sex cells of earlier development stage were seen, up to spermatogonies. This may be understood as generation of sex cells for polycyclic spawning.

State of gonads of migratory fish. All ovaries of thunders at the age 3+ and 4+ in September are at the maturity stage III and contain oocytes of the vitellogenesis period 163–911 μm in diameter. Male

thunders at the age 4+ and 5+ in September have testes at the maturity stage III without noticeable difference in the cytological structure from the gonads of other ecological and cytological groups. Thus, a single brief visit to the sea does not accelerate maturation of anadromous specimens.

The ovaries of anadromous females of age classes 4+, 5+, 6+, and 7+ in June contain vacuolized oocytes of vitellogenesis (stage III) and oocytes with not yet fused large yolk granules (up to 100–200 μm) (stage IV) (Fig. 6c). Diameters oocytes with vacuoles are 574–1277 μm , and those containing yolk granules

are 1129–2426 μm . The membrane of an oocyte with yolk granules consists of the formed zona radiata, a layer of follicle cells, and a two-layer theca.

The testes of mature anadromous males have no noticeable cytological distinctions from gonads of fish of other ecological and age groups. The gonads of anadromous males at maturity stage II are characterized by similar characters of spawning at the previous year, similarly to precocious males, expressed lumina of seminal canaliculi.

DISCUSSION

The local stock of Dolly Varden from the Kol River is a complicated system comprising a wide range of intrapopulation groups and ensuring realization of the life cycle by two major strategies: anadromous or resident. Such significant level of the intraspecies ecological diversity is closely connected to environmental conditions. The Kol River system is characterized by a high level of geomorphological complexity and a high productivity ensured by biogens of marine origin brought by numerous stocks of Pacific salmon of the genus *Oncorhynchus* (Pavlov et al., 2009; Kuzishchin, 2010). It is remarkable that processes of intraspecies differentiation occur in Dolly Varden juveniles, similarly to other salmonid species, in the period of the early freshwater phase of its life cycle (Gross, 1987; Thorpe, 1994; Klemetsen et al., 2003; Pavlov et al., 2009; Gruzdeva et al., 2013).

In the Kol River basin, the freshwater phase of the life cycle of Dolly Varden occurs all over the river basin. However, the leading role in the existing of the population belongs to numerous and relatively small tributaries and floodplain water bodies where density of juveniles is elevated and where the main part of precocious males is concentrated. Diversity of life history strategies in the Dolly Varden population occurs in tributaries where precocious males reach maturity and the juveniles realizing life cycle by anadromous type attain smoltification. For this local population of Dolly Varden, the river mainstream is mainly a transient zone of the aquatic system where catadromous migration is made by smolts, thunders, and by spawners that were spent in the sea, and also where anadromous migration of thunders takes place for feeding to the spawning grounds of Pacific salmon and to anadromous spawners to spawning grounds. At the same time, the mainstream plays a leading role in formation of riverine resident males and females.

In the Kol River basin, formation of diversity of life history strategies in a generation of Dolly Varden is rather long, taking up to 5 years. A generation is differentiated in various ways in males and in females (Fig. 8).

The first act of differentiation in females takes place during the first summer of life (0+). Back calculations of growth by otoliths demonstrated that the most rapidly growing specimens in a generation fur-

ther retain a high growth rate and adopt resident life history pattern (Fig. 8a). Such fish in a population are not numerous: a few such females are noted in spawning grounds among spawners. They attain maturity at the age 5+.

Further differentiation of females is related to their smoltification and migration to the sea. Duration of the freshwater phase of the life cycle varies in different specimens from 2 to 4 years and directly depends on the growth rate. As back calculation of growth by otoliths demonstrated that the most rapidly growing part of a generation is smoltified and migrated to the sea (Fig. 8a). Thus, the number of years while a female stayed in fresh water depend on its attaining a minimum critical body size. This is confirmed by the data on other salmonids (Chernitskii, 1993; Thorpe, 1994; Klemetsen et al., 2003). Thus, slower-growing specimens stay longer in the river.

Histology demonstrated in female smolts at the age 2+ that the state of gonads differs insignificantly from the gonads of parr of various age classes, while the number of specimens with gonads at a later maturity stage (III) is somewhat higher. The part of specimens with ovaries at maturity stage III in smolts at the age 3+ is much higher than in parr of the same age (75 vs. 33%). Thus, in smolts at the age 2+ and 3+, the ovaries are somewhat more developed than in parr of the same age, and all smolts without exception have gonads at stage III up to the age 4+. NCR of previtellogenous oocytes of smolts is somewhat larger than in parr. This, on the contrary, indicates to slower growth of sex cells in smolts. The two centenary conclusions may depend on inhomogeneity of structure of the investigated fish groups: some parr of age 2+ in one year would form a new group of smolts. There is no doubt that the revealed inhomogeneity of structure of the Kol River Dolly Varden, including the state of its gonads, depends, at least partly, on different environmental conditions. Unfavorable conditions may render a considerable influence on gametogenesis rate in fish. Thus, inadequate food resources at the background of infestation with helminthes may lead to missing of spawning in Arctic charr *Salvelinus alpinus* with significant anomalies of structure of gonads (Selyukov et al., 2012). In morphology of sex cells and glands of Dolly Varden, we also did not find considerable anomalies, i.e., negative influence of environmental conditions was expressed just as a small retardation of the growth rate of oogenesis.

A considerable variability of size of previtellogenic oocytes observed in gonads of thunders (4+) may depend on the fact that a part of early oocytes (smallest cells) do not manage to get ripened in due time, which decreases the final fecundity. It seems that the gametogenesis is influenced by temporary transition of fish to seawater. It is known that morphological and physiological changes in osmoregulation require considerable expenditures of energy (Jonsson B. and Jons-

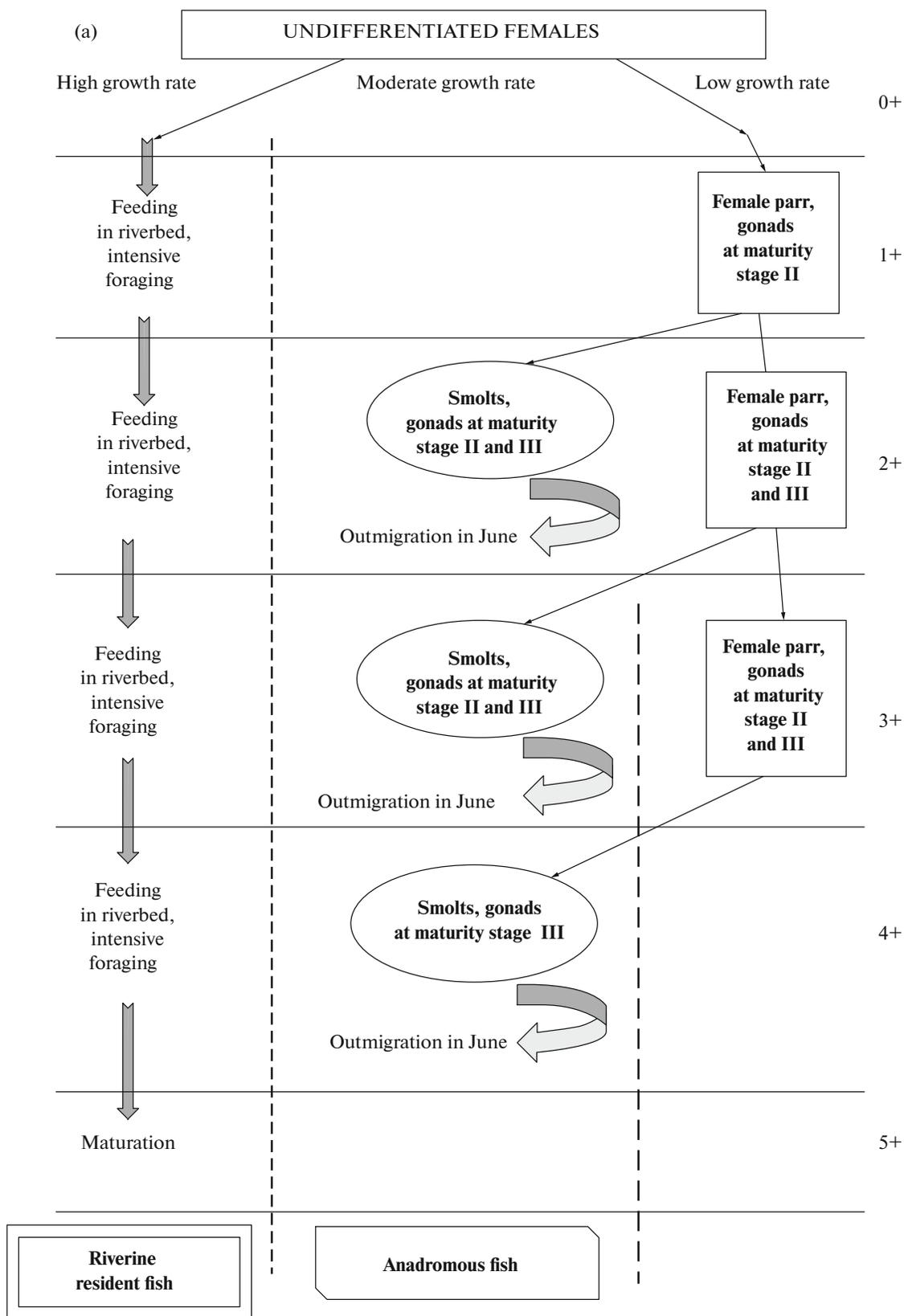


Fig. 8. Scheme of differentiation of a generation of (a) females and of (b) males in the Kol River.

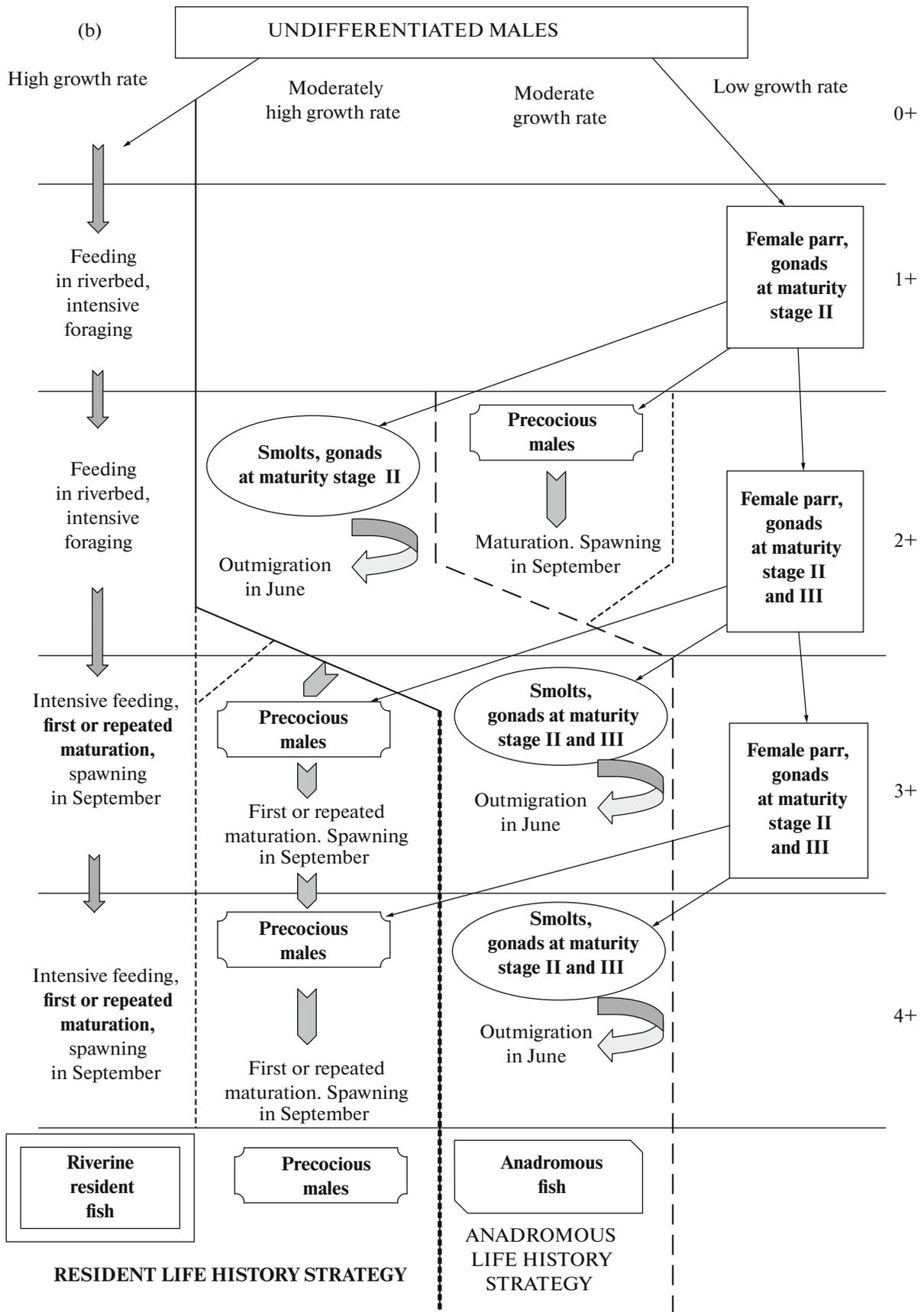


Fig. 8. (Contd.).

son N., 2011) therefore energy deficiency leads to decrease of sex cell able to attain maturity. This is confirmed by the fact that, on average, the oocytes of the vacuolization phase are noticeably larger ($p < 0.001$) than in parr, smolts, and residents of the same age.

In contrast to females, the life cycle of males in a generation is variable and is invariant during the first 4 years of the freshwater phase during which differentiation in the generations into different life strategies occurs (Fig. 8b). Similarly to resident females, formation of males with different life history strategy takes place in the first summer of life (0+): they become resident at a high growth rate. Resident males attain maturity at the age 3+. Further, at the age 1+–4+ among parr, there are processes of formation of smolts of different age and of precocious males, but large resident males are not formed any more. At the second year of life (1+) in the generation, the male parr may be discerned with moderate somatic growth. In such fish, the smoltification process starts at retarded maturation. In the next year (2+), such fish get smoltified and migrate to the sea. Further on, their life cycle is confined to an anadromous life strategy. At the same time, no one case of maturation of precocious males is recorded at the age 1+.

In the third year of life (2+), already in the beginning of summer, three individual groups may be seen in males: (1) undifferentiated parr with a low growth rate and gonads at early developmental stages; (2) specimens with moderate growth rate and gonads at early developmental stages (process of smoltification starts in this group, they migrate to the sea the next year); (3) the fish with moderate but lower growth rate than in the second group (up to the autumn, they attain maturity and become precocious males).

Further differentiation of the male generation occurs also by the dichotomic principle. However, the specimens smoltifying at the age 3+ and 4+ grow slower than the precocious males attaining maturity at the age 3+ and 4+.

Histologically, testes are at maturity stage II in an absolute majority of parr and in all smolts at the age 2+. In smolts of the age 3+, the part of gonads at maturity age III is considerably lower than in parr of the same age. Thus, the rate of spermatogenesis in parr is higher than in smolts. The obtained results agree with previous studies on *Salmo trutta labrax* (Pavlov et al., 2014) indicating that spermatogenesis in a resident form is more intensive than in a migratory one, and oogenesis, on the contrary, is slower. Smoltification is a process involving energy expenses, and it may suppress and maturation of sex cells. In addition to smoltification, the second fundamental factor is the rate of somatic growth. It is known (Gritsenko, 2002; Savvaitova et al., 2004; Pichugin et al., 2008) that stream groups of Southern Malma from Sakhalin and the Kurils are characterized by a simple age structure, brief life, early inhibition of somatic growth, and by

accelerated maturation. Thus, the growth rate of males whose ontogenesis would follow the anadromous life history strategy is in the reverse correlation with development of gonads.

More rapidly growing part of the parr generation of the fourth (3+) and fifth (4+) years of life are transformed into precocious males. Their sexual maturation proceeds in summer identically, irrespective of their age. Resident males, as well as precocious males, may reproduce several times in the course of life, probably every year.

With consideration of the obtained data, we may conclude that the formation of the anadromous part of the male generation of Dolly Varden proceeds differently: at an early age (2+ and 3+), the specimens with moderate rate of somatic growth become anadromous, while those with a low rate of somatic growth become anadromous at later age, as was noted for other salmonids (Gross, 1991, 1996; Thorpe, 1994). It is remarkable that, in the case of males in fresh water, their further life cycle becomes strictly channelized towards a resident life history strategy (resident specimens and precocious males). The precocious males in the generation always formed of the fish whose weight growth prevails of linear growth. Thus, for formation of smolts, the foremost significance has redistribution of resources of the organism for somatic growth (accumulation of resources of the organism blocking sex maturation). Formation of precocious males needs combination of moderate growth and fat accumulation.

Diversity in life history strategies in the population of Kol River Dolly Varden depends on the cumulative effect of complicated and closely interrelated processes of growth, accumulation of stock substances, and sexual maturation. Foraging success of juvenile fish—growth, maturation, or smoltification—are controlled to a considerable degree by abundance and dynamic of food resources in the habitats. Precocious males and river resident specimens feed on various allochthonous and autochthonous invertebrates. It should be noted that, in tributaries and in the floodplain waterbodies, the food resources are variable during the season but are always abundant, and satiation of fish is always high (Kuzishchin et al., 2015). A great impact on the growth of Dolly Varden of different groupings during foraging season is rendered by Pacific salmon, since a considerable part of juveniles in autumn, especially in tributaries, feed on eggs *Oncorhynchus gorbuscha*, *O. keta*, and *O. kisutch* as well as insect larvae which destruct their dead bodies. A high growth rate of the resident specimens in the river channel depends on its predatory life, when they consume salmonid outmigrants.

Thus, the traits of ontogenesis in the local Dolly Varden population gave reason to believe that the ratio of fish with different type of life history strategy in a generation is a fluctuating characteristic that depend-

ing on a complex of environmental factors and density of juveniles in biotopes. Previously, similar relationships were found in other fish species (Gross et al., 1998). This is the reason why the ratio of migratory spawners and precocious males on the spawning grounds changes from year to year. In addition, the ratio of age of precocious males also varies. In rainy years on spawning ground, the number of precocious males is somewhat higher, probably due to better growth in tributaries receiving more terrestrial insects (Kuzishchin et al., 2015). We also noted that abundance of riverine resident specimens increases in the river mainchannel in the years of high abundance of pink salmon *O. gorbuscha* and, especially, of chum salmon *O. keta* (2002–2004, 2006).

At present, the intrapopulation structure of the Kol River Dolly Varden is drastically shifted towards the migratory component, the principal reproduction occurring by the anadromous females. The role of resident females in the population is extremely small due to their low abundance. In spite of their high abundance, the role of precocious males in the reproduction of the population seems to be rather a reserve one, since the probability of their active participation in spawning in the presence of larger males is low.

Significance of the role of riverine resident specimens and precocious males for existence of the population should not be underestimated. The precocious males occur widely in the Asian part of the Dolly Varden range (Tiller, 2007). Resident females are found in some rivers of Kamchatka and the Kuril Islands (Gritsenko et al., 2012; Pichugin, 2015). Thus, the existence of a significant resident component is a typical event for the species. According to many authors, ripe specimens that manage without travel to the sea make the populational reserve ensuring the survival of the species in dramatic change of the environment and in suboptimum conditions (Reist, 1989; Quinn and Adams, 1996; Hendry and Stearns, 2004; Quinn, 2005). It is known that, in the case of physical obstacles preventing migration of juvenile fish to the sea, the capacity of Dolly Varden to get maturity in fresh waters results in the formation of bisexual self-reproducing isolated populations. Such examples are described for Kamchatka (Esin, 2015).

The revealed diversity of life history strategy in Dolly Varden and of patterns of its formation reflect the ability of the species to form in each generation the groups adequate to impact the environment creating “excess of functional possibilities of a species” sensu Severtsov (2008). Such superfluousness provides a flexible fitting of Dolly Varden populations to oscillating life conditions in boreal water bodies, thus working to conserve the ecological niche of the species and supporting its stable existence in space and time.

CONCLUSIONS

Formation of diversity of life history strategies of the Kol River Dolly Varden is a result of epigenetic processes of growth and gametogenesis in the individual ontogenesis. The observed variation in the population is individual and the population structure is dynamic and results from complex interaction of fish with their environment. For Dolly Varden, the following patterns of individual development are elucidated: both in females and in males, the resident life history strategy is determined in the first summer of life. This type of life history strategy is characteristic of the rapidly growing specimens. Formation of anadromous life history strategy in early age is characteristic of specimens with a moderate rate of somatic growth, while it is characteristic of those with a low rate of somatic growth at a later age. Males realize ontogenesis by alternative life strategies during the first 4 years. The life cycle of females from the second summer is channelized towards the anadromous life history strategy. The sex maturation in fresh water predetermines the life cycle of males and females only by the resident type. The type of life strategy of traits of its formation depends on individual growth and gonad development under influence of the environment. All spawners of Dolly Varden are characterized by interoparity: irrespective to confinement to different life history strategy type, reproduction occurs several times during life.

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REFERENCES

- 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.
- Bohlin, T.L., Pettersson, J., and Deregman, E., Population density of migratory and resident brown trout (*Salmo trutta*) in relation to altitude: evidence for a migration cost, *J. Anim. Ecol.*, 2001, vol. 70, pp. 683–692.
- 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, MD: Am. Fish. Soc. 1990, vol. 1, pp. 363–387.
- Chernitskii, A.G., Migration and living in marine water of juveniles of genus *Salmo* in natural and artificial reproduction, *Extended Abstract of Doctoral (Biol.) Dissertation*, Moscow: VNIRO, 1993.
- Chmylevskii, D.A., On periods of oogenesis of Teleostei (a review), *J. Ichthyol.*, 2003, vol. 43, no. 4, p. 296.

- Debat, V. and David, P., Mapping phenotypes: canalization, plasticity and developmental stability, *Trends Ecol. Evol.*, 2001, vol. 16, pp. 555–561.
- Elliott, J.M., *Quantitative Ecology and the Brown Trout*, Oxford: Oxford Univ. Press, 1994.
- Esin, E.V., Stream resident Dolly Varden *Salvelinus malma* of Kamchatka Peninsula, *J. Ichthyol.*, 2015, vol. 55, no. 2, pp. 224–239.
- Gritsenko, O.F., *Prokhnodnye ryby ostrova Sakhalin (sistematika, ekologiya, promysel)* (Anadromous Fishes of Sakhalin Island: Systematic, Ecology, and Fishery), Moscow: VNIRO, 2002.
- Gritsenko, O.F., Savvaitova, K.A., Pichugin, M.Yu., et al., *Ryby Kuril'skikh ostrovov* (Fishes of the Kuril Islands), Moscow: VNIRO, 2012.
- Gross, M.R., Evolution of diadromy in fishes, *Am. Fish. Soc. Symp.*, 1987, vol. 1, pp. 14–25.
- Gross, M.R., Salmon breeding behavior and the life history evolution in changing environments, *Ecology*, 1991, vol. 72, pp. 1180–1186.
- Gross, M.R., Alternative reproductive strategies and tactics: diversity within sexes, *Trends Ecol. Evol.*, 1996, vol. 11, pp. 92–98.
- Gross, M.R., Coleman, R.M., and McDowell, R.M., Aquatic productivity and the evolution of diadromous fish migration, *Science*, 1998, vol. 239, pp. 1291–1293.
- Gruzdeva, M.A., Kuzishchin, K.V., and Malyutina, A.M., Species composition and distribution of salmon juveniles and fish-like species in longitude continuum of the main channel of Kol' river (Western Kamchatka), *Mater. XII mezhdunarodnoi nauchnoi konferentsii "Sokhranenie bioraznoobraziya Kamchatki i prilegayushchikh morei," Tezisy dokladov* (Proc. XII Int. Sci. Conf. "Conservation of Biological Diversity of Kamchatka and Adjacent Seas," Abstracts of Papers), Petropavlovsk-Kamchatskii: Kamchatpress, 2011a, pp. 215–218.
- Gruzdeva, M.A., Kuzishchin, K.V., and Malyutina, A.M., Role of side system of salmon river as the fattening space for salmon juveniles, *Mater. XII mezhdunarodnoi nauchnoi konferentsii "Sokhranenie bioraznoobraziya Kamchatki i prilegayushchikh morei," Tezisy dokladov* (Proc. XII Int. Sci. Conf. "Conservation of Biological Diversity of Kamchatka and Adjacent Seas," Abstracts of Papers), Petropavlovsk-Kamchatskii: Kamchatpress, 2011b, pp. 94–97.
- Gruzdeva, M.A., Malyutina, A.M., Kuzishchin, K.V., Belova, N.V., P'yanova, S.V., and Pavlov, D.S., 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, *J. Ichthyol.*, 2013, vol. 53, no. 8, pp. 585–599.
- Gruzdeva, M.A., Kuzishchin, K.V., and Malyutina, A.M., Specific distribution of salmon juveniles in the mosaic river habitats during the summer fattening: the dynamics of group, *Mater. XV mezhdunarodnoi nauchnoi konferentsii "Sokhranenie bioraznoobraziya Kamchatki i prilegayushchikh morei," Tezisy dokladov* (Proc. XV Int. Sci. Conf. "Conservation of Biological Diversity of Kamchatka and Adjacent Seas," Abstracts of Papers), Petropavlovsk-Kamchatskii: Kamchatpress, 2014a, pp. 259–263.
- Gruzdeva, M.A., Kuzishchin, K.V., and Malyutina, A.M., Preferred sites for the salmon juveniles in the channel of Kol' River (Western Kamchatka), *Mater. XV mezhdunarodnoi nauchnoi konferentsii "Sokhranenie bioraznoobraziya Kamchatki i prilegayushchikh morei," Tezisy dokladov* (Proc. XV Int. Sci. Conf. "Conservation of Biological Diversity of Kamchatka and Adjacent Seas," Abstracts of Papers), Petropavlovsk-Kamchatskii: Kamchatpress, 2014b, pp. 255–258.
- Gruzdeva, M.A., Bush, A.G., Kuzishchin, K.V., et al., The life strategy of Dolly Varden trout population of Kol' River (Western Kamchatka), *Mater. XVI mezhdunarodnoi nauchnoi konferentsii "Sokhranenie bioraznoobraziya Kamchatki i prilegayushchikh morei," Tezisy dokladov* (Proc. XVI Int. Sci. Conf. "Conservation of Biological Diversity of Kamchatka and Adjacent Seas," Abstracts of Papers), Petropavlovsk-Kamchatskii: Kamchatpress, 2015, pp. 281–285.
- Hendry, A.P. and Stearns, S.C., *Evolution Illuminated: Salmon and Their Relatives*, Oxford: Oxford Univ. Press, 2004.
- Hutchings, J.A., Norms of reaction and phenotypic plasticity in salmonid life histories, in *Evolution Illuminated: Salmon and Their Relatives*, Oxford: Oxford Univ. Press, 2004, pp. 154–174.
- Hutchings, J.A. and Jones, M.E., Life history variation and growth rate thresholds for maturity in Atlantic salmon, *Salmo salar*, *Can. J. Fish. Aquat. Sci.*, 1998, vol. 55, no. 1, pp. 22–47.
- James, F.C. and McCulluch, C.E., Multivariate analysis in ecology and systematic: panacea or Pandora's box? *Ann. Rev. Ecol. Syst.*, 1990, vol. 21, pp. 129–166.
- Jonsson, B. and Jonsson, N., *Ecology of Atlantic Salmon and Brown Trout*, Dordrecht: Springer-Verlag, 2011.
- Kalish, J.M., Use of otolith microchemistry to distinguish the progeny of sympatric anadromous and non-anadromous salmonids, *Fish Bull U.S.*, 1990, vol. 88, no. 4, pp. 657–666.
- Klemetsen, A., Amundsen, P.-A., Dempson, J. B., et al., Atlantic salmon *Salmo salar* L., brown trout *Salmo trutta* L. and arctic charr *Salvelinus alpinus* L., a review of aspects of their life histories, *Ecol. Freshwater Fish.*, 2003, vol. 1, no. 2, pp. 1–59.
- Kouřil, J., Mikodina, E., Mikulin, A., et al., Different sensitivity between adult salmonids fish species and grayling to an anesthetic clove oil, *Proc. Int. Conf. "Aquaculture Europe 2009," Abstracts of Papers*, Trondheim, 2009.
- Kuzishchin, K.V., Development and adaptive role of intraspecific ecological diversity of salmon fishes (family Salmonidae), *Extended Abstract of Doctoral (Biol.) Dissertation*, Moscow: Moscow State Univ., 2010.
- Kuzishchin, K.V., Gruzdeva, M.A., Savvaitova, K.A., Pavlov, D.S., and Stanford, J.A., Seasonal races of chum salmon *Oncorhynchus keta* and their interrelations in Kamchatka Rivers, *J. Ichthyol.*, 2010, vol. 50, no. 2, pp. 159–173.
- Kuzishchin, K.V., Malyutina, A.M., and Gruzdeva, M.A., Seasonal dynamics of feeding and food relationships of juveniles of Salmonidae in the basin of the Kol River (Western Kamchatka), *J. Ichthyol.*, 2015, vol. 55, no. 3, pp. 323–350.
- Lakin, G.F., *Biometriya* (Biometry), Moscow: Vysshaya Shkola, 1990.
- Makeeva, A.P., *Embriologiya ryb* (Fish Embryology), Moscow: Mosk. Gos. Univ., 1992.
- Mikodina, E.V., Sedova, M.A., P'yanova, S.V., et al., *Rukovodstvo po primeneniyu anestetika "gvozdičnoe maslo"*

- v *akvakul'ture* (Manual for Implementation of Anesthetic Clove Oil in Aquaculture), Moscow: VNIRO, 2011.
- Mina, M.V., *Mikroevolyutsiya ryb* (Microevolution of Fishes), Moscow: Nauka, 1986.
- Murza, I.G. and Khristoforov, O.L., *Opređenje stepeni zrelosti gonad i prognoziranje vozrasta dostizheniya polovoi zrelosti u atlanticheskogo lososya i kumzhi* (Determination of Gonad Maturity and Forecasting of the Puberty Age of Atlantic Salmons and Brown Trout), Leningrad: Gos. Nauchno-Issled. Inst. Rechn. Ozern. Rybn. Khoz., 1991.
- Myers, R.A., Hutchings, J.A., and Gibson, R.J., Variation in male parr maturation within and among populations of Atlantic salmon, *Salmo salar*, *Can. J. Fish. Aquat. Sci.*, 1986, vol. 43, pp. 1242–1248.
- Pavlov, D.S. and Savvaitova, K.A., On the problem of ratio of anadromy and residence in salmonids (Salmonidae), *J. Ichthyol.*, 2008, vol. 48, no. 9, pp. 778–791.
- Pavlov, D.S. and Skorobogatov, M.A., *Migratsii ryb v zaregulirovannykh rekakh* (Fish Migrations in the Regulated Rivers), Moscow: KMK, 2014.
- Pavlov, D.S., Savvaitova, K.A., Kuzishchin, K.V., et al., *Sostoyanie i monitoring bioraznoobraziya lososevykh ryb i sredy ikh obitaniya na Kamchatke (na primere territorii zakaniznika "Reka Kol")* (Status and Monitoring of Biological Diversity of Salmon Fishes and Their Habitats in Kamchatka by Example of Reka Kol' Nursery), Moscow: KMK, 2009.
- Pavlov, D.S., Kuzishchin, K.V., Gruzdeva, M.A., Polyakov, M.P., and Pelgunova, L.A., Life history strategy diversity in the Kamchatka Dolly Varden char *Salvelinus malma* (Walbaum) (Salmonidae, Salmoniformes): ontogenetic reconstructions based on the data of X-ray fluorescence analysis of the microchemistry of recording structures, *Dokl. Biol. Sci.*, 2013, vol. 450, no. 1, pp. 142–145.
- Pavlov, D.S., Pavlov, E.D., Ganzha, E.V., Kostin, V.V., and Ponomareva, V.Y., Cytological status of the gonads and the level of thyroid and sex hormones in juvenile Black Sea trout, *Salmo trutta labrax*, of two phenotypic forms, *J. Ichthyol.*, 2014, vol. 54, no. 7, pp. 476–484.
- Pavlov, D.S., Samoilov, K.Yu., Kuzishchin, K.V., Gruzdeva, M.A., and Pelgunova, L.A., Diversity of life strategies of pikepech *Sander lucioperca* (L.) in the Lower Volga (by the data of microelement composition of otolithes), *Inland Water Biol.*, 2016, vol. 9, no. 4, pp. 382–389.
- Persov, G.M., *Differentsirovka pola u ryb* (Gender Differentiation in Fishes), Leningrad: Leningr. Gos. Univ., 1975.
- Pichugin, M.Yu., Peculiarities of growth and skeletal system development of prelarvae, larvae, and fingerlings of Dolly Varden trout *Salvelinus malma malma* inhabiting the rivers of Western Kamchatka in regard to the temperature regime of the spawning grounds, *J. Ichthyol.*, 2015, vol. 55, no. 4, pp. 549–566.
- Pichugin, M.Yu., Osinov, A.G., and Gritsenko, O.F., On morphological diversity of southern Dolly Varden trout *Salvelinus malma* Krascheninnikovi from water bodies of Sakhalin, *J. Ichthyol.*, 2008, vol. 48, no. 5, pp. 367–390.
- Pravdin, I.F., *Rukovodstvo po izucheniyu ryb* (Manual for Fish Analysis), Moscow: Pishchepromizdat, 1966.
- Quinn, T.P., *The Behavior and Ecology of Pacific Salmon and Trout*, Washington: Univ. Wash. Press, 2005.
- Quinn, T.P. and Adams, D.J., Environmental changes affecting the migratory timing of American shad and sockeye salmon, *Ecology*, 1996, vol. 77, pp. 1151–1162.
- Radtke, R.L., Dempson, J.B., and Ruzicka, J., Microprobe analyses of anadromous Arctic charr, *Salvelinus alpinus*, otoliths to infer life history migration events, *Polar Biol.*, 1997, vol. 19, no. 1, pp. 1–8.
- Reist, J.D., Genetic structuring of allopatric populations and sympatric life history types of charr, *Salvelinus alpinus/malma* in the western Arctic, Canada, *Physiol. Ecol. Jap. Spec.*, 1989, vol. 1, pp. 405–420.
- Rohlf, J.F., *BNSYS-pc Numerical Taxonomy and Multivariate Analysis System*, New York: Exeter Software Press, 1993.
- Romeis, B., *Mikroskopische Technik*, Munich: Oldenbourg Verlag, 1968.
- Sakun, O.F. and Butskaya, N.A., *Opređenje stadii zrelosti i izuchenie polovykh tsiklov ryb* (Determination of Maturity Degree and Analysis of Sexual Cycles of Fishes), Murmansk: Glavrybvod, 1968.
- Savvaitova, K.A., *Arkticheskie gol'tsy (struktura populyatsionnykh sistem, perspektivy khozyaistvennogo ispol'zovaniya)* (Arctic Chars: Structure of Population Systems and Prospective Economic Use), Moscow: Agropromizdat, 1989.
- Savvaitova, K.A., Gruzdeva, M.A., Kuzishchin, K.V., et al., The creek chars of genus *Salvelinus* in northern Kuril Islands, *Vopr. Ichthyol.*, 2004, vol. 44, no. 1, pp. 89–101.
- Selyukov, A.G., Shuman, L.A., and Nekrasov, I.S., Status of gonads of Salmon fishes in subarctic lakes of Yamal and Gydan, *Vestn. Tyumen. Gos. Univ.*, 2012, no. 6, pp. 31–40.
- Sevrtsov, A.S., *Evolutsionnyi stazis i mikroevolyutsiya* (Evolutionary Stasis and Microevolution), Moscow: KMK, 2008.
- Thorpe, J.E., Smolting versus residency developmental conflicts in salmonids, *Am. Fish. Soc. Symp.*, 1987, vol. 1, pp. 244–252.
- Thorpe, J.E., Reproductive strategies in Atlantic salmon *Salmo salar* L., *Aquacult. Res.*, 1994, vol. 25, no. 1, pp. 77–87.
- Thorpe, J.E., Mangel, M., Metcalf, N.B., and Huntingford, F.A., Modeling the proximate basis of salmonid life-history variation, with application to Atlantic salmon, *Salmo salar* L., *Evol. Ecol.*, 1998, vol. 12, pp. 581–599.
- Tiller, I.V., Anadromous Dolly Varden trout (*Salvelinus malma*) of Kamchatka, *Issled. Vodn. Biol. Resur. Kamchat. Sev.-Zap. Chasti Tikh. Okeana*, 2007, no. 9, pp. 79–95.
- Zimmerman, C.E., Kuzishchin, K.V., Gruzdeva, M.A., Pavlov, D.S., Stanford, J.A., and Savvaitova, K.A., Experimental determination of the life history strategy of the Kamchatka mykizha *Parasalmo mykiss* (Walb.) (Salmonidae, Salmoniformes) on the basis of analysis of the Sr/Ca ratio in otoliths, *Dokl. Biol. Sci.*, 2003, vol. 389, nos. 1–6, pp. 138–143.
- 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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