Distribution of migratory fish in the stream (depth, velocity, body size, predators)

A. A. Chemagin

Tobolsk Complex Scientific Station of UrB RAS, Tobolsk, Russia

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In order to supplement the available information for the eco-hydraulic approach to designing fish passages, taking into account the taxonomic, dimensional structure, as well as taking into account the presence of predatory fish in the stream, the distribution of migratory fish of the boreal plain faunistic complex (Russian Federation) was studied. Three depth-velocity sections from the shore to the midstream were investigated: 5 m and 27.8 cm/s, 8 m and 44.4 cm/s, 11 m and 55.6 cm/s. Analysis of the migration distribution of fish showed that in the direction from the shore to the midstream, the proportion of representatives of Cyprinidae decreases from 41.8–24.3% and that of Percidae decreases from 25.0–18.4%. For individuals of two groups: the Acipenseridae and Lotidae, Coregonidae and Esocidae, patterns of distribution in the structure of migratory fish are opposite – their share increases with increasing speed and depth characteristics: 23.0–40.2% and 10.2–17.1%, respectively. An assessment of the dimensional structure revealed a feature of increase in the size range of fish from the shore to the midstream: the dominance of small individuals (<10 cm) in the shore area is replaced by the dominance of large fish (> 30 cm) in the area of higher speeds and depths. A significant difference in the distribution for all studied taxonomic fish groups between the shore and the midstream was shown. Thus, it has been established that for Cyprinidae during the migration period, the choice shifts in favour of minimizing energy costs, and the choice to avoid the risk of predation from individuals of the groups: Coregonidae and Esocidae, and also Percidae, shifts in favour of the former. The distribution of perch is influenced by the reduction of energy costs and the simultaneous avoidance of predation and cannibalism. For the fish group Acipenseridae and Lotidae, their predominance in the deeper area is due to their less developed visual orientation mechanism in the stream because they are bottom-living fish species.

Keywords: fish migration; antipredator behaviour; predation risk; body size fish; fishway.

Introduction

The movement and migration of fish is important for maintaining populations of various fish species, including river fish. The development of hydro-construction changes the natural flow regimes and can fragment habitats, creating insurmountable barriers (Santos et al., 2016; Mao, 2018; Beesley et al., 2019) not only for anadromous and potamodromous, but also for resident fish species (Enders et al., 2017), as a result of which the number of fish may decrease (Radinger & Wolter, 2014; Santos et al., 2016). To overcome the artificial barriers, special fish passages are being built – fish passages that help the fish to reach their spawning and feeding grounds. At the same time projects of fish passages rarely fully take into account the behaviour, energy and biomechanics of fish (Bunt et al., 2012; Silva et al., 2015; Enders et al., 2017). For the design and construction of these technically complex structures, ichthyologists carry out a large number of studies in order to assess the physiological capabilities of fish depending on their age, species, gender, and phenotype. The obtained data allow one to correctly calculate the technical characteristics of the bottom substrate, the flow rate, the availability of resting places, etc., which in turn ensures the accessibility of the habitat with certain physical parameters for the realization of life potential by the fish community (Beachum et al., 2016, Booker, 2016; Bravo-Córdoba et al., 2018; Stuart & Marsden, 2019).

Certain authors (Maddock et al., 2013) examine traditional methods for obtaining criteria used in the design and construction of fish passages, while emphasizing the importance of an ecohydraulic approach in studying fish migration. Based on this approach, it is possible to ensure consistency between environmental and engineering knowledge (Silva et al., 2017; Bravo-Córdoba et al., 2018). Currently the most common approach is still the traditional approach (Newbold et al., 2016) to developing criteria for the passage of fish, which mostly is based on experimental studies

of fish locomotion movement and held in controlled and homogeneous hydraulic conditions. In turn, it is worth emphasizing the difficulty of working under experimental conditions, as among fish only a limited number of size classes and species are usually tested (Amaral et al., 2016; Newbold et al., 2016; Link et al., 2017; Stuart & Marsden, 2019). Thus there is no research on motion and distribution of migratory fish in the stream (*in situ*) which take into account the presence of predatory fish in the community structure. The predatory factor is important since trophic-defensive relationships can cause changes in the spatial distribution of individuals, both predators and prey (Goldenberg et al., 2014; Murray et al., 2015). To improve further the structures and characteristics of fish passages, to increase the efficiency of the passage of several species of one family, as well as individuals of different taxonomic groups, it is necessary to quantify the efficiency and migration behaviour of fish in realistic hydraulic conditions with a large variety of different environmental parameters (Noonan et al., 2012; Silva et al., 2015; Amaral et al., 2016).

In this regard, the aim of this work is to determine the features of the spatial distribution of migratory fish in the river flow, taking into account their dimensional and taxonomic structure.

Materials and methods

The studies were performed in the time interval of 17–18 hours in the spring period on dates 9.05, 10.05, 13.05, 15.05–20.05.2017 in a first order tributary of the Irtysh River – near the mouth of the River Konda (0–1 km from the mouth) in the Khanty-Mansiysk district of the Khanty-Mansi Autonomous District in the coordinates: 60°42'13.8" N, 69°40'13.8" E. In the period of observations on the Konda River, there is a mass migration of fish in the flooded floodplain-channel complex. To register the number of migratory fish and their size composition, we used the software-technical sonar complex NetCor (LLC Promhydroaco-

ustics, Petrozavodsk). With the help of this complex we made a stationary round-the-clock registration of fish migrating both upstream and downstream, the recording and transmitting equipment was fixed on hydroacoustic buoys, which with the help of anchors were installed in the Konda riverbed (Fig. 1).
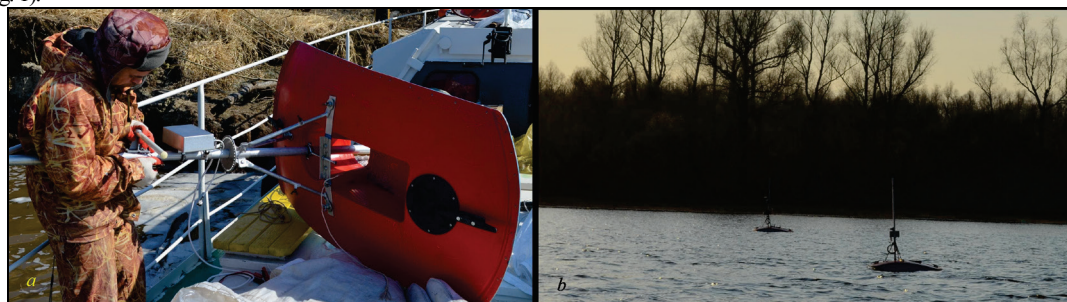

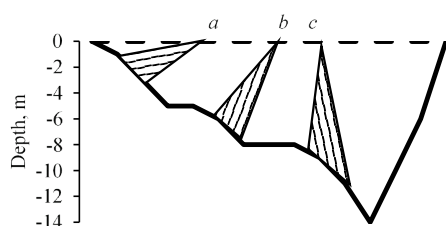**Fig. 1.** Hydroacoustic complex "NetCor": *a* – assembly, *b* – installation into the riverbed

Fig. 2. Schematic representation of the location of the studied depth-velocity sections of the cross-section of the Konda River flow scanned by the complex "NetCor": *a* – section No. 1, *b* – section No. 2, *c* – section No. 3

The installation sites of the complex were chosen in view of preventing the creation of obstacles to ship traffic, since passenger and cargo shipping is conducted along the Konda. On each buoy, a "Slave" module was installed that registered the movement of fish; this radio information was transmitted to the "Master" module additionally installed on one of the buoys. With the help of the "Master" module, the obtained information was recorded as files on a flash memory card, and then the generated files are processed in the laboratory with the help of special application software. The work of the "Slave" and "Master" modules used a 12 V battery, which was replaced daily from a motorboat. The area of the controlled living section of the flow with each Slave module was ≈ 8.75 m².

The taxonomic composition of migratory fish in the depth-velocity sections was determined using a computerized complex "AsCor" (LLC Promhydroacoustics, Petrozavodsk) with an operating frequency of 50 kHz. Hydroacoustic surveys were carried out along isobathic lines of selected sections with depths of 5, 8, 11 m, covering a distance downstream of 0.5 km to the fixed hydroacoustic buoys (Fig. 3).
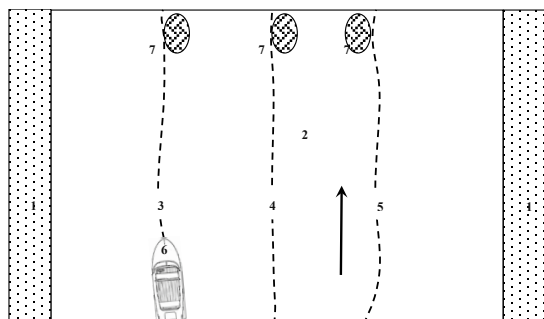

Fig. 3. Schematic representation of the sonar survey of depth-speed sections of the river: *1* – shores, *2* – water area of the river, *3* – isobathic line with a depth of 5 m, *4* – isobathic line with a depth of 8 m, *5* – isobathic line with a depth of 11 m, *6* – motorboat, *7* – hydroacoustic buoys with "NetCor" complexes; the arrow shows the direction of the flow of the river and the movement of the motorboat

For the installation of hydroacoustic buoys, three depth-speed sections were selected with an increase in the depth and speed characteristics of the flow from the shore to the midstream: 5 m and 27.8 cm/s, 8 m and 44.4 cm/s, 11 m and 55.6 cm/s respectively (Fig. 2).

The hydroacoustic data files were later processed in the laboratory using the software "Taxonomy". The algorithm used in this program allows, according to the swim bladder shape, the registered fish to be classified into the following four groups: Cyprinidae, Percidae, Coregonidae and Esocidae, Acipenseridae and Lotidae (Borisenko et al., 2006).

To control their species composition and biological state, the fish were caught with control stationary and smooth nets (mesh size 14, 25, 35, 45, 55, 65 mm, net length 35–75 m).

Thus, in three depth-speed sections of the river we performed and analyzed 27 hours of stationary and 13.5 km of moving sonar survey, and took 81 measurements of the flow velocity (3 replicates).

To measure the flow velocity, a river flow meter was used, which was lowered to a depth of 1.0–1.5 m, in the alignment of the hydroacoustic buoys' installation. Statistical analysis was performed using Statistica 10.0 (Statsoft Inc., USA). ANOVA analysis of variance was performed after checking the normal distribution of the data.

Results

According to the control fishing data, the ichthyofauna of the Konda River is represented by: sterlet (*Acipenser ruthenus* Linnaeus, 1758), siberian sturgeon (*A. baerii* Brandt, 1869), nelma (*Stenodus leucichthys nelma* Pallas, 1773), peled (*Coregonus peled* Gmelin, 1788), roach (*Rutilus rutilus* Linnaeus, 1758), ide (*Leuciscus idus* Linnaeus, 1758), Eurasian dace (*Leuciscus leuciscus* Linnaeus, 1758), bream (*Abramis brama* Linnaeus, 1758), gold crucian (*Carassius carassius* Linnaeus, 1758), silver crucian (*C. auratus* Linnaeus, 1758), European perch (*Perca fluviatilis* Linnaeus, 1758), Eurasian ruffe (*Gimnocephalus cernuus* Linnaeus, 1758), zander (*Sander lucioperca* Linnaeus, 1758), northern pike (*Esox lucius* Linnaeus, 1758), burbot (*Lota lota* Linnaeus, 1758). Among the cyprinids, the dominant species were the silver crucian, roach, dace, ide and bream. The proportion of roach, dace and crucian in the catches decreased in the direction from the shore to the midstream, while for ide and bream it increased. Perch and zander dominated among percids, the ruff was rare in the catches. In the direction from the shore to the midstream, the share of the perch decreased, while that of zander increased. Sterlet dominated in the sturgeons' group; individuals of Siberian sturgeon were rare in the catches. In the group of Coregonidae and Esocidae, pike and nelma dominated, peled were present in negligible quantity. Pike were more numerous in the direction to the shore of the river; nelma were caught only in the midstream. Burbot were also rarely caught; therefore, we can assume that the group of Acipenseridae and Lotidae was represented mainly by sterlet.

The number of fish and dimensional structure. The number of migratory fish through a comparable cross-section of the stream decreased in the direction from the shore (section No. 1) to the midstream of the river (section No. 3), while the flow velocity increased. For the period of observations on the depth-speed section No. 1 we recorded 1215 individuals of fish, No. 2 and 3 – 796 and 390 individuals of fish, respectively, while the average flow velocity in sections No. 1, 2 and 3 was 27.8, 44.4 and 55.6 cm/s (Fig. 4). Analysis of data on the number of

migratory fish and the percentage of their size groups revealed significant differences. In the depth-speed section No. 1, more than 1/3 of the individuals were represented by two size groups of 5 and 5–10 cm, their total share was 33.6%, the share of size groups 10–15, 15–20, 25–30, 30–35 cm decreased in the range 10.0–5.3% of the total number of fish registered in this section (Fig. 5a).
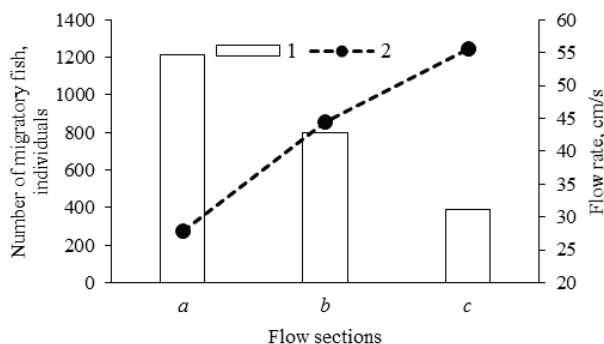

Fig. 4. The number of migrant fish (*1*) and average flow rates (*2*) recorded in the depth-velocity sections of the Konda river flow: *a* – section No. 1, *b* – section No. 2, *c* – section No. 3
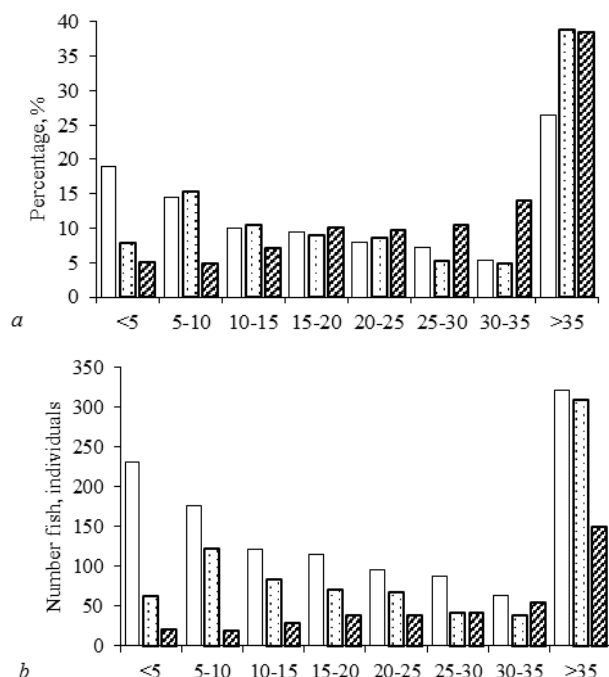

Fig. 5. The distribution of the size groups of migratory fish upstream of the River Konda in the flow along the depth-velocity sections: here abscissa is the size groups of fish (cm): *a* – absolute number, *b* – percentage; white background – section No. 1, dotted background – section No. 2, striped background – section No. 3

The proportion of the largest fish with body sizes greater than 35 cm was 26.5%. The number of the first two size groups was 408 individuals, the number of individuals with a body length of 10–15, 15–20, 25–30, 30–35 cm – 485 individuals, > 35 cm – 322 individuals. (Fig. 5b). In the depth-velocity area No. 2, larger individuals of the size group > 35 cm dominated, their share was 38.8%, the proportion of size groups of fish <5, 15–20, 20–25 cm did not exceed 10%, and the shares of groups 25–30 and 30–35 cm was about 5%. In numerical terms, the number of fish by size groups in the area under consideration was 309, 63, 71, 68 and 41, 38 individuals, respectively. The greatest difference in both the number and size structure was noted between the depth-velocity section No. 3 and the two previous ones. In section No. 3 we noted the predominance of larger fish, while their number was less in comparison with areas No. 1 and No. 2. The proportion of the size group > 35 cm was 38.5%, and the number of individuals 150. In the

direction of reduction of the size of groups of fish from 30–35 cm to < 5, 5–10 cm, we also observed a decrease in their share from 14.0–5.1% to 4.9%, respectively. At the same time, the number of individuals in the groups ranged from 55–20 and 19 individuals in the respective size classes.

As a result of the analysis of the taxonomic structure of fish migrating in depth-speed sections, it was established that in the direction from the shore to midstream, that is, with an increase in bathymetric and speed characteristics of flow, the proportion of cyprinid and percid fish decreased from 41.8–24.3% and 25.0–18.4% respectively. At the same time, the share of two groups: Acipenseridae and Lotidae, Coregonidae and Esocidae fish increased from 10.2–17.1% and 23.0–40.2% (Fig. 6).
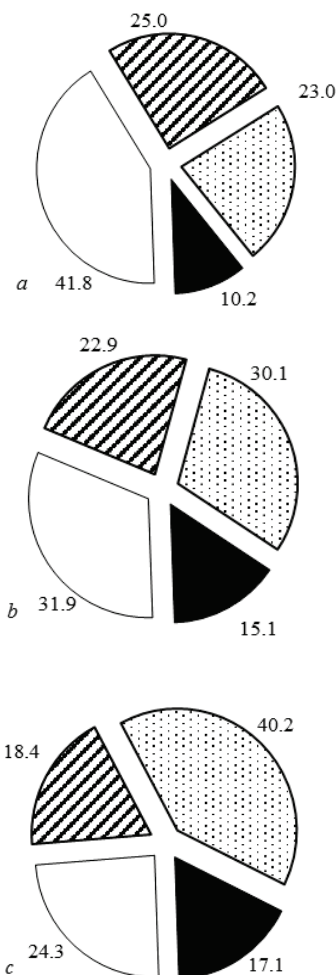

Fig. 6. Distribution of groups of migratory fish in the flow along the depth-velocity sections of the Konda River: *a* – section No. 1, *b* – section No. 2, *c* – section No. 3; white background – Cyprinidae, striped background – Percidae, dotted background – Coregonidae and Esocidae, black background – Acipenseridae and Lotidae

It should be noted that the distribution of taxonomic groups of fish according to size ranges recorded by hydroacoustic method in the depth-velocity sections under study also had differences and regularities. A comparative analysis of section No. 1 and 2 showed that for cyprinids there was a general tendency to reduction in the share of size groups 5–10, 10–15, 15–20, 20–25, 25–30, 30–35, > 35 cm: 66.7–58.1, 47.1–28.7, 37.8–20.8, 34.8–27.5, 32.0–27.8, 38.2–20.5, 27.0–19.1%, respectively (Fig. 7).

Comparison of sections No. 2 and 3, showed a slight increase in the proportion of fish in size groups of 10–15, 15–20 and 30–35 cm to 34.6%, 23.4% and 29.5%, respectively, while the shares of fish groups of the other size classes continued to decrease.

For percids, distribution of the different size classes in the flow was different. In the area No. 1, the smallest group of fish < 5 cm dominated; its share was 50% of the ichthyofauna belonging to this size group in

this section. More than 1/3 (35.3%) were represented by the size group of 15–20 cm, the proportion of size groups 5–10, 10–15, 20–25, 25–30 cm varied from 20.6–25.3%, the larger individuals with body sizes of 30–35, > 35 cm were less significant (5.9–4.8%, respectively). When comparing sections No. 2 and 3 with section No. 1, there was a decrease in the proportion of the smallest group of fish to 25.0 and 15.4%, respectively; an increase of 1.4–1.6 times in the share of medium-sized individuals from 5 to 20 cm; a 3–4 times increase in the proportion of larger fish with a body length of 30–35 cm to 26.1% and 16.7% in the respective sections. The share of the other size classes is comparable. For the group Coregonidae-Esocidae, it was established that the distribution of the size classes in the considered sections occurred more evenly. When considering sections from the shore to the midstream, the proportion of size groups 20–25 and 30–35 cm decreased slightly from 25.8–23.7% and 33.3–23.9%. Alongside this, the proportion of larger individuals with body sizes of 25–30 and > 35 cm increased from 30.0–44.3% and 50.8–66.9%. It should be noted that, among this group, in all the sections, large individuals with body sizes of 25 cm and more predomi-

nated. Individuals with a body length of < 5 cm in this group of fish were not registered. For the group Acipenseridae-Esocidae, the smallest individuals were not noted in sections No. 1 and 2; in section No. 3 their share was 15.4%. With an increase in the speed characteristics of the studied sections from No. 1 to 3, the share of the other size groups slightly increased.

Statistically significant differences were noted when comparing the number of the studied groups of fish in the depth-velocity sections, that is, in their distribution in the stream. Thus, for the cyprinids, it was established that the numerical indicators differed statistically significantly when comparing sections No. 1 and 2, 3 ($P < 0.05$). For three groups (Percidae, Coregonidae and Esocidae, and Acipenseridae and Lotidae) a comparative analysis revealed significant statistically significant differences when comparing sections No. 1 and 3 ($P < 0.05$), which in turn shows the preference for certain biotopes by these groups of fish: smaller individuals dominated in less high-speed sections, larger – in more high-speed sections (Table 1). However, in terms of numbers, migratory fish dominated in the lower velocity section of the river.
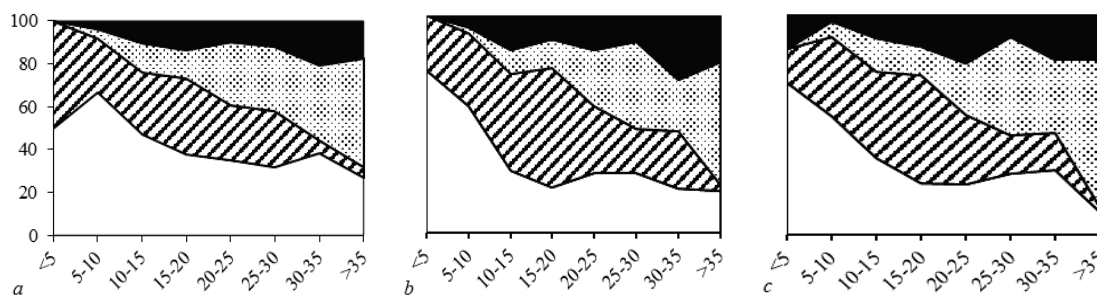

Fig. 7. Dimensional structure of migratory fish in depth-speed areas: abscissa – size groups of fish (cm); ordinate – percentage (%); *a* – section No. 1, *b* – section No. 2, *c* – section No. 3; white background – Cyprinidae, striped background – Percidae, dotted background – Coregonidae and Esocidae, black background – Acipenseridae and Lotidae

Table 1
Reliability of differences in the number of migratory fish of registered taxonomic groups in the depth-velocity sections of the Konda River according to the level (P) of the Tukey criterion

Depth-velocity sections	Cyprinidae			Percidae			Coregonidae and Esocidae			Acipenseridae and Lotidae		
	1	2	3	1	2	3	1	2	3	1	2	3
1	–	0.002	>0.001	–	0.469	0.044	–	0.096	0.009	–	0.536	0.020
2	–	–	0.475	–	–	0.375	–	–	0.543	–	–	0.182

Note: 1, 2, 3 – depth-velocity sections of flow of Konda River.

Discussion

The maximum number of small fish was registered in section No. 1, which is most closely located to the shore. This is explained by the fact that (Newbold et al., 2016; Wang & Chanson, 2018) small-sized fish minimize their energy expenditure by moving in low-speed and often high turbulence watercourse areas. Such areas are usually formed in areas of contact between the bottom surface and the river flow itself. It is worth noting that with sufficiently high turbulence, the efficiency of fish swimming may decrease (Tritico & Cotel, 2010), on the other hand, due to the hydraulic heterogeneity of the aquatic environment, the energy consumption of fish can be minimized, while the swimming characteristics of fish individuals increase (Enders et al., 2017).

In this regard, some researchers have suggested that for small-sized fish, one of the main criteria for migration is the presence of low-velocity areas in the flow (Clark et al., 2014). The preference of fish for these areas is characteristic of both non-predators (Dockery et al., 2017) and predatory species (Crisp & Hurley, 1991). By the example of cyprinids, it is shown (Dockery et al., 2017) that when migrating, individuals of this family actively choose low-speed sections located along the bottom, while adhering to the station retention behaviour at higher water velocities. For juvenile trout, in turn, preference is given to lower flow rates compared with older individuals (Crisp & Hurley, 1991). High indicators of the total number of fish in the shoreline section of the stream in comparison with the deeper sections may be due to excesses imposed by the latter environment over the physiological threshold of the body of fish, which suffer exhaustion and, therefore, move towards areas of lower flow rate to avoid activity (Peake & Farrell, 2006).

In turn, it is shown (Meuthen et al., 2019) that in the dimensional structure of the fish community from sections with a high number of predators, which corresponds to our sections No. 1 and 2, small fish predominate (juveniles). It has been established (Roy & Bhat, 2018; Meuthen et al., 2019) that smaller fish are bolder; therefore, small-sized cyprinids predominate in sections of the river No. 1 and 2, although here was also the largest share of percids from the all studied sections at 25.0% and 22.9%, respectively, against 18.4%.

The presence of different size classes of cyprinids, both in the near shore zone and on the midstream of the river, was caused by the difference in individual behaviour of individuals, resulting from a compromise between the energy costs of swimming in the turbulent zones near the bottom of the shore area and sections with higher speeds of flow in the midstream section (Newbold et al., 2016). Also in an earlier study (Pavlov, 1979) it was shown that the same species of fish can swim at different speeds, which affects the distribution of the same taxonomic groups of fish in different depth-velocity sections of the stream. Thus, differences in the behaviour and selection of the flow area are manifested not only within the same family of fish, but also within species. The increase in the share of larger fish in the core part of the river is explained (Pavlov, 1979; Crisp & Hurley, 1991; Dockery et al., 2017) by an increase in the indicators of threshold and critical flow rates for fish during ontogenesis, i.e. with increasing body length, the swimming efficiency of fish increases. This feature is confirmed in our study: the proportion of small-sized individuals decreases from the shore to the deep stream and, on the contrary, the proportion of medium-sized and larger fish increases. This ensures the even distribution of fish in the stream and reduces the risk of predation (Magoulick, 2004) and less ex-

pensive movement of fish in terms of the metabolic energy costs of individuals during their locomotion. For representatives of non-predatory fish of the Cyprinidae family – roach showed dominance in the shore zone in the presence of predatory species (Sharma & Borgstrøm, 2008), including pike, zander and large perch, that is, the presence of predators has a corresponding impact on the prey's choice of habitat (Šmejkal et al., 2018).

For sturgeon juveniles, it has been shown (Deslauriers & Kieffer, 2012) that the maximum steady swimming speed at which the fish are able to move can reach values of 18.0–22.3 cm/s, while it is assumed that keeping the station in sturgeon can be an important energy saving strategy during swimming (Deslauriers & Kieffer, 2011). It has been established (Deslauriers & Kieffer, 2011) that sturgeon juveniles cannot move for long periods at high speeds. Also, one field study of migration of representatives of sturgeon in North America conducted with the help of acoustic equipment showed (McElroy et al., 2012) that the representatives of this family can still minimize energy consumption by using low-speed areas during migration. When studying the physiology of juvenile Siberian sturgeon (Yuan et al., 2016), as well as for individuals of Chinese sturgeon (Cai et al., 2014), it was found that their individuals, due to the metabolic characteristics of the organism, have a high ability to recover the energy spent on movement in the stream. This feature explains the pattern of increase in the share of the group Acipenseridae and Lotidae in the structure of ichthyofauna from the shore zone to midstream, from 10.2–17.1%, and for almost all size classes. Also, their dominance on the deep stream is explained by a less developed visual mechanism, which is typical for bottom-dwelling fish. By contrast, pelagic fish (cyprinids, percids), have a more developed visual orientation mechanism in the stream (Pavlov, 1979). Thus, the bottom-dwelling fish, moving near the bottom of the river, even in the midstream, use less high-speed areas of flow, and getting to areas with a high flow velocity, they can quickly recover. In this regard, it is natural that while the proportion of the groups Acipenseridae and Lotidae increases midstream alongside an increase in the proportion of predators – nelma and pike, their vertical distribution is divided (Reshetnikov, 2003). It should be noted that the nelma, being a typical predator, actively consumes the juveniles of various species of fish, including pike (Stuby, 2018). Our observations show that a decrease in the share of percids occurs with a simultaneous increase in the share of other predatory fish from the Coregonidae and Esocidae group (nelma and pike). This pattern is traced in the direction from the shore to the midstream with an increase in the depth-velocity characteristics in the river flow. This is explained (Mikheev et al., 2006) by a change in the behaviour of juvenile perch: with visual detection of pike. Its smell acts as an additional stimulus that enhances the effects of visual signals during the daytime, which cause a congenital natural response in the perch – avoiding the predator and reducing the proportion of large prey in its diet, as well as reducing the overall consumption of food objects (Mikheev et al., 2006). At the same time, percids have morphological protection in response to the threat of predation (Šmejkal et al., 2018).

Conclusion

During the upstream migration of fish, their distribution in the stream is uneven in both size and taxonomic groups. For Cyprinidae and Percidae fishes, it was shown that their share in the structure of migratory fish decreases with increasing depth and speed characteristics of the flow in the direction from the shore to the midstream section, for two groups: Coregonidae and Esocidae, Acipenseridae and Lotidae fishes, on the contrary, it increases. The share of one group of predatory (percids) fish decreases with an increase in the proportion of larger predators: pike and nelma – the former avoid the latter. The change in the size range of migratory fish in the direction from the shore to the midstream of the studied depth-velocity sections occurs as follows: the dominance of small-sized groups of fish < 10 cm is replaced by the dominance of larger individuals > 30 cm. In numerical terms, the maximum indicators are noted in the shore area, the minimum in the midstream. According to analysis of the distribution of fish in the stream, it was shown that in cyprinids the choice of depth-speed sections is firstly dominated by the

minimization of the energy costs of migration, and secondly by the avoidance of the risk of predation from the group Coregonidae and Esocidae. Despite the maximum indicators of the number and relative share of percids in the shore area, the number of individuals of cyprinids here also has the highest indicators. At the same time, the distribution of percids apparently is influenced by two factors – the reduction of energy costs and the simultaneous avoidance of predation and cannibalism. For the group Acipenseridae and Lotidae, due to their river bottom distribution and less developed visual mechanism of orientation in the stream, maximum share in the midstream is characteristic.

Thus, the distribution of migratory fish in the stream should be considered not only from the point of view of changing characteristics of swimming individuals depending on body size, but also from that of the predator-prey system, taking into account the structure of the fish community, namely the presence and distribution of predatory species.

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