

Spatial and Biotopic Distribution Patterns of Semianadromous Burbot, *Lota lota* L. (Lotidae), Early Larvae in the Lower Ob Floodplain

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Burbot larvae passively migrate downstream from spawning sites to shallow areas of the floodplain (Evropeitseva, 1946; Meshkov, 1967; Volodin and Ivanova, 1968; Sorokin, 1976; Pavlov et al., 1981; Bogdanov, 1989; etc.), where they undergo the second stage of development involving transition to active feeding. Their size in this period varies from 3.9 to 9 mm (Pavlov et al., 1981; Sorokin, 1976). In the middle and at the end of this stage, the larvae usually avoid open waters and areas with strong current, keep near the surface, and show positive phototaxis (Girsa, 1972; Pavlov et al., 1981). Early-juvenile burbot choose zones where the water is well warmed (Kjellman and Eloranta, 2002).

Miler and Fischer (2004), who studied the foraging of burbot larvae in Lake Constance, attributed their distribution by depth and along water temperature gradients to movements of copepods and rotifers, which are the main food objects of this larval stage. According to Harzevili et al. (2003), burbot larvae kept at relatively high water temperatures (above 16°C) grow more rapidly but have higher mortality, while at lower temperatures (below 12°C) their growth is retarded but survival rate is the highest. These authors conclude that the optimum temperature for burbot larvae after transition to active feeding is 12–16°C. Burbot larvae are more tolerant of fluctuations in water temperature, pH, and oxygen content than the larvae of other fish species (Sorokin, 1976). However, strong water acidification (to pH below 5.5) can result in their retarded development or even mass mortality (Kjellman and Hudd, 1996; Hudd and Kjellman, 2002).

The purpose of this study was to reveal the distribution patterns of semianadromous burbot larvae at the second stage of their development in the Lower Ob floodplain, one of the world's largest floodplain systems (Fig. 1).

Field studies (2000–2006, 2008) were performed in a 385-km segment of the floodplain between the Azovskaya Channel and Shchuch'ya River mouth. Samples were taken at the same sites every year.

The ecological density (Odum, 1986) of burbot larvae in their foraging areas was estimated after the end of their downstream migration from spawning tributaries. Samples were taken in the shallow near-bank zone (with depths of no more than 0.6 m), using a trap bag made of nylon bolting cloth no. 21 with a 60 × 40-cm aperture. The collected larvae were preserved in 4% formaldehyde solution.

The ecological density of the larvae at these sampling stations (ρ_{ec} , ind./m²) was calculated by the formula

$$\rho_{ec} = m/lD,$$

where m is catch size, ind.; l is trap movement distance, m; and D is trap width, m.

Sampling stations in larval foraging areas were grouped with regard to their distance from spawning tributaries (Fig. 1) and biotope type (Koporikov, 2004). This approach allowed us to single out the individual effects of the above two factors on the ecological density of burbot larvae.

By the criterion of biotope type, we distinguished three basic types of foraging areas characterized by certain water depth, temperature, vegetation, and bottom substrate. They were conditionally named “floodplain meadow” (FM), “sand–pebble beach,” and “steep undercut riverbank” (SR). The type “sand–pebble beach,” in turn, was divided into two subtypes, with still or flowing water (SB and FB, respectively).

By the criterion of distance from the spawning tributary, the foraging areas were divided into four zones (Fig. 2): (1) the floodplain–lake system of a spawning tributary (S_0); (2) nearby floodplain areas lying less than 30 km downstream of the mouth of the spawning tributary (S_1); (3) medium-distance foraging areas (S_2) within a 20- to 30-km stretch downstream of S_1 ; and (4) distant foraging areas (S_3) downstream of S_2 to the mouth of the next spawning tributary.

The indicated lengths of S_1 , S_2 , and S_3 stretches are approximate, because they can vary from year to year and between different spawning tributaries depending on specific hydrological conditions in different seg-

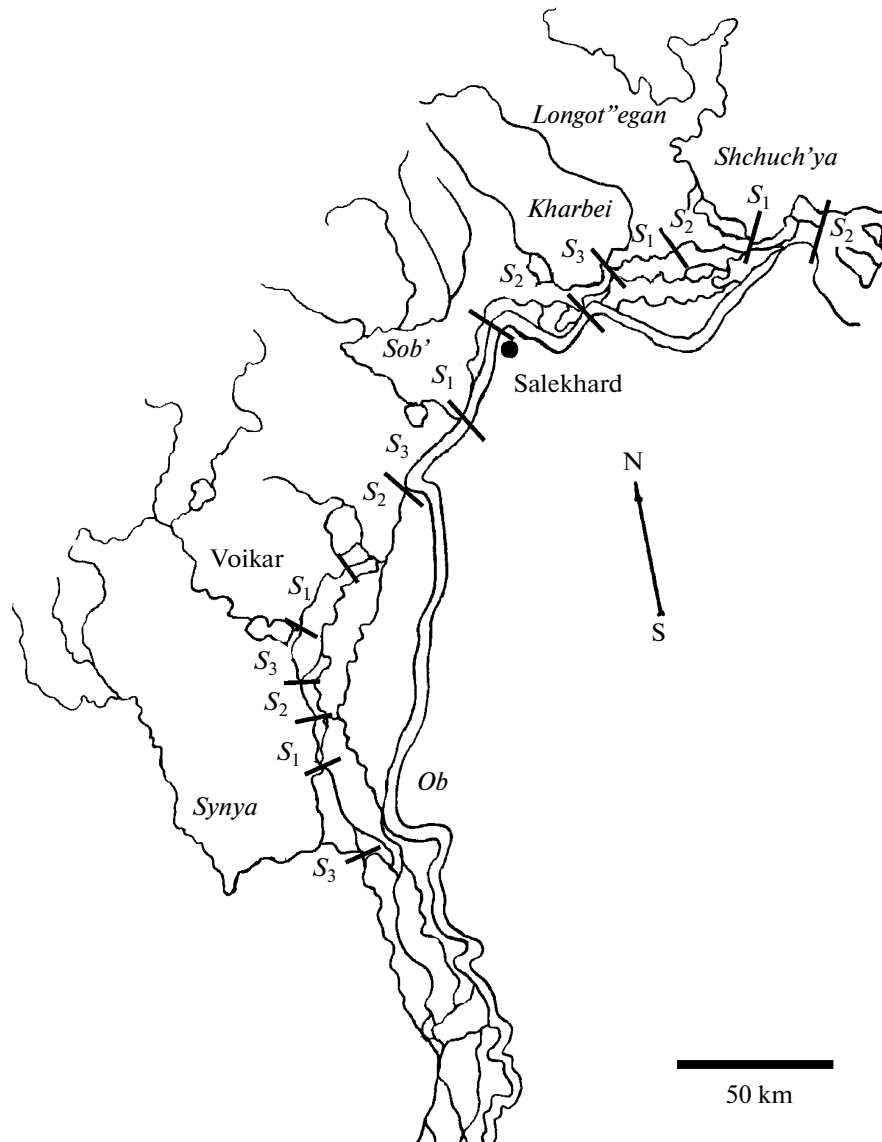


Fig. 1. Schematic map of the Lower Ob River with the main zones of burbot larvae sampling in foraging areas (for characteristics of these zones, see the text).

ments of the Lower Ob floodplain. A particular case of division into zones is shown in Fig. 2b.

The significance of differences in the distribution of burbot larvae between foraging areas differing in biotope type and distance from the mouth of the spawning tributary was estimated by the nonparametric Mann–Whitney test.

The eight-year monitoring of burbot larvae foraging in the Lower Ob floodplain allowed us to reveal several trends in their distribution over this water area. During the first month of foraging, the larvae occurred significantly more often ($p \leq 0.01$) in near-bank areas with a low current speed (the FM and SB biotopes), with their ecological density reaching a peak in the former biotope type (Table). This is explained prima-

rily by favorable environmental conditions: the small water depth and the absence of appreciable current allow effective water warming and rapid development of food organisms in sufficient amounts; therefore, the growth and survival rates of the larvae are the highest in such biotopes. In the other two biotope types (SR and FB), the current speed is relatively high, and water temperature is close to that in the mainstream; consequently, the abundance of food organisms is relatively low, and the larvae collected in such biotopes have a low growth rate. Due to their small body size, early-juvenile burbot cannot swim for long against the current and are swept along with it.

In years with a high or medium flood level—over 820 cm according to the Muzhi weather station

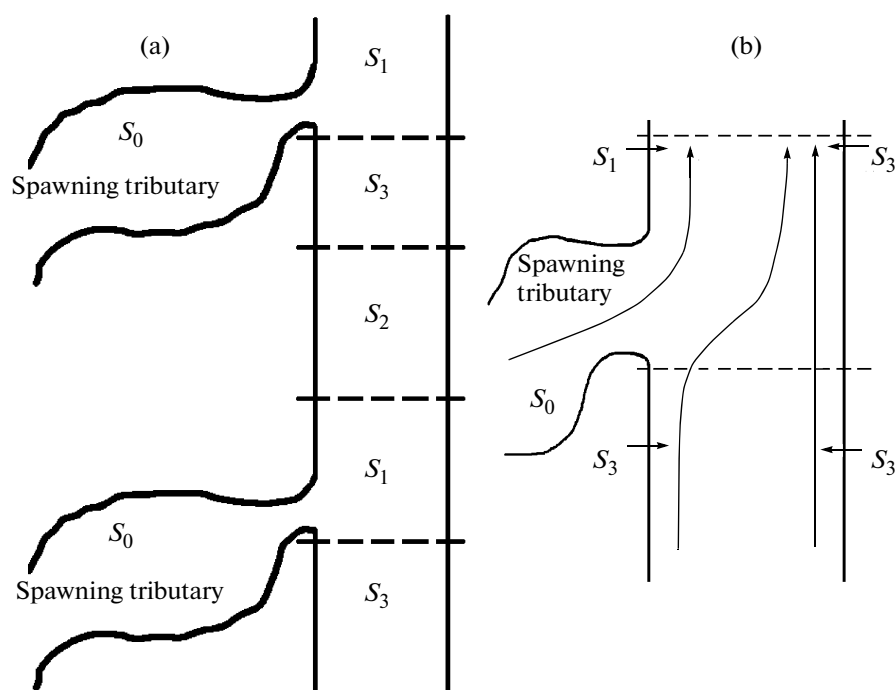


Fig. 2. (a) Scheme of the division of a floodplain area into zones by the criterion of distance from spawning tributaries (for characteristics of the zones, see the text) and (b) a particular case of delimitation between zones S_3 and S_1 depending on hydrological conditions.

(Fig. 3)—burbot larvae move out of river current and settle immediately near the mouth of the spawning tributary, in the S_1 zone (table). In years with a low flood level, the larvae are distributed over the downstream areas of the floodplain more or less evenly, and no significant differences in ecological density are observed between zones S_1 , S_2 , and S_3 (table).

The conclusion that the distance of the downstream distribution of burbot larvae depends on a certain (820 cm) flood level was confirmed by the Spearman rank correlation test ($r_s = -1$, indicating a strong, highly significant correlation). This study gave no statistical confirmation to the existence of a distribution pattern where early-juvenile burbot remain in the river

Ecological density of semianadromous burbot larvae in the Lower Ob floodplain (2000–2008)

Year	Flood level, cm	Abundance of downstream-migrating larvae, million ind.		Average ecological density of larvae, ind./m ²						Significance of floodplain area for larval feeding*
		<i>Synya River</i>	<i>Voikar River</i>	Floodplain area			Biotope type			
				S_1	S_2	S_3	FM	SB	SR + FB	
2000	802	67	874	2.6	1.9	0.3	2	—	0.1	$S_1 = S_2 = S_3$
2001	833	289	2911	19.3	2.3	0.1	8.4	5.4	0	$S_1 > S_2, S_3$
2002	848	2.3	15.5	1.5	0.4	0	0.9	—	—	$S_1 > S_2, S_3$
2003	815	297	530	0.8	0.8	0	0.8	0	0	$S_1 = S_2 = S_3$
2004	824	1282	143	3.5	1.6	0	2.9	1.6	0	$S_1 > S_2, S_3$
2005	800	168.4	6.8	0.8	2.8	7.5	2.1	0.05	0	$S_1 = S_2 = S_3$
2006	796	205	1589	1.3	1.4	—	0.7	3.5	0	$S_1 = S_2 = S_3$
2008	790	336	3506	14.8	3.9	3.9	9.1	1.1	0	$S_1 = S_2 = S_3$

* Differences in the ecological density of larvae are significant at $p \leq 0.01$; (—) no data.

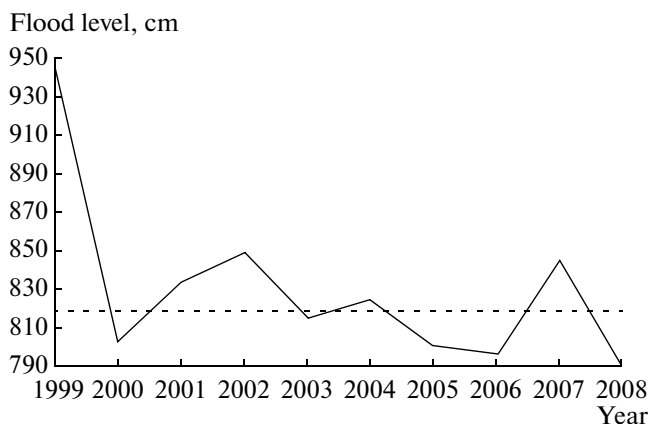


Fig. 3. Changes in the maximum spring flood level in the Lower Ob floodplain over the study period (according to data from the Muzhi weather station). If the flood rises above the level indicated by the dashed line, foraging burbot larvae concentrate in zone S_1 ; if the flood level is lower, they are distributed more or less evenly over the floodplain.

current for a long time and are washed far downstream from the mouth of the spawning tributary.

Differences in the distribution of burbot larvae in years with different flood levels can be explained by the fact that when the water level is below 820 cm, their optimal foraging areas in the FM biotopes (hay meadows on top of floodplain hillocks) remain above the surface, which makes them inaccessible to the larvae. In such years, floodplain watercourses return to their main channels, which provides for an increase in the number of SR and FB biotopes (with a relatively high current speed).

With the onset of the second stage of larval development (transition to active feeding), which coincides with the arrival of drifting larvae to the floodplain system, they usually move out of the main river channel into shallow near-bank foraging areas. In low-water years, however, the larvae drift with the current to floodplain areas lying farther downstream. Thus, the distance of their passive migration depends on the presence of accessible foraging biotopes.

It has been found that conditions for burbot larvae are optimal at a medium flood level, when all typical foraging biotopes in the floodplain become accessible to them. When this level is low (below 820 cm), the number of such biotopes sharply decreases, and the larvae concentrate in local sites of the water area. Their ecological density in these sites is high, although the larval generation as a whole usually shows an increased mortality rate in such years. When the flood level is high, most of the typical foraging areas are deep underwater, with strong current flowing over the FM biotopes, and burbot larvae disperse over floodplain areas not commonly used for foraging, such as flooded forest and shrub thickets. Foraging success in such years is low, the growth of larvae is retarded, and their mortality is increased. Conversely, burbot larvae foraging in shallow,

well-warmed areas of the floodplain (in floodplain lakes) show the highest growth rates. Studies by other authors (Kjellman and Eloranta, 2002; Harzevili et al., 2003) confirm that water temperature has a strong effect on the growth of early-juvenile burbot.

Thus, the distribution of anadromous burbot larvae over foraging areas shows a regular pattern depending on the spring flood level. However, a general trend is that, irrespective of this level, the second-stage larvae prefer biotopes with a low current speed, with their ecological density reaching a peak in biotopes of the floodplain meadow (FM) type. When the spring flood level is low and hay meadows on top of floodplain hillocks remain above the water surface, the larvae more or less evenly disperse over favorable biotopes in downstream floodplain areas. When the flood level is medium or high, the larvae forage in the immediate vicinity of the mouths of spawning tributaries. Their growth rate increases at high water temperatures in foraging areas.

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