ISSN 1067-4136, Russian Journal of Ecology, 2016, Vol. 47, No. 2, pp. 167–178. © Pleiades Publishing, Ltd., 2016.
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Trophic Factor during the Transition of Peled (*Coregonus peled* Gmelin) Larvae to Active Feeding in Their Native Range

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Received October 9, 2015

Abstract—With regard to published data on the ecology of early peled larvae acclimated in lakes or reared under experimental or fish farm conditions, interannual variability of feeding and environmental conditions during the transition to exogenous feeding has been demonstrated for peled larvae in a control water body located in the floodplain of the main spawning tributary of the lower Ob River. The conditions that govern exogenous food consumption by early peled larvae and largely determine the fate of a given generation depend on both biotic (the concentration of food organisms) and abiotic factors (wind regime). The trophic optimum during the transition of larvae to exogenous feeding, which ensures the level of gut filling sufficient for their survival and growth in the control water body, is determined by a complex of natural events. The results of this study may be extrapolated to the entire native range of the Ob River peled population and used for planning the release of peled larvae into natural water bodies of Western Siberia to compensate for losses to their biological resources.

Keywords: early peled larvae, endogenous, mixed, and exogenous feeding, trophic factor, biotic and abiotic conditions, survival rate, floodplain water body, the Severnaya Sosva River (a tributary of the lower Ob)

DOI: 10.1134/S1067413616020041

Knowledge of ecological aspects of early fish ontogeny is necessary for improving the efficiency of controlled fish reproduction. In case of coregonid fishes, extensive data are available on the embryonic and larval development, growth, and variation of juveniles acclimated in lakes or reared under experimental or fish farm conditions, but their early ontogeny in natural water bodies (especially river ecosystems) have not been studied sufficiently, although information on the life of the larvae in their natural environment is necessary for optimizing fish culture regimes.

The purpose of this study was to estimate the optimum of trophic factor for the larvae of peled (*Coregonus peled* Gmelin) from the Ob River population during their transition to active feeding in a natural water body within their native range. The term "trophic factor" refers here to a set of conditions that are indispensable for the search, capture, and digestion of food organisms. Success in this transition may depend mainly on biotic (food supply and endogenous energy resources) or abiotic conditions (the temperature, water-level, wind, illumination, and gas regimes of the water body).

The peled is the most abundant commercial species among coregonids inhabiting the Ob River and the preferred species for coregonid fish farming. The reason for our choice of the study site—a floodplain lagoon lake (locally named as sor) on the Severnaya Sosva River, a right-hand tributary of the Ob—is that the lower reaches of the Ob are the zone of ecological optimum for the peled within its vast native range (Reshetnikov, 1983), with the Severnaya Sosva being the main spawning river for this species (Bogdanov, 1997).

On the basis of data on the ontogeny of coregonid species from the Ob (Bogdanov, 1998), we adhere to the concept of those researchers who consider that the larval period of development starts at the moment of hatching (Balon, 1975; Lebedeva, 1976; Kamler, 2002).

MATERIAL AND METHODS

Studies were performed in Pol'khostur Sor, a temporary lagoon lake in the right-bank floodplain of the Severnaya Sosva, 195 km from its mouth. The lake is shallow (no deeper than 4 m), with a low flow rate, and its surface area in high-water years reaches 24 km^2. Peled larvae were sampled from three water areas (Fig. 1) from 8 to 11 a.m. using a drag net of nylon gauze nos. 11 and 21. In parallel, samples of zooplankton were taken at the same sites by passing 100 L of

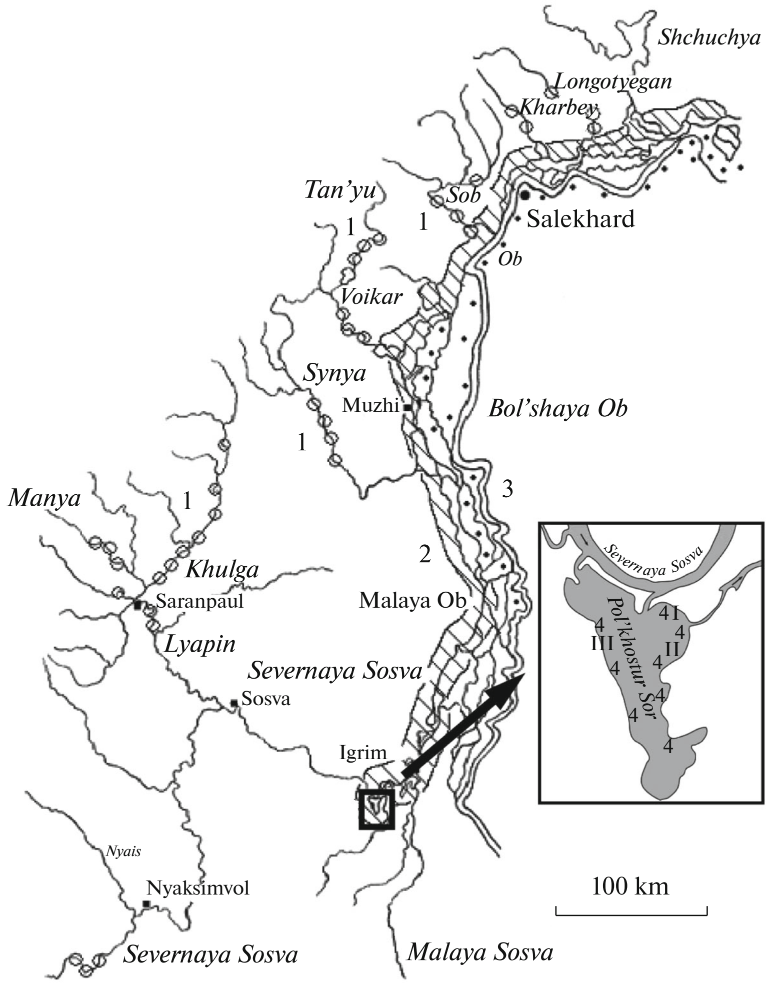

Fig. 1. Schematic map of feeding areas for early fish larvae in the lower Ob floodplain and Pol'khostur Sor: (1) coregonid spawning grounds, (2) feeding areas for coregonid larvae with high ecological density, (3) sites of single catches of feeding coregonid larvae, (4) ichthyological and hydrobiological stations; (I–III) water areas differing in food supply to fish larvae.

water through a quantitative plankton net with mesh no. 77 (1982, 1985–1999). This was done to characterize food supply to the larvae, i.e., the part of total food resources of the water body that is consumed by a given fish species at a certain stage of ontogeny. The material on the feeding of larvae and their food supply was processed and analyzed by conventional methods (*Metodicheskoe posobie*..., 1974; *Metodicheskie rekomendatsii*..., 1982). The food spectrum of the larvae was characterized using the index or relative significance (*IR*) (Popova and Reshetnikov, 2011).

Statistical analysis of test parameters involved the calculation of arithmetic means (*M*), their errors (*m*), and variation coefficients (*CV*). The effects of relevant factors on the level of gut filling, the amount of endogenous resources, and the survival or larval generations were evaluated by means of correlation analysis in the Statistica v. 10.0 program package (StatSoft, Inc., 2012)

Species identification of the larvae was based on the descriptions given by Bogdanov (1998). A total of 625 peled larvae were examined for the presence of yolk, fat drop, and food bolus in the gut (1985–1990, 1992–1999), and 238 larvae, for the composition of food organisms in the bolus (1985–1989). The body length of the larvae (from the snout tip to the end of the notochord) varied from 8.1 to 9.2 mm; body weight, from 2.5 to 3.6 mg. They were at one of the three developmental stages characterized by endogenous, mixed, or exogenous feeding (Volkova, 1965; Bogdanov, 1998). We classified them as early larvae. The material presented below concerns the larvae in the period of their mass entry from the river to Pol'khostur Sor, since it is these larvae that determine the fate of the generation.

RESULTS

The drift of peled larvae from spawning grounds down the Severnaya Sosva continues for 10 to 35 days (in most years, 16–17 days), and their entry to

Table 1. Proportions of early peled larvae at different stages of development at the time of approaching the near-shore waters of Pol'khostur Sor, %

Year	Stages of development			
	Endogenous feeding	Mixed feeding	Exogenous feeding	
			feeding individuals	nonfeeding individuals (risk group)
1985	0	15.2	74.8	10.0
1986	5.8	0	83.0	11.2
1987	1.6	3.2	82.5	12.7
1988	9.5	1.2	71.4	17.9
1989	4.4	0	36.8	58.8
1990	0	0	37.5	62.5
1992	0	0	90.0	10.0
1993	0	0	75.0	25.0
1994	0	5.0	80.0	15.0
1996	41.7	8.3	12.5	37.5
1997	0	0	81.2	18.8

Pol'khostur Sor takes place throughout this period. The earliest entry was recorded on May 8 (in 1995), and the latest, on June 11 (in 1985 and 1999). The bulk of the larvae enter the sor within a short time interval (1–2 or less frequently, 3–4 days) on different calendar and phenological dates, depending on the year. Some larvae are then carried away by the current and drift farther downstream, while others are dispersed over the sor by water flow or wind and come to near-shore shoals, where they move actively and, under a certain combination of abiotic and biotic conditions, undergo the transition to exogenous feeding. Such larvae either contain the remains of the yolk sac (0.10 to 0.60 mm long and 0.09 to 0.55 mm high), or the yolk has already been completely resorbed. Over the long observation period, the proportion of peled larvae with an endogenous food reserve among those arriving to the shoals averaged only 14.7%. The absence of the yolk sac in all the larvae was recorded in 33.3% of the study years; its retention in no less than half of the larvae, in 26.7%; in other years, only a few larvae still contained the yolk sac (Table 1). The difference between the proportions of larvae with the yolk sac during their entry to the sor and upon their arrival to feeding areas in the shoals varied between years ($CV = 46\%$) (Fig. 2).

In different years, early peled larvae containing different combinations of endogenous and exogenous food could be found in Pol'khostur Sor. As a rule (in 10 out of 11 years), the larvae at the stages of endogenous and mixed feeding were scarce (Table 1). Among the larvae with resorbed yolk sacs, individuals with exogenous food in the gut dominated in 8 out of

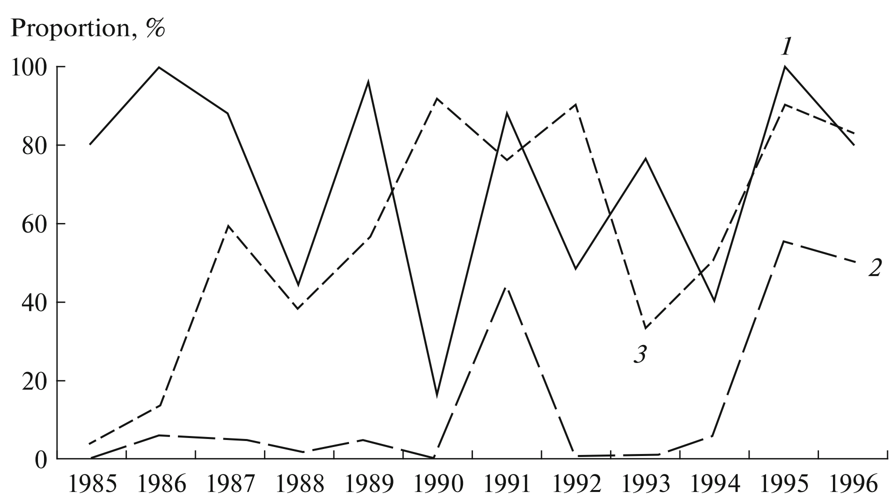

Fig. 2. Proportions of peled larvae with yolk and fat drop in Pol'khostur Sor: (*1*) proportion of larvae with yolk during entry to the sor, (*2*) proportion of larvae with yolk in near-shore shoals, (*3*) proportion of larvae with fat drop in near-shore shoals.

Table 2. Gut filling in feeding peled larvae upon transition to exogenous feeding in Pol'khostur Sor in different years

Year	Number of larvae	Number of prey per larva			Index of gut filling, ‱		
		$M \pm m$	Min–max	CV, %	$M \pm m$	Min–max	CV, %
1985	16	1.81 ± 0.20	1–3	46	15.49 ± 4.68	0.12–57.67	120
1986	33	4.48 ± 0.70	1–18	89	52.46 ± 11.40	9.60–80.00	124
1987	13	2.15 ± 0.53	1–8	88	36.32 ± 16.82	5.38–230.77	167
1988	18	2.78 ± 0.38	1–6	59	90.20 ± 36.66	3.00–372.09	172
1989	15	1.66 ± 0.23	1–4	54	7.52 ± 2.23	0.10–11.22	115

Table 3. Gut filling in peled larval generations upon transition to exogenous feeding in Pol'khostur Sor

Year	Number of larvae	Number of prey per larva			Index of gut filling, ‱		
		$M \pm m$	Min–max	CV, %	$M \pm m$	Min–max	CV, %
1985	40	0.72 ± 0.16	0–3	143	6.20 ± 2.20	0–57.67	224
1986	48	3.08 ± 0.56	0–18	126	36.07 ± 8.57	0–280.00	165
1987	46	0.61 ± 0.20	0–8	228	10.26 ± 5.20	0–30.77	345
1988	44	1.14 ± 0.25	0–6	151	36.90 ± 16.22	0–372.09	291
1989	42	0.59 ± 0.15	0–5	162	2.68 ± 0.96	0–11.22	232

11 years (72.7% of the observation period); in other years, a major proportion of the larvae belonged to the risk group, i.e., did not yet start exogenous feeding after depletion of endogenous food resource. Some larvae contained no fat drop. Their proportion varied between years from 8.0 to 93% but in most cases did not exceed 60% (Fig. 2).

The diet of early peled larvae included typical zoo- and meroplanktonic organisms. The former were represented by copepods at nauplius and copepodite stages, juvenile cladocerans (*Bosmina, Ceriodaphnia, Macrothrix, Polyphemus,* and *Sida*), and rotifers (*Euchlanis, Brachionus,* and *Keratella*); the latter, by chironomid and mayfly larvae with a body length of up to 1.9 mm.

In the gut of feeding larvae with the remains of yolk (the mixed feeding stage), we usually found unidentifiable food remains or, rarely, one or two prey organisms such as rotifers (*Keratella* and *Euchlanis*), copepod nauplii, or juvenile cladocerans (*Daphnia* and *Sida*). The size of prey ranged between 0.12 to 0.32 mm, with the index of gut filling (calculated for the feeding larvae only) varying between years from 0.12 to 42.86‱.

In the larvae without the yolk sac (the exogenous feeding stage), copepod nauplii were the preferred food and played a major role in the diet throughout the study period. The corresponding *IR* value was the highest (from 51.2 to 81.1% in the larvae of different generations), and their proportion (the number of prey per larva) varied between years from 40.2 to 69.7%. At some sampling stations, the diet of the larvae in certain years included major proportions of cyclopoid copepodites (*IR* = 82.8%), mayfly larvae (*IR* = 78.2%), juvenile *Sida* (*IR* = 71.4%), chironomid larvae (*IR* = 35.1%), and juvenile *Bosmina* (IR = 26.9%). Rotifers were found in the guts of the larvae in only two years, with a low frequency (19.4% and 2.0%), and their relative significance was also low (*IR* = 0.9 and 3.1%). The average size of prey consumed by the larvae at the exogenous feeding stage varied between years from 0.21 to 0.43 mm; the minimum size, from 0.19 to 0.35 mm; and the maximum size, from 0.40 to 1.90 mm. The degree of gut filling in individual larvae and their generations as a whole also varied from year to year (Tables 2, 3).

Despite interannual differences in the rate of development of spring zoo- and meroplankton in Pol'khostur Sor (Fig. 3), its composition in any year was fairly rich and constant at the time when the early peled larvae arrived to their feeding grounds in near-shore shoals. Among 20 generic and infrageneric components of the animal plankton, about 40% were recorded every year. They included cyclopoid nauplii and copepodites, juvenile cladocerans (*Daphnia, Chydorus, Bosmina,* and *Ceriodaphnia*), chironomid and mayfly larvae. In different years, the food supply for the early peled larvae consisted of 32.7 to 95.1% of the total zoo- and meroplankton, excluding adult copepods of the orders Cyclopiformes and Calaniformes, adult cladocerans of the genera *Dahpnia, Scapholeberis,* and *Eurycercus*, insect larvae with a body length of more than 1.9 mm, and rotifers of the genus *Asplanchna*.

The abundance of food organisms for the early peled larvae markedly varied both between years (Fig. 4) and between different water areas in the same year (Table 4). The food supply for the larvae was usually the richest in area III and the poorest in area I (in 62.5% of the

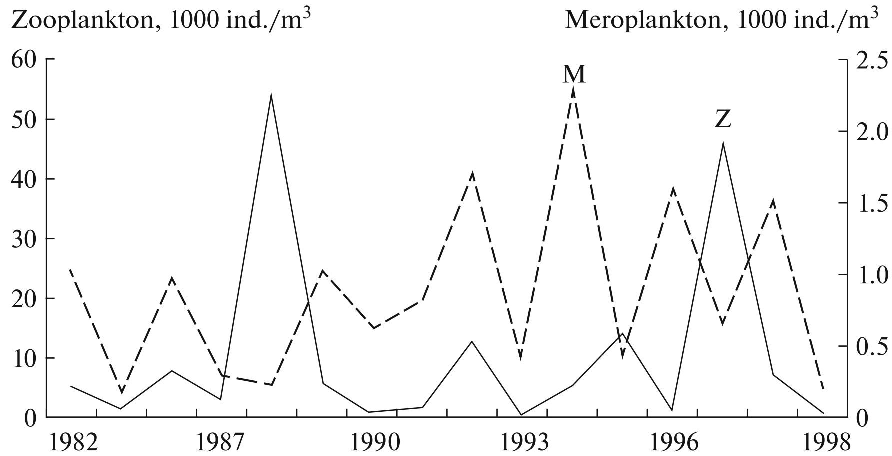

Fig. 3. Concentrations of (Z) zooplankton and (M) meroplankton in Pol'khostur Sor 2 weeks after spring flood (data on 1983 and 1984 are absent).

study years). Over the 16-year study period, the abundance of all food organisms in near-shore shoals averaged 13.69 ± 3.18 ($0.30–93.75$) $\times 10^3$ ind./m^3, and that of copepod nauplii, 5.14 ± 1.91 ($0–72.75$) $\times 10^3$ ind./m^3.

The contribution of meroplankters to the total abundance of food organisms was relatively low (from 0.4 to 32.2% in different years, averaging 8.4% over the 16-year period), while that of copepod nauplii was markedly higher (0.6 to 80.0%, averaging 37.5%).

The concentrations of food organisms most frequently recorded in near-shore shoals were less than 5000 ind./m^3. The concentration of copepod nauplii was less than 5000 ind./m^3 in 73.0% of cases, less than 2500 ind./m^3 в 66.7% of cases, and no nauplii were recorded in 6.3% of cases (Table 5).

In the years when the risk group comprised more than 25% of early peled larvae, the concentrations of food organisms at most stations were below 4000 ind./m^3, and those of copepod nauplii, below 1000 ind./m^3.

The correlation of food supply for the early larvae with water temperature and level in Pol'khostur Sor was weaker than that with the period from its flooding in spring to the approach of the larvae to near-shore shoals. This period varied between years from 7 to 39 days but usually lasted for 15–20 days (in 65.5% of the study years) (Table 6). A negative correlation was revealed between the mortality rate of the larvae at 10 days after their entry to the sor and the concentration of food organisms at the time of their transition to active feeding ($r = -0.761$).

The rate of water warming after spring flood in Pol'khostur Sor differed between years. In the period of dispersal of early peled larvae over the sor, water temperature remained unchanged in some years but usually increased by 1–2°C, rarely more. Peled larvae of different generations started active feeding when the water warmed up above 5°C, usually to 8–10°C or, in 7 out of 20 years, to 12–15°C (Fig. 5).

In spring, northerly and westerly winds prevailed in the region of Pol'khostur Sor (in 14 out of 20 years); no-wind conditions were observed less frequently (in 6 out of 20 years). Due to the prevailing wind directions, biotopes with favorable conditions for the transition of peled larvae to exogenous feeding are formed at the leeward northern and western shores of the sor. These are warmed-up shoals with submerged last year's herbaceous vegetation or small willow scrub and sufficient food resources that are accessible to the larvae due to the absence of waves.

The amplitude of the long-term dynamics of water level in Pol'khostur Sor during the spring flood is considerable, with the difference in water level between the highest-water and the lowest-water years reaching 3.1 m (Fig. 5).

Illumination conditions for the early peled larvae entering Pol'khostur Sor differ between years, even

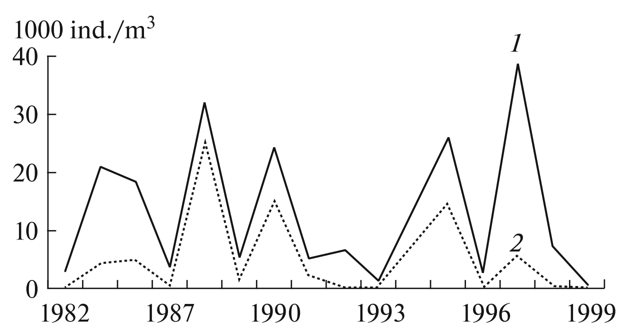

Fig. 4. Food supply to peled larvae during transition to exogenous feeding in Pol'khostur Sor: (*1*) all food organisms, (*2*) copepod nauplii (data on 1983 and 1984 are absent).

Table 4. Total concentrations of food organisms for early peled larvae (above the line) and concentrations of food organisms preferred by them (below the line) in Pol'khostur Sor, 1000 ind./m^3 (average data over 16 years)

Area	$M \pm m$	Min–max	CV, %
I	$\frac{5.34 \pm 1.34}{0.24 \pm 0.12}$	$\frac{0.13–22.53}{0–1.63}$	$\frac{101}{187}$
II	$\frac{7.75 \pm 2.17}{4.01 \pm 1.35}$	$\frac{0.30–26.50}{0.02–16.01}$	$\frac{112}{130}$
III	$\frac{27.97 \pm 7.89}{11.16 \pm 5.45}$	$\frac{1.08–93.75}{0–72.75}$	$\frac{112}{189}$

Table 5. Occurrence frequencies of different total concentrations of food organisms for early peled larvae (above the line) and concentrations of food organisms preferred by them (below the line) in Pol'khostur Sor, average data over 16 years

1000 ind./m^3	0–4.99	5.00–9.99	10.00–14.99	15.00–19.99	20.00–24.99	Over 25.00
Frequency, %	$\frac{43.7}{73.0}$	$\frac{20.8}{8.2}$	$\frac{10.4}{4.2}$	$\frac{6.3}{2.1}$	$\frac{4.2}{0}$	$\frac{14.6}{6.2}$

Table 6. Dependence of food supply to early peled larvae in Pol'khostur Sor on abiotic factors

Factor	Correlation coefficient
Duration of the period from flooding to mass approach of peled larvae to near-shore shoals	0.760
Sum of temperatures over the period from flooding to mass approach of peled larvae to near-shore shoals	0.653
Water level during spring flood	–0.451

though it is located at 63° N, where the polar day begins in the spring. When the larvae drifting from spawning grounds approach the sor on early dates (in the second half or, more frequently, in the third 10-day period of May), the daily period of low illumination (below 10–20 lx) lasts for 3–4 h; when this occurs relatively late (at the end of the first 10-day period of June), this period is only about 1 h (Fig. 6).

The sor system of the lower Ob River and its mountain tributaries after the spring flood is characterized by a favorable gas regime. At the time when the early peled larvae approached their foraging grounds in Pol'khostur Sor, the dissolved oxygen concentration was never below 8 mg/L.

DISCUSSION

It is considered that coregonid fish larvae normally start exogenous feeding while they still contain the yolk (Shkorbatov et al., 1959; Bogdanova, 1975; Lebedeva, 1981; Kugaevskaya, 1983a; Bolotova, 1986; Aver'yanova, 1990). As noted by some researchers (Gorbunova, 1967; Lebedeva, 1985), the mixed feeding stage begins when only a small amount of yolk remains. Thus, Shirobokov (1988) found that the transition to exogenous feeding in the larvae of Baikal lacustrine whitefish, omul, and peled under experimental conditions occurred when the relative weight of yolk was reduced to less than 5% of the initial; if this parameter was higher, only single individuals began to consume exogenous food. According to other data (Maksimova et al., 1967), when food organisms are in excess and water temperature is high, coregonid larvae start exogenous feeding while having a yolk sac of considerable size; moreover, an early transition to exogenous feeding (e.g., in the Baikal omul) leads to more active yolk resorption, and the larvae are more resistant to diseases and grow more rapidly than in the case of late transition (Toporkov, 1972; Volkova, 1988). The mixed feeding stage may be fairly long; for example, its duration in the whitefish *Coregonus lavaretus ludoga* reared in a fish farm at 6.0–9.5°C is 6–8 days (Bogdanova, 1972). Coregonid larvae undergoing the transition to exogenous feeding after complete yolk resorption or upon long-term starvation can survive for some time on account of internal nutrient resources and, later, at the expense of relatively differentiated tissues, but soon die because of irreparable dystrophic changes in body structures (Maksimova et al., 1967; Kugaevskaya,1983a; Dmitrieva and Voi-

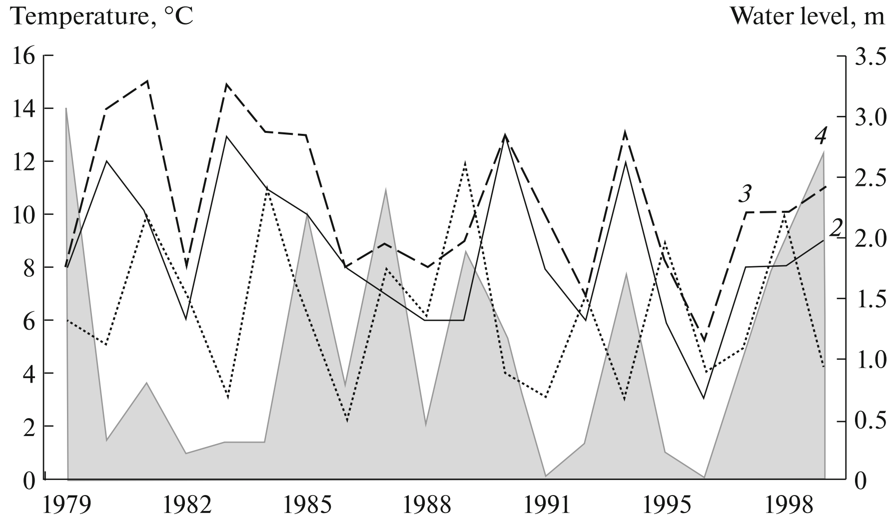

Fig. 5. Water temperature and level in Pol'khostur Sor in spring (water level in 1991 and 1996 is taken as baseline): (*1*) water temperature 2–2.5 weeks after flooding, (*2*) water temperature during mass entry of peled larvae to the sor, (*3*) water temperature during mass approach of peled larvae to feeding areas in near-shore shoals, (*4*) water level during spring flood.

nova, 1988; Semenchenko, 1988). The period of survival under such conditions directly depends on water temperature and the body size and morphological condition of the larvae (Korovina and Vasil'eva, 1976). Thus, coregonid larvae reared in a fish farm tolerated starvation (without impairment of viability) for a maximum of 10 days at 0.2–1.5°C and 5 days at 4–5°C (Sergienko, 1995). It has been shown that the larvae of Baikal omul acquire the universal type of energy metabolism and enter the period of rapid growth only after completing the transition to exogenous feeding (Dmitrieva and Voinova, 1988).

Peled larvae drifting from the upper and lower spawning grounds down the Severnaya Sosva to their foraging water bodies cover considerable distances, about 400 and 280 km, respectively. The conditions of their downstream migration vary both between years and during the same season (Bogdanov and Bogdanova, 2012), and this factor, along with qualitative differences between the larvae during hatching (Lebedeva and Meshkov, 1980; Bogdanov, 1998), largely accounts for their heterogeneity with respect to the amount of energy resources. Peled larvae approaching Pol'khostur Sor either contained the residual amount of yolk or were completely depleted of it, but all of them retained the fat drop (Bogdanov and Bogdanova, 2012). Active resorption of the yolk and fat drop continued during the short period (1–3 days) of their dispersal over the sor. According to average data over several years, yolk resorption was completed during downstream drift in 28.7% (0 to 84% in different years) and continued in the sor in 57.1% of the larvae (16.0 to 94.2%); the fat drop also disappeared in a considerable proportion of the larvae (up tom 94% in some years). Thus, the majority of peled larval generations in Pol'khostur Sor start exogenous feeding while retaining a small endogenous food reserve. However, this reserve was absent in 36.4% of generations, which could be conditioned to some extent by relatively high water warming (above 10°C) in the sor ($r = -0.552$).

Not all peled larvae in Pol'khostur Sor could change over to exogenous feeding. The proportion of larvae with food in the gut varied between years but was usually significant (over 72.6%); they included individuals at the mixed feeding stage, whose proportion was consistently low: 1.2 to 16.0% in different years, usually being less than 8.3%. The proportion of larvae that expended their internal energy resources but failed to start active feeding varied significantly: from 10.0 to 15.0% in 66.7% of the study years and from 37.5 to 72.0% in other years. The correlation of mortality rate with the proportion of larvae without the yolk and food in the gut was

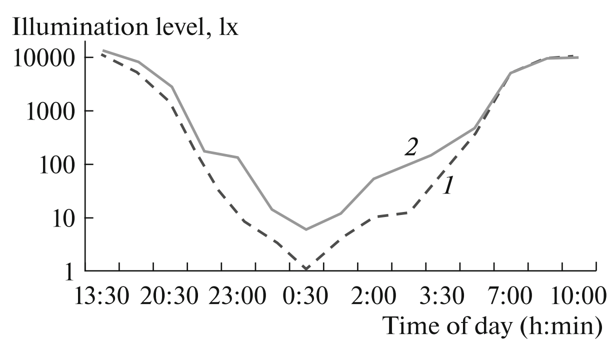

Fig. 6. Illumination levels during the transition of peled larvae to exogenous feeding in Pol'khostur Sor in cases of their (*1*) early and (*2*) late downstream drift (on May 22 and June 6, 1996, respectively).

relatively weak ($r = -0.460$), but we consider that it is such larvae that have the lowest chance to survive and, hence, refer to them as the risk group. The food spectrum of the early peled larvae from Pol'khostur Sor and those reared in other region is similar (Volkova, 1965; Gorbunova, 1967; Bogdanova, 1986; Bolotova, 1986; Shirobokov, 1988; Vesnina, 1990) and includes the majority of zoo- and meroplanktonic organisms inhabiting the water body (Bogdanova, 1992), with limitations on prey size. It has been shown that the maximum possible size of prey for fish depends on mouth opening (Ivlev, 1955). The recorded sizes (body lengths) of prey consumed by peled larvae in Pol'khostur Sor were in some years slightly greater than their normal mouth opening (0.25 mm) (Sergienko, 1995) and greater than the optimum prey size (0.25–0.29 mm) calculated for early peled larvae with a body length of 8.1–9.2 mm (Skoptsov and Pitrukov, 1988). However, taking into account body proportions (in particular, a small dorsoventral size) of the main food organisms, we consider that the aforementioned sizes of prey for peled larvae during their transition to exogenous feeding are in line with the general concept of the optimum prey size depending on the trophic status of fish (Ivlev, 1955), including juveniles feeding on zooplankton (Mikheev, 1984).

Concentrations of starting food for early peled larvae estimated by different authors are relatively low: 1.00–5.00 × 10^3 ind./m^3 (Shirobokov, 1988), 0.37–14.40 × 10^3 ind./m^3 (Vesnina, 1990), 10–12 × 10^3 ind./m^3 (Skoptsov, 2005), or 0.03–0.05 g/m^3 (Semenchenko, 1988; Shirobokov, 1988). Under experimental conditions, the minimum concentration of food organisms sufficient to fully satisfy the food requirements of peled larvae of different ages was determined at 25–30 × 10^3 ind./m^3 (Skoptsov and Pitrukov, 1988). In Pol'khostur Sor, the transition of peled larvae to exogenous feeding in most years also proceeded at a low food concentration. In years with a high larval mortality (over 95%), the concentration of their starting food in near-shore shoals did not exceed 8000 ind./m^3; therefore, we took this value as the threshold concentration. As a rule, concentrations above this threshold were rarely observed in areas I and II (7.5 and 31.3% of cases, respectively), being more frequent in area III (65.5% of cases). Food concentrations sufficient to fully satisfy the requirements of early peled larvae were recorded rarely: in 18.8% of cases, with area III accounting for 14.6%. Thus, the most favorable feeding conditions for early peled larvae (with respect to the composition and concentration of food organisms) are formed only in certain areas of the foraging water body. We agree with the researchers (e.g., Kukharchuk, 1986; Shirobokov, 1988) who consider that the ability of coregonid fish larvae to actively feed in nature at low concentrations of food organisms is an adaptation to the conditions of northern water bodies in spring.

The survival of early peled larvae in Pol'khostur Sor depends on the degree of gut filling ($r = -0.975$). In all study years, the larvae at the exogenous feeding stage consumed their food less actively than at the mixed feeding stage. However, the average parameters of food consumption (gut filling) in individual peled larvae foraging in the sor (to say nothing about their generations) cannot be regarded as high, compared to published data on the feeding of coregonid larvae from other water bodies. For example, the average index of gut filling in the early larvae of Shuya River whitefish developing in lakes reached 256‱ (Aver'yanova, 1990); in vendace larvae, 320 and 590‱ in different years; in whitefish larvae from Syamozero Lake, 660‱ (Bushman and Pervozvanskaya, 1981); in peled larvae (weighing no more than 0.03 g) reared in fishponds, 401‱ (Dmitrenko et al., 1990). However, the highest values of this index recorded in Pol'khostur Sor provide evidence that peled larvae in this water body are physiologically capable of feeding with higher intensity. Gut filling in peled generations directly depends on the level of development of their food resources, namely, the total amount of food organisms ($r = 0.770$) and the amounts of copepod nauplii ($r = 0.653$), meroplankton ($r = 0.576$), and typical zooplankters ($r = 0.761$). In addition to the concentration of starting food, this parameter depends on abiotic factors, which can have both direct and indirect effects. Thus, the index of gut filling in early peled larvae from Pol'khostur Sor was higher at westerly, northwesterly, and northerly winds ($r = 0.860$) than at southerly, southeasterly, and easterly winds ($r = -0.835$). Strong waves not only cause direct mechanical damage to the larvae (Bogdanov and Bogdanova, 2010) but also make food organisms less accessible to them. However, when westerly, northwesterly, or northerly winds blow over the sor, the larvae can securely feed in leeward biotopes with sufficient concentrations of food organisms (primarily in area III).

The water level in Pol'khostur Sor is the factor determining long-term variation in foraging conditions for early peled larvae, i.e., the area of near-shore shoals, the rates of water warming and development of zoo- and meroplankton, the level of wave disturbance, etc. Correlation analysis revealed a negative relationship between gut filling in the larvae and the water level in the sor ($r = -0.931$), which indirectly reflects dependence on the level of development of food zooplankton (Bogdanova, 1972). It should be noted that biotopes favorable for the feeding of larvae (see above) disappear when the water level is extremely low.

The temperature regime of a water body is one of the most important environmental factors, and many studies performed in fish farms and under laboratory conditions deal with its effect on various aspects of growth, development, and survival of fish larvae (Brett, 1983; Dgebuadze, 2001; Golovanov, 2013). In coregonid fish larvae, parameters that inversely depend on water temperature include the duration of endogenous and mixed feeding stages (*Pelyad'*..., 1989) and the survival period of starving individuals (Korovina et al., 1975; Nikitin, 1976; Shirobokov, 1988), while direct dependence on this factor has been shown for the rates of yolk sac resorption (Kugaevskaya, 1983a) and transition to exogenous feeding (Korovina et al., 1975). In laboratory and field experiments, early larvae of coregonid fishes, including the peled, tolerated temperature fluctuations within the range of 2 to 24°C (Shirobokov, 1988). Early peled larvae reared in a fish farm were shown to cease moving at 25°C and, at 10-day age, fall into shock at 26.5–28.5°C (Shkorbatov, 1966; Sergienko and Kugaevskaya, 1990). There is an opinion that the range of temperatures most favorable for peled larvae after hatching is fairly wide, 7–20°C (Radenko, 1994) or 8–18°C (Golovanov, 2013). The lower and upper limits of water temperatures at which peled larvae begin to consume their starting food were also estimated experimentally in fish farms. Thus, only a few larvae began to catch prey (1–3 ind. each) at 4–6°C, whereas most of them proved to actively feed at 6–8°C (Kugaevskaya, 1983b; Sergienko and Kugaevskaya, 1990). The upper temperature limit was determined at 23°C (Kugaevskaya and Sergienko, 1985).

Throughout the study period, the water temperature in Pol'khostur Sor during the arrival of peled larvae to near-shore shoals was above the lower and below the upper limit, remaining within a range of 8–11°C in 60% of years. No dependence of gut filling in the larvae and their mortality on water temperature was revealed. We have good reason to agree with Shirobokov (1988) that the indirect effect of temperature conditions on the survival of coregonid larvae (e.g., via the development of food resources in the water body) is sufficiently strong; however, it is unlikely that, in nature, water temperature may be an immediate cause of their death. This conclusion is confirmed by the negative correlation between gut filling in peled larval generations and the rate of water warming in the sor ($r = -0.752$). Such a correlation indirectly reflects the level of food supply to the larvae in different years, because rapid water warming provides for a high rate of development of crustacean plankton (Bogdanova, 1992).

It is known that the optimum dissolved oxygen concentrations for coregonid larvae are high and range widely, e.g., from 6.9 to 12.5 mg/L for Baikal omul larvae (Kozlova, 1997). According to experimental data from fish farms, the requirements for this factor increases as the larvae grow and develop (Kozlova, 1997; Kugaevskaya and Sergienko, 1985). The lower limit of dissolved oxygen concentration for peled larvae at 20°C was estimated at 1.39 mg/L prior to the transition to exogenous feeding and at 1.60 mg/L during this transition (Kugaevskaya and Sergienko, 1985). We never recorded oxygen concentrations below 9 mg/L in the waters of Pol'khostur Sor in spring and, hence, consider that this factor does not limit the process of transition to exogenous feeding in peled larvae.

The effect of light on fishes is multifaceted (Girsa, 1981; Radenko, 1994; Dgebuadze, 2001). In "visual" consumers, such as early peled larvae (Skoptsov, 2005), illumination level largely determines the level of food intake and assimilation, growth, and development (Protasov and Sbikin, 1970; Radenko, 1994; Vlasov et al., 2013). Each fish species is characterized by a certain range of illumination levels that is optimal for the functioning of its body systems (Ruchin, 2008). The threshold visual sensitivity markedly changes in the course of ontogeny and shows an inverse dependence on fish body size and a direct dependence on water temperature (Blaxter, 1968; Pavlov and Sbikin, 1967; Pavlov et al., 1967). However, we have not found definite values of these parameters for peled larvae in available publications. It has only been found experimentally that early peled larvae reared in fish farms do not eat in the dark (Kugaevskaya and Sergienko, 1985; Sergienko and Kugaevskaya, 1988; Sergienko, 1995) and show no deviations in behavior at illumination levels of 320 to 20000 lx (Radenko and Terent'ev, 1988). Omul larvae aged 0.5–1.0 days cannot search for food at 5–10 lx but actively chase prey at 100 lx (Volkova, 1981). These data suggest that the threshold illumination level allowing early peled larvae to feed actively is at about 10–20 lx. In all study years, including those with the extremely early dates of larval drift, the periods of low illumination insufficient for prey finding did not exceed 4 h, while it has been shown that continuously feeding peled larvae can fully satisfy their need for food within no more than 6 h (Skoptsov, 2005). Thus, illumination is not a factor that can interfere with the transition of peled larvae to exogenous feeding in Pol'khostur Sor.

CONCLUSIONS

The results of this study confirm the opinion that the transition to exogenous feeding can be a critical period for coregonid fish larvae, but not in terms of implementation of intrinsic (inherited) defects, which occurs independently of environmental factors (Vladimirov, 1964), but rather as a manifestation of the organism–environment unity (Eremeeva, 1967). The external morphology of the larvae and the state of their digestive system and locomotor and visual organs at his stage of development already allow them to successfully change over to exogenous feeding if this is not hindered by the trophic factor (Kovalev, 1962; Bogdanova, 1972, 1975).

We have shown that trophic conditions for peled larvae during their transition to exogenous feeding in Pol'khostur Sor are characterized by significant interannual variation and, in some years, determine the mortality rate of the larval generation, which varies between 65.1 and 98.2% (Bogdanov and Bogdanova, 2010). Factors that can directly prevent this transition are insufficient concentration of food organisms (below 8000 ind./m^3) and unfavorable wind regime responsible for the formation of waves and their impact on the most favorable foraging biotopes, which not only results in the death of larvae but also makes food organisms less accessible to them. In addition, the thermal and hydrological regimes (the level of spring flood) are the factors that can act indirectly, by affecting the development of food resources and increasing fall of the waves. The trophic situation for early peled larvae is most difficult in years when a late spring flood coincides with early larval drift or the sor is flooded early but the larvae arrive there on late dates. In the latter case, the situation may be aggravated due to a high rate of water warming, which results in the growth of food organisms (primarily copepods) to excessive size.

A distinctive feature of all peled larval generations at the transition of active feeding in Pol'khostur Sor is an insignificant amount or complete absence of endogenous food resources, which increases their sensitivity to adverse weather conditions. The optimum trophic conditions for such larvae, which ensure the level of gut filling sufficient for their survival and growth in Pol'khostur Sor, are as follows: the concentration of food organisms close to $20–30 \times 10^3$ ind./m^3, with prevalence of juvenile copepods (especially nauplii); westerly, northwesterly, and northerly winds or no-wind conditions; the presence of favorable biotopes with submerged last year's herbaceous vegetation or small willow scrub; water temperature between 8 and 10°C; the level of spring flood that does not approach the extreme values; and the medium dates of mass larval drift.

Studies on trophic aspects of early coregonid fish ontogeny, especially in the native range, have recently acquired special significance in view of increasingly acute problem of compensating damage to aquatic bioresources, which in Western Siberia is solved by releasing the larvae of valuable fish species (most frequently, the peled) into natural water bodies. Characteristics of the trophic factor and its optimal parameters for peled larvae at the transition to active feeding, which we obtained during studies in a water body located in the Severnaya Sosva floodplain, can be used for modeling analogous processes in floodplain water bodies on the lower Ob River and its spawning tributaries.

ACKNOWLEDGMENTS

This study was supported by the Basic Research Program of the Presidium of the Russian Academy of Sciences, project nos. 15-15-4-28 and 15-12-4-28).

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Translated by N. Gorgolyuk