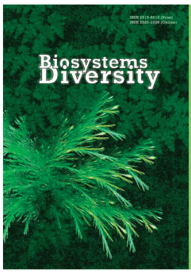

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Effects of temperature and water levels on dynamics of density and structure of the fish population of the channel-floodplain complex of a large river in the period of spring floods

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The article discusses the features of the dynamic process of migration of ichthyofauna from wintering sites to the wetlands of a large boreal river for feeding and spawning. The influence of factors of temperature and water level on various groups of fish is estimated, and the role of water bodies of various types during fish migration in a flooded floodplain is also established. The research was performed during the spring flood in the floodplain-channel complex of the Irtysh River (Western Siberia, Russian Federation) in the water area of the conjugate water bodies: the lotic and lentic parts of the riverbed depression and the mouth of the tributary – transit section of the migration pathway of fish to the flooded floodplain. The research work was performed by "AsCor" – computerized hydroacoustic complex, hydroacoustic survey data were processed in the laboratory. The "AsCor" complex remotely performs taxonomic identification of abundant species of fish at the family level by groups (Cyprinidae, Percidae, Coregonidae–Esocidae, Acipenseridae–Lotidae). It was found that after the breakup of ice cover, maximum densities of fish were observed in the wintering sections – the initial location of the spring migration. During the 30-days observation period in the wintering sections and conjugate water bodies, the density of fish decreased from 4 to 13 times due to their migration to the floodplain. The response to a decrease in the overall density of fish in the year-round functioning lotic part of the riverbed depression to the influence of factors of water level and temperature regimes was >0.300 in general for ichthyofauna and for all groups of fish registered by hydroacoustic method (Cyprinidae, Percidae, Coregonidae–Esocidae, Acipenseridae–Lotidae). We constructed regression models of changes in the density of fish in the wintering sections of the river depending on the considered factors. Use of ANOVA analysis of variance confirmed the adequacy of the choice and the acceptability of the constructed models. We established a high statistically significant inverse correlation between the density of the fish, the water level and temperature regime for the mouth of the Konda River and the lentic part of the riverbed depression, which are transit sections of the migration pathway of fish in the floodplain. The lentic part of the riverbed depression may perform the function of a temporary station of fish during migration to the floodplain, which is beneficial from the point of view of bioenergetics resources. During the observation period, in the river flows there was a decrease in the proportion of larger fish and an increase in smaller individuals; in the lentic part of the riverbed depression, on the contrary, there was a reduced proportion of small fish and increase in the proportion of larger individuals.This pattern is explained by the reduced risk of predation by small fish in more turbulent conditions, as well as by an initial entry into the flooded floodplain of larger individuals of fish for spawning, followed by the smaller ones for feeding.

Keywords: wetlands ecosystem; fish migration; factors influencing fish migration; upstream spring fish migration; spawning migration; boreal fish communities.

Introduction

Seasonal changes in hydrological (Dutterer et al., 2013; Walton et al., 2017; Jin et al., 2019) and temperature conditions (Dutterer et al., 2013; Espínola et al., 2016) are significant factors in the dynamics of fish populations in floodplain-channel systems of large rivers and their tributaries. At the same time, the study of the distribution and dynamics of fish in wetlands ecosystems is an important, relevant and little-studied direction of modern ichthyological researches (Górski et al., 2013; Reinhold et al., 2016; Naus & Adams, 2018).

Floodplain-channel ecosystems are, on the one hand, economically valuable and highly productive (Van de Wolfshaar et al., 2011; Batzer et al., 2018) and, on the other – ecologically vulnerable (Batzer et al., 2018). Understanding the functioning and disclosure of the role of all types of water bodies depending on the season and environmental factors in these ecosystems will accurately determine the potential extent of damage and the negative consequences for fisheries as a result of anthropogenic impact on the components of the wetlands ecosystem (Vaughan et al., 2009; Batzer et al., 2018; Goulding et al. 2019; Jin et al., 2019).

Researchers have studied the duration and direction of migration in the floodplain-channel complexes of the Amazon (Goulding et al., 2019), Yangtsi (Jin et al., 2019; Wang et al., 2019) and Parana Rivers (Baumgartner et al., 2018), and investigated the abundance and structure of the fish population, its dimensional taxonomic features in the areas of flooded floodplains, that is, either in the middle or at the end of the migration pathway, even on the territory of the Russian Federation, for example, in the Volga-Akhtuba river system (Van de Wolfshaar et al., 2011).

At the same time there is a gap in research on characteristics of the structure and dynamics of the number of fish surviving extreme effects of abiotic factors of the boreal zone (oxygen deficiency, ice cover, low temperatures) in the initial location of the migration pathway – wintering sections (riverbed depressions) and water bodies conjugated with them in the course of their spring migration to a flooded floodplain.

Researchers have noted (Goulding et al., 2019; Wang et al., 2019) the importance of studying the problem of fish community dynamics in floodplain-riverine ecosystems, taking into account their lentic and lotic parts, but these works are rare. In addition, currently there is a lack of information on the mechanisms of the effect of abiotic factors on the migration of fish from non-salmon families (Walton et al., 2017). It is worth noting that the Irtysh River is a habitat for various fish species, the most abundant are Cyprinidae, Percidae, Esocidae, Lotidae, while to a lesser extent the most valuable species are represented – Coregonidae, Acipenseridae, which increases the relevance of this study. In this connection, the purpose of this work is to determine the dynamics of the structure and density of the fish at the wintering section and the associated areas of the floodplain-channel complex of the Lower Irtysh during the spring flood, and construct the regression model of changes in density of different taxonomic groups of fish in response to the level and temperature water factors in the initial location.

Material and methods

The study was performed in the floodplain-channel complex of the Lower Irtysh in Khanty-Mansiysk district of the Khanty-Mansiysk Autonomous Okrug (Western Siberia, Russian Federation) in May 2017 during break up of ice cover and spring floods. Assessment of fish density and the proportion of size groups in the water area of the Kondinskaya riverbed depression (90–91 km from the mouth of the Irtysh River) and the conjugated mouth part of the Konda River (0–1 km from the mouth of the Konda River) was carried out daily using a computerized sonar complex "AsCor" (LLC Promgidroakustika, Petrozavodsk) with the subsequent post-processing analysis of hydroacoustic surveys in laboratory by the "AsCor" software application. With the application "Taxonomy" taxonomic fish identification of the following groups was performed remotely: Cyprinidae (CPR), Percidae (PRC), Coregonidae–Esocidae (CRG-ESC) and Acipenseridae-Lotidae (ACP–LTD) (Borisenko et al., 2006). To carry out surveys in the water area of the studied water bodies, we zigzagged in a motorboat according to generally accepted methods (Yudanov et al., 1984). To control the species composition and biological state of fish, fishing was used with static and swimming control gill nets (mesh size 14, 25, 35, 45, 55, 65 mm, length 35–75 m). Water temperature was determined using a multiparameter water quality assessment system Horiba-22U (Horiba, Japan). The dynamics of the water level regime were recorded daily using a measuring rod installed in the shore zone. Statistical analysis was performed using Statistica 10.0 (StatSoft Inc., USA). After checking the normality of the distribution of the data, the Spearman correlation coefficient was calculated. ANOVA was used for the analysis of variance. The correlation was estimated according to the following scale: weak (0.1–0.3), moderate (0.3–0.5), noticeable (0.5–0.7), high (0.7–0.9), very high (0.9–1.0).

The Kondinskaya riverbed depression – a fairly large area of the Irtysh River, both in area and in bathymetric characteristics, is located in geographic coordinates 60°42'28.21" N, 69°40'34.88" E. It consists of lotic and lentic parts with an area of 117 and 42.6 hectares, respectively (Fig. 1). The first is located in the channel of the Irtysh River, the maximum depth at the end of the observation period exceeding 43 m, and the lentic area is located on the left bank of the floodplain, its depth reached 10 m. These sections are separated by flooded banks overgrown with willow scrub.

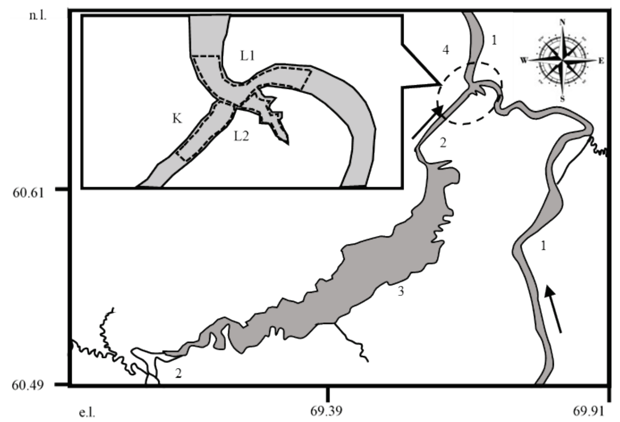

Fig. 1. Map of the study area and components of the floodplain-channel complex (scale 1: 3 500 000): *1* – Irtysh River, *2* – Konda River, *3* – Kondinskoe flowing lake; *L1* – lotic part of the riverbed depression, *L2* – lentic part of the riverbed depression, *K* – mouth section of the Konda River; the arrows indicate the direction of the flow of rivers

Mouth of Konda River – is associated with the lotic and lentic parts of the Kondinskaya riverbed depression in the left-bank part of the Irtysh River, the area of the study section is 77.5 hectares, and the maximum depth of 12 m. The studied water bodies according to the direction, complexity and intensity of currents are assigned on a macroscale to 3 types: the lotic part having several multidirectional high-intensity streams occurring among themselves, located on a meander with a high curvature of the channel (Chemagin, 2018) is a high-turbulent section of the flow; in the lentic part, the movement of water masses occurs mainly with wind mixing, change in the water level in the Irtysh and Konda rivers, it is a low-turbulent water body with a slow water exchange.

The rectilinear flow prevails at the mouth of the Konda River, the considered section is laminar with an average degree of flow turbulence. In the aggregate, the conjugate studied water bodies form a laminar-turbulent environment within the aquatic ecosystem.

Results

According to the control fishing in the study area, the ichthyofauna is represented by typical species abundant in the Lower Irtysh: 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), dace (*L. leuciscus* Linnaeus, 1758), bream (*Abramis brama* (Linnaeus, 1758)), golden crucian (*Carassius carassius* Linnaeus, 1758), silver crucian (*C. auratus* Linnaeus, 1758), perch (*Perca fluviatilis* Linnaeus, 1758), ruff (*Gimnocephalus cernuus* Linnaeus, 1758), zander (*Sander lucioperca* Linnaeus, 1758), pike (*Esox lucius* Linnaeus, 1758), burbot (*Lota lota* Linnaeus, 1758).

Inside the complex of a wintering riverbed depression consisting of lotic (L1) and lentic (L2) sections located in the Irtysh River and the mouth of the Konda River associated with them (K), during the observation period we noted differences in taxonomic and size structure of fish communities, as well as in the dynamics of fish density. In the water area of the lotic part of the riverbed depression (Irtysh River) and the mouth of the Konda River, cyprinids dominated, their shares being 51.1–61.4% and 42.3–74.4% of the total number of registered fish in them, respectively (Fig. 2).

Among cyprinids in the lotic part of the riverbed depression the following species dominated: ide, bream; in the lentic part – roach, ide, bream, in the water area of the mouth of the Konda river – silver crucian, roach, ide, bream. Zander and perch dominated among the percids in the riverbed depression, ruff to a lesser extent, perch and zander prevailed at the mouth of the Konda River, and ruff was also represented slightly. From the group of Coregoniae–Esocidae in the lotic part of the riverbed depression and in the mouth of the Konda River nelma dominated until the end of the 1st decade of the observation period, then pike, the individual peled were rarely present in the catches. The group of Acipenseridae–Lotidae throughout the entire observation period was represented predominantly by sterlet and to a lesser extent by siberian sturgeon; individuals of burbot are rare. Individuals of the siberian sturgeon were immediately and with the least damage released back into their natural habitat.

It is worth noting that in the direction of reduction of the flow and intensity of turbulence of water bodies from the lotic to the lentic part of the riverbed depression, the pattern was established of increase in the proportion and density of representatives of percids: 22.0 ± 0.2%, 18.4 ± 0.8%, 28.3 ± 1.3%, and the maximum values of the density of representatives of the fish of this family amounted to 2.88 in the lotic part of the riverbed depression, 3.81 in the lentic part, and Konda 2.25 thousand individuals/ha.

The average densities of percids in the lotic and lentic parts of the riverbed depression, as well as in the water area of the mouth of the Konda River were 0.95 ± 0.10, 0.90 ± 0.20, 0.54 ± 0.11 thousand individuals/ha, respectively (Fig. 2). The maximum values of fish density in the waters of all studied water bodies were noted at the beginning of the observation period (May 2, 2017), which coincided with the breaking of ice cover, ice drift, lack of flooding of floodplain areas and the onset of spawning temperatures for the abundant species fish in the floodplain-channel complex of the Irtysh River (Fig. 3).

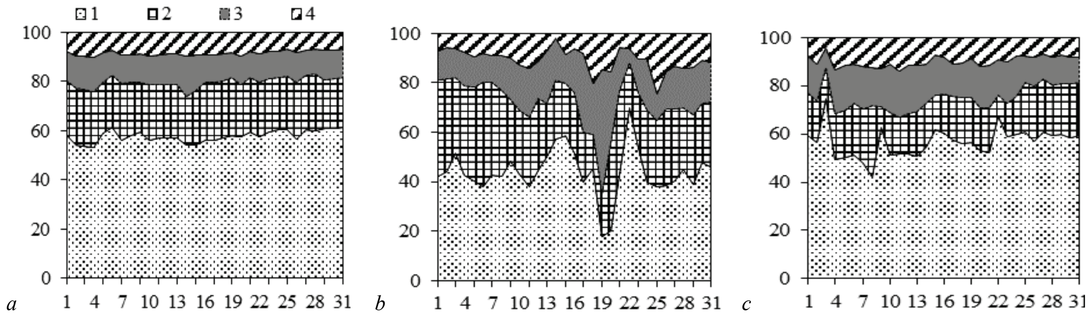

Fig. 2. Dynamic of the taxonomic structure of the ichthyofauna of the floodplain-channel complex of the Irtysh River during the spring flood: here abscissa is the dates of observation (May, 2017); ordinate is percentage (%); *a* – lotic part of the riverbed depression, *b* – lentic part of the riverbed depression, *c* – mouth section of the Konda River; *1* – Cyprinidae, *2* – Percidae, *3* – Coregonidae–Esocidae, *4* – Acipenseridae–Lotidae

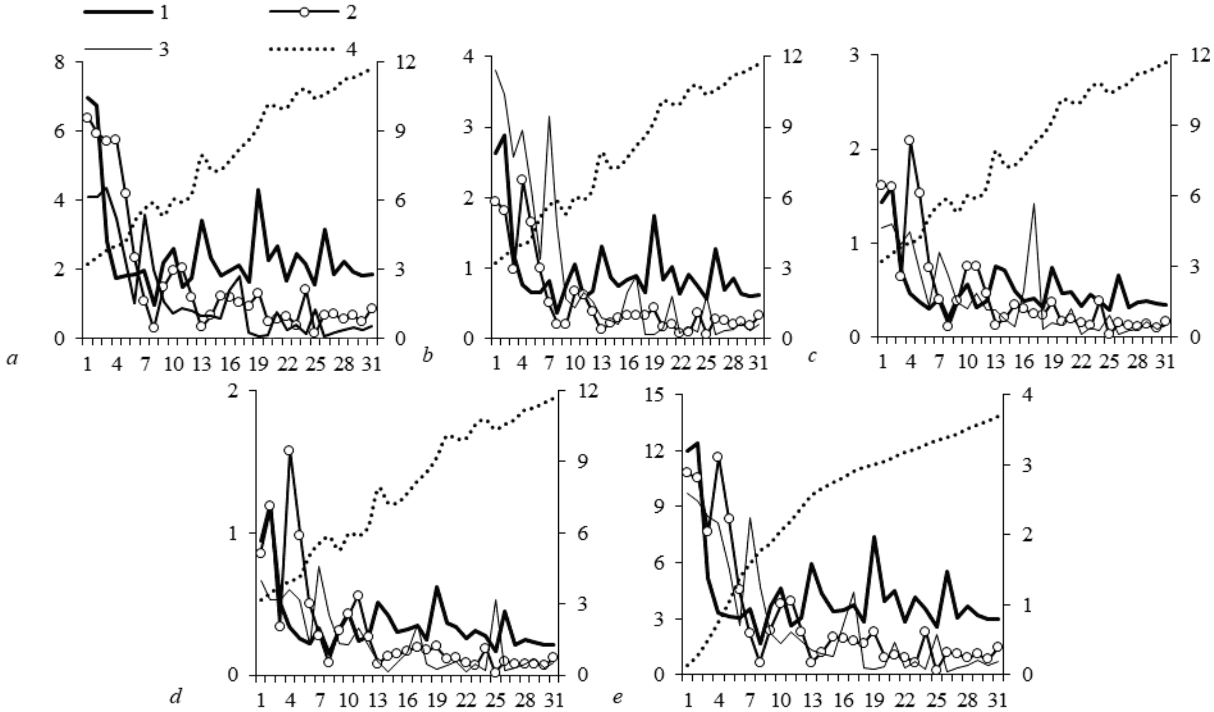

Fig. 3. Dynamic of density of taxonomic groups of fish in the floodplain-channel complex of the Irtysh River depending on temperature and water level: here abscissa is the dates of observation (May, 2017); basic ordinate is fish density (thousands individuals/ha); *a*–*b* – auxiliary ordinate is temperature of water (ºC), *e* – auxiliary ordinate is water level (m); *1* – lotic part of the riverbed depression, *2* – mouth of the Konda River, *3* – lentic part of the riverbed depression, *4* – temperature (*a*–*d*) and water level (*e*); *a* – Cyprinidae, *b* – Percidae, *c* – Coregonidae–Esocidae, *d* – Acipenseridae–Lotidae, *e* – total density

In the lotic part of the riverbed depression, the fish density reached 12.42, in the lentic 9.73, in the mouth part of the Konda river 11.67 thousand individuals/ha, the temperature of the water 3.5 ºC.

Subsequently, with the development of the flood process and a rise in the level and temperature of the water in the study area, a decrease was observed in the density of fish for all registered groups. In the middle of the observation period (15 May, 2017), the water temperature was 7.3 ºC and the total rise in the water level was 2.464 m, which in turn amounted to 74.6% of the total rise in the water level in May 2017. By the closing day of the observation period (May 31, 2017), the total rise in the water level during the study period was 3.318 m, the water temperature was 11.7 ºC, the density of fish, decreased in the lotic part of the riverbed depression by 4.12 times, in the lentic – 13.17 times, in the mouth section of Konda River by 7.89 times, respectively. Their values were 3.01, 0.74, 1.48 thousand individuals/ha, respectively. The greatest dynamics in reduction in the density of fish during the rise of flood waters and water temperature were established for the lentic part of the riverbed depression: for the group of Cyprinidae – 12.05 times, Percidae – 18 times, Coregonidae–Esocidae – 10.14 times, Acipenseridae–Lotidae – 6.03 times. The maximum dynamics of changes in the density of fish of the group of Acipenseridae–Lotidae at the beginning and end of the observation period were established for the lotic part of the riverbed depression and for the mouth of the Konda River, the 10 fold decrease reached the values of 0.21 and 0.12 thousand individuals/ha. It is worth noting that the periods of rising density of fish of the group Cyprinidae in the Irtysh river: 2.05–4.05, 5.05–7.05, 8.05–10.05, 12.05–13.05, 18.05–19.05, 20.05–21.05, 22.05–23.05, 25.05–26.05, either coincided with an increase in this indicator in the lentic part of the riverbed depression and the mouth of the Konda River, or preceded them; the same pattern is observed for the groups Percidae and Coregonidae–Esocidae during the periods 2.05–4.05, 6.05–7.05, 8.05–10.05, 13.05–17.05, 18.05–24.05 and 1.05–4.05, 8.05-10.05, 10.05–17.05, 18.05–20.05, 21.05–25.05 (Fig. 3).

For the Acipenseridae–Lotidae group, almost the entire observation period was characterized by a decrease in density in the Irtysh River with a simultaneous increase in the Konda River. With a decrease in the density of fish of this group in the Konda River and the lentic part of the riverbed depression, their density, and accordingly, the number in the Irtysh River somewhat increased.

The dynamics of the size structure. As a result of the analysis of the size structure of the ichthyofauna during the observation period, it was found that individuals with body sizes of 5–10 cm dominated among the cyprinids in the lotic part of the riverbed depression, their proportion of the total number of fish of this group varied from 69.3% in the middle to 75.5% at the end of the observation period. The percentages of larger fish with a body size from 20 cm or more were characterized by a decline from the beginning to the end of the observation period (Fig. 4*a*, *b*).

For percids, it was established that in the lotic part of the riverbed depression, individuals with a body size of 5–10 cm were dominant, their proportion was 67.3–74.5% of the total number of fish of this group (Fig. 4*c*, *d*).

The shares of larger fish with a body size of 20 cm increased from the beginning to the middle of the observation period, then a decrease was observed. When analyzing the distribution of size groups among the fish of the group Coregonidae–Esocidae it was noted that individuals with body sizes of 5–10 cm, 10–15 cm dominated, their shares varied 40.6–53.8% and 25.7–28.4%, respectively (Fig. 4*e*, *f*). The proportion of fish individuals of this group with the body size >20 cm was maximal in the middle of the observation period, minimal at the end. The group Acipenseridae–Lotidae in the lotic part of the riverbed depression was characterized by a similar distribution across the size groups during the observation period (Fig. 4*g*, *h*).

An analysis of the size structure of the ichthyofauna of the lentic part of the riverbed depression revealed its difference from the lotic part during the observation period. Among cyprinids, groups of individuals with body sizes of 5–10 and 10–15 cm dominated only at the beginning of the observation period, their shares were 39.9% and 29.6% in the middle and the end of the observation period, the main part of the cyprinids consisted of larger individuals, while it is worth noting that their shares were on average higher than in the lotic part of the riverbed depression (Fig. 5*a*, *b*). Percids consisted predominantly of individuals with body sizes of 5–10, 10–15, and 15–20 cm; in the middle and at the end of the observation period, large individuals (25–30, >35 cm) were absent. When considering the observation period in the aspect of increasing the water level and its temperature, the general pattern for percids in the lentic part of the riverbed depression was characterized by a decrease in the proportion of small-sized individuals (5–10, 10–15 cm) and an increase in the proportion of larger fish (Fig. 5*c*, *d*).

For the group Coregonidae–Esocidae, the dominance of larger individuals with body sizes >20 cm was observed during almost the entire observation period (Fig. 5*e*, *f*).

In the group Acipenseridae–Lotidae, the pattern of the dynamics of the size structure was similar to the percids – at the beginning smaller individuals dominated, in the middle and the end of the observations larger size groups dominated (Fig. 5*g*, *h*).

For cyprinids and percids, in the water area of the mouth section of the Konda River in the beginning and middle of the observation period, the predominance of larger individuals with a body size >20 cm was found. At the end of the observation period, dominance shifted to the small-sized group of 5–10 cm, the shares of this group among cyprinids and percids were 75.5% and 74.5%, respectively (Fig. 6*a*–*d*).

The general regularity of the decline in the proportion of large individuals at the end of the observation period and the dominance of small-sized groups (5–10 cm) was also characterized by groups of Coregonidae–Esocidae, Acipenseridae–Lotidae. Among them, large individuals dominated until the middle of the observation period (Fig. 6*e*–*h*).

To investigate the relationship between the overall density of the dynamics of individual fish and taxonomic groups, as well as environmental factors – the level of flood water and temperature of water in the tested water bodies, the Spearman correlation coefficient was calculated (Table 1).

The analysis of the dynamics of fish density in the lotic and lentic parts of the riverbed depression revealed the presence of a reliable direct correlation connection ($R = 0.49$, $P < 0.05$), when comparing the densities in the Irtysh River and the Konda River we also noted a direct correlation relationship ($R = 0.56$, $P < 0.05$). The greatest direct correlation between the dynamics of fish density is established between the lentic part of the riverbed depression and the Konda River mouth ($R = 0.81$, $P < 0.05$) (Table 1).

When analyzing the relationship between the dynamics of the total density of fish, the density of taxonomic groups of fish in the lentic part of the riverbed depression and the Konda River and the water level and temperature factors during the spring flood, we established a reliable inverse high correlation (R from –0.70 to –0.90, $P < 0.05$) (Table 2).

As a result of the analysis of the relationship of these factors with the indicators of the total density of fish, the density of taxonomic groups, the presence of an inverse moderate correlation was noted (R from –0.30 to –0.50, $P < 0.05$).

An analysis of the relation between the water level factor and the density of the groups Coregonidae–Esocidae, Acipenseridae–Lotidae showed the presence of a moderate statistically significant inverse correlation (R from –0.50 to –0.70, $P < 0.05$). An analysis of the relationship within the water bodies between the dynamics of fish density in different taxonomic groups revealed a statistically significant high and very high correlation (Table 2). To determine the reliability of differences in the density of the registered taxonomic groups of fish in the studied water bodies of the floodplain-channel complex of the Irtysh River we performed analysis of variance ANOVA for decades (Table 3).

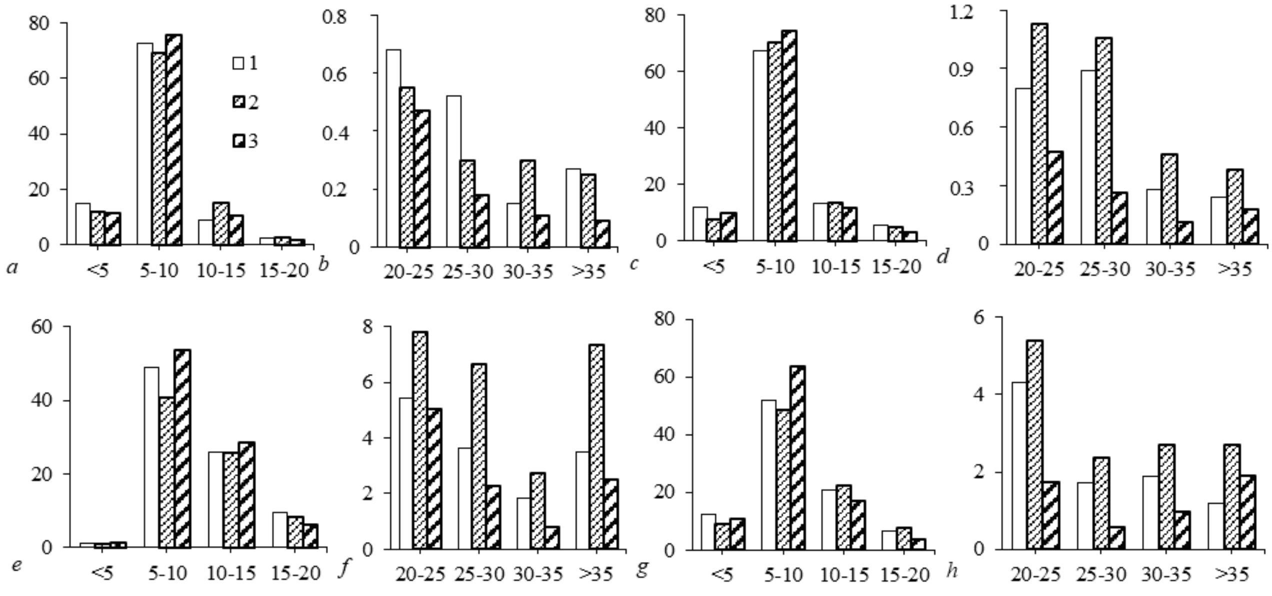

Fig. 4. Dynamics of the size structure of the ichthyofauna (as a percentage of the appropriate groups of fish) of the lotic part of the riverbed depression at the beginning (*1*), middle (*2*) and end (*3*) of the observation period (Irtysh River): here abscissa is the size groups of fish (cm); ordinate is percentage (%); *a*, *b* – Cyprinidae, *c*, *d* – Percidae, *e*, *f* – Coregonidae–Esocidae, *g*, *h* – Acipenseridae–Lotidae

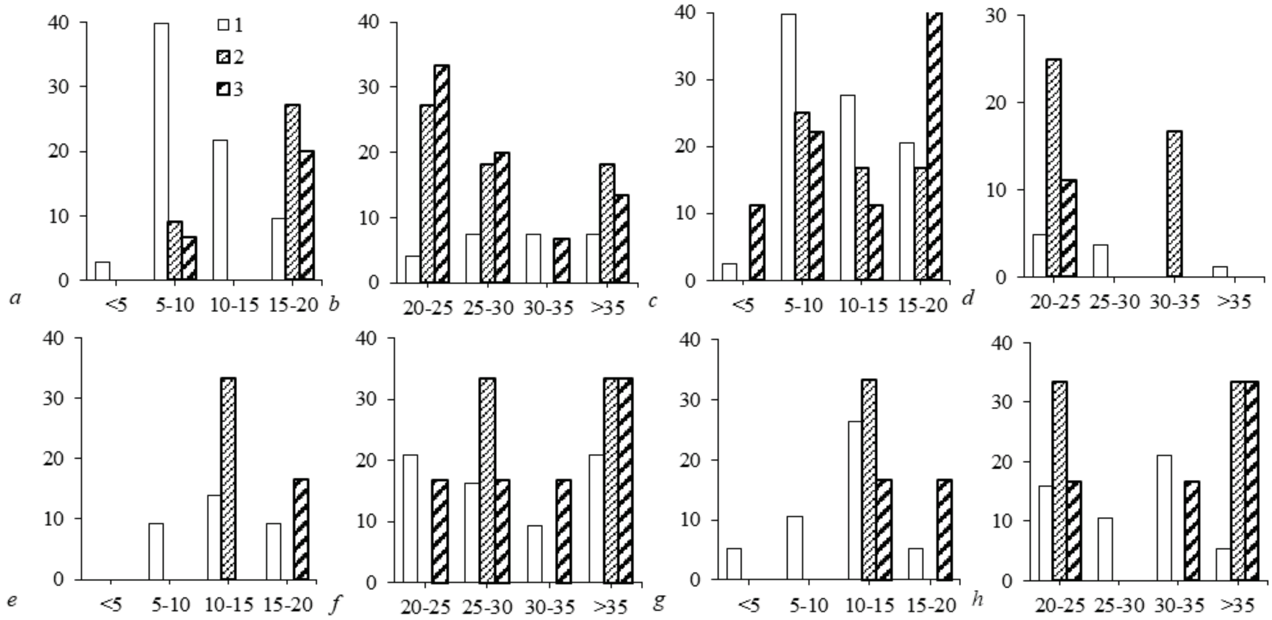

Fig. 5. Dynamics of the size structure of the ichthyofauna (as a percentage of the appropriate groups of fish) of the lentic part of the riverbed depression at the beginning (*1*), middle (*2*) and end (*3*) of the observation period: here abscissa is the size groups of fish (cm); ordinate is percentage (%); *a*, *b* – Cyprinidae, *c*, *d* – Percidae, *e*, *f* – Coregonidae–Esocidae, *g*, *h* – Acipenseridae–Lotidae

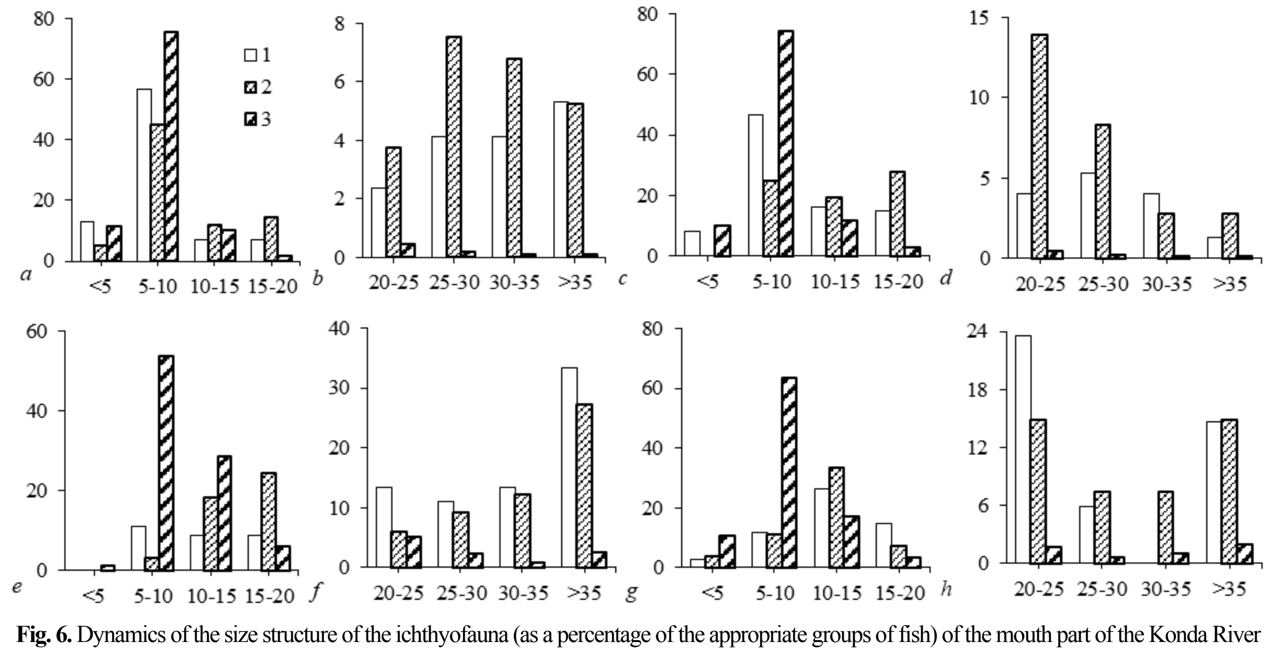

Fig. 6. Dynamics of the size structure of the ichthyofauna (as a percentage of the appropriate groups of fish) of the mouth part of the Konda River at the beginning (*1*), middle (*2*) and end (*3*) of the observation period: here abscissa is the size groups of fish (cm); ordinate is percentage (%); *a*, *b* – Cyprinidae, *c*, *d* – Percidae, *e*, *f* – Coregonidae–Esocidae, *g*, *h* – Acipenseridae–Lotidae

As a result of the analysis, a significant difference was established ($P < 0.05$) in the density of fish groups during the observation period, with the exception of the 1st decade for the groups Cyprinidae and Acipenseridae–Lotidae, as well as during the first and second decades for the group Coregonidae–Esocidae, due to the close values of their density in these time intervals in the conjugate water bodies (Table 2, Fig. 2).

Statistically significant differences were noted when comparing the lotic part of the riverbed depression with the lentic part and mouth of the Konda River ($P < 0.05$). Comparative analysis for the lentic part of the riverbed depression and the mouth of the Konda River did not reveal any statistically significant differences, which in turn reflects the similarity of these water bodies in their ecological role for the life cycle of fish – a transit section of the migration pathway to the floodplain-channel complex (Table 3). To assess the degree of influence of level and temperature factors on the density of fish in the water area of the year-round functioning lotic part of the riverbed depression during the spring flood period, we conducted a regression analysis with the construction of equations. As a result of the analysis performed, it was established that the proportion of the influence of these factors on the density of groups of fish registered by the hydroacoustic method is from 0.312 for a group of Acipenseridae–Lotidae to 0.390 Coregonidae–Esocidae (Table 5).

It should be noted that for the group Acipenseridae-Lotidae, the temperature factor turned out to be unreliable; therefore, it was excluded from the regression analysis. With analyzing ichthyofauna structure in the lotic part of the riverbed depression, the share of the influence of these factors on the total density of fish was 0.374. The determinant, or the indicator of the value of influence of factors exceeding the value of 0.300, reflects the adequacy of the choice of the factors considered by us of the level and temperature of water. The following ANOVA analysis of variance also confirms the adequacy of the choice of factors and the acceptability of the constructed model (equation) for both the total fish density and the density of individual taxonomic groups ($P < 0.05$) (Table 6).

Table 1
Analysis of the mutual correlation of the density of the registered fish groups
in the conjugate water bodies of the floodplain-channel complex of the Irtysh River

		Fish groups	Water bodies										
			L1			K				L2			
			PRC	CRG–ESC	ACP–LTD	CPR	PRC	CRG–ESC	ACP–LTD	CPR	PRC	CRG–ESC	ACP–LTD
Water bodies	L1	CPR	0.99***	0.97***	0.96***	0.57***	0.50**	0.46**	0.39*	0.45*	0.50**	0.40*	0.25
		PRC	–	0.97***	0.98***	0.60***	0.52**	0.48**	0.42*	0.50**	0.52**	0.44*	0.28
		CRG–ESC	–	–	0.98***	0.63***	0.55**	0.51**	0.46**	0.53**	0.55**	0.45*	0.30
		ACP–LTD	–	–	–	0.63*	0.55**	0.53**	0.48**	0.54**	0.56**	0.49**	0.31
	K	CPR	–	–	–	–	0.94***	0.91***	0.87***	0.83***	0.83***	0.71***	0.67***
		PRC	–	–	–	–	–	0.98***	0.96***	0.76***	0.83***	0.69***	0.67***
		CRG–ESC	–	–	–	–	–	–	0.98***	0.71***	0.78***	0.66***	0.65***
		ACP–LTD	–	–	–	–	–	–	–	0.69***	0.75***	0.66***	0.64***
	L2	CPR	–	–	–	–	–	–	–	–	0.97**	0.90**	0.89**
		PRC	–	–	–	–	–	–	–	–	–	0.86**	0.91**
		CRG–ESC	–	–	–	–	–	–	–	–	–	–	0.83**
		ACP–LTD	–	–	–	–	–	–	–	–	–	–	–

Note: CPR – Cyprinidae, PRC – Percidae, CRG–ESC – Coregonidae–Esocidae, ACP–LTD – Acipenseridae–Lotidae; L1 and L2 – the lotic and lentic parts of the riverbed depression; K – mouth of the Konda River; * – correlation is significant at P < 0.05; ** – correlation is significant at P < 0.01; *** – correlation is significant at P < 0.001.

Table 2
Analysis of the mutual correlation of the density of the registered fish groups in the conjugate water bodies of the floodplain-channel complex of the Irtysh River and with the total density and factors of the level (WL) and temperature regimes (T) of water

	Fish groups		Σ_{L1}	Σ_K	Σ_{L2}	WL	T
Water bodies	L1	CPR	1.00***	0.54**	0.46**	–0.47**	–0.33
		PRC	1.00***	0.56**	0.50**	–0.49**	–0.37*
		CRG–ESC	0.98***	0.59***	0.53**	–0.54**	–0.43*
		ACP–LTD	0.98**	0.60***	0.54**	–0.56**	–0.45*
	K	CPR	0.60***	0.98***	0.82***	–0.87***	–0.77***
		PRC	0.52**	0.98***	0.79***	–0.84***	–0.74***
		CRG–ESC	0.48**	0.97***	0.74***	–0.83***	–0.76***
		ACP–LTD	0.42*	0.94***	0.72***	–0.79***	–0.73***
	L2	CPR	0.49**	0.80***	0.99***	–0.89***	–0.80***
		PRC	0.52**	0.83***	0.99***	–0.90***	–0.79***
		CRG–ESC	0.42*	0.71***	0.91***	–0.77***	–0.73***
		ACP–LTD	0.27	0.68***	0.92***	–0.78***	–0.73***
		Σ_{L1}	–	0.56**	0.49**	–0.49**	–0.37*
		Σ_K	–	–	0.81***	–0.87***	–0.77***
		Σ_{L2}	–	–	–	–0.89***	–0.80***
		WL	–	–	–	–	0.96***

Note: CPR – Cyprinidae, PRC – Percidae, CRG–ESC – Coregonidae–Esocidae, ACP–LTD – Acipenseridae–Lotidae; L1 and L2 – the lotic and lentic parts of the riverbed depression; K – mouth of the Konda River; Σ – the total density of fish in the relevant water bodies; ** – correlation is significant at P < 0.05; ** – correlation is significant at P < 0.01; *** – correlation is significant at P < 0.001.

Table 3
Significance of differences of the density of the registered fish groups in the conjugate water bodies of the floodplain-channel complex of the Irtysh River by level of its significance of Tukey's criterion for decades of observations (I, II, III)*

Fish groups	Water bodies	Decades								
		I			II			III		
		L1	K	L2	L1	K	L2	L1	K	L2
CPR	L1	–	0.816	0.940	–	<0.001	<0.001	–	<0.001	<0.001
	K	0.816	–	0.615	<0.001	–	0.497	<0.001	–	0.134
	L2	0.940	0.615	–	<0.001	0.497	–	<0.001	0.134	–
PRC	L1	–	0.992	0.065	–	<0.001	<0.001	–	<0.001	<0.001
	K	0.992	–	0.051	<0.001	–	0.896	<0.001	–	0.992
	L2	0.065	0.051	–	<0.001	0.896	–	<0.001	0.992	–
CRG-ESC	L1	–	0.316	0.846	–	0.334	0.512	–	<0.001	<0.001
	K	0.316	–	0.628	0.334	–	0.943	<0.001	–	0.727
	L2	0.846	0.628	–	0.512	0.943	–	<0.001	0.727	–
ACP–LTD	L1	–	0.487	1.000	–	0.020	0.001	–	0.001	0.002
	K	0.487	–	0.485	0.020	–	0.532	0.001	–	0.925
	L2	1.000	0.485	–	0.001	0.532	–	0.002	0.925	–

Note: see Table 2.

Discussion

Flood-channel complexes, or wetland ecosystems are dynamic and among the most productive and diverse due to their spatial and temporal heterogeneity caused by changes in the water level and the presence of systems of lotic and lentic reservoirs (Ward & Stanford, 1995; Dudgeon et al., 2006; Röpke et al., 2016; Wang et al., 2019) are optimal places for feeding and spawning of river fish (Janáč et al., 2010; Górski et al., 2011). At the same time, flood impulses are the main drivers for the dynamics of aquatic communities, biodiversity and fish numbers (Wang et al., 2019) in floodplains (Baumgartner et al., 2018). The developed floodplain-channel complex of the Lower Irtysh is also a feeding and a spawning place for various species of fish. Fluctuations in temperature and water level are the two main factors affecting the life of hydrobionts, including fish in river floodplain ecosystems (Abrial et al., 2019), while the importance of both hydrological and temperature fluctuations is noted as necessary for interpreting the complex life cycle of fish.

Table 4
ANOVA analysis of variance to detect a significant effect of differences in the density of the registered fish groups in the conjugate water bodies of the floodplain-channel complex of the Irtysh River by Tukey's criterion (F) and the level of its significance (P) by decades of observations (I, II, III)*

Fish groups	Decades	Indicators	
		F	P
CPR	I	1.22	0.329
	II	8.96	<0.001
	III	30.39	<0.001
PRC	I	4.39	0.008
	II	8.05	<0.001
	III	14.93	<0.001
CRG–ESC	I	1.42	0.256
	II	1.32	0.290
	III	11.92	<0.001
ACP–LTD	I	0.59	0.674
	II	11.16	<0.001
	III	4.41	0.008

Note: CPR – Cyprinidae, PRC – Percidae, CRG–ESC – Coregonidae–Esocidae, ACP–LTD – Acipenseridae – Lotidae.

Table 5
Regression analysis and model of fish density dynamics in the lotic part of the riverbed depression during the spring flood depending on the water level (L) and water temperature (T) factors*

Fish groups	Variables and constant of the equation	Indicators		Regression equation
		P	R^2	
CPR	CONST	<0.001	0.366	2.75 – 2.47*L + 0.65*T
	WL	0.002		
	T	0.016		
PRC	CONST	<0.001	0.368	1.15 – 0.97*L + 0.25*T
	L	0.004		
	T	0.027		
CRG–ESC	CONST	<0.001	0.390	0.68 – 0.51*L + 0.12*T
	L	0.005		
	T	0.044		
ACP–LTD	CONST	<0.001	0.312	0.65 – 0.13*L
	L	0.001		
Σ	CONST	<0.001	0.374	5.09 – 4.29*L + 1.10*T
	L	0.003		
	T	0.027		

Note: CPR – Cyprinidae, PRC – Percidae, CRG–ESC – Coregonidae–Esocidae, ACP–LTD – Acipenseridae–Lotidae; CONST – calculated constant; R^2 determinant (share of factor influence); Σ – the total density of fish in the lotic part of the riverbed depression.

Table 6
ANOVA variance analysis of acceptability of model (equation)*

Fish groups	Indicators	
	F	P
CPR	8.05	0.002
PRC	8.14	0.002
CRG-ESC	8.94	0.001
ACP–LTD	13.13	0.001
Σ	8.35	0.001

Note: CPR – Cyprinidae, PRC – Percidae, CRG–ESC – Coregonidae–Esocidae, ACP–LTD – Acipenseridae–Lotidae; Σ – the total density of fish in the lotic part of the riverbed depression.

The decrease in the number of cyprinids in the riverbed depression with an increase in the water level and temperature is explained by their transition to the floodplain, since it is shown (Li et al., 2013) that these are the most significant factors of their spawning activity, for pike migration the most significant factor is water temperature, with males migrating earlier than females (Pauwels et al., 2014). In general, it was established (Górski et al., 2013) that as a result of floods, a heterogeneous environment of the flooded floodplain forms, thus creating habitats for fish with different variations in requirements for environmental factors, which in turn leads to a high diversity of fish communities of the floodplain. It is worth noting that due to the rise in the water level as a result of floods, a connection is formed between parts of the floodplain-channel system of rivers, as a result of which migratory fish are redistributed in different parts of the waters bodies of these systems with heterogeneous and differing habitat conditions, as a result of the flooding of land plants, the availability of food resources and spawning sites increases (Agostinho et al., 2009; Fernandes et al., 2009). Thus, the factor of water level is of fundamental importance in the dynamics of the number and structure of the fish communities in river floodplains (Junk et al., 1989; Wang et al., 2019).

The change in the size structure of the ichthyofauna in water bodies of various types in the floodplain-channel complex of the Irtysh River is primarily due to the mass approach of fish to potential feeding and spawning sites. It is also shown (Sommer et al., 2014) that the structure of fish concentrations and the presence of migrants in floodplain-channel complexes changes as a result of seasonal fluctuations of the factors we are considering – temperature and water level. For fish that migrate to the floodplain for feeding, low water temperature is one of the factors that reduce the success of catching prey (Watz & Piccolo, 2011) and restrain them in the main river. During the period of water level increase (Reinhold et al., 2016), we noted the predominant migration of small fish from the main river to its tributaries, and not vice versa, which was established during the observation period in the Irtysh and Konda rivers.

It is interesting to note that the greatest dynamics of the decrease in the density of fish by the final day of observations were established exactly in the lentic part of the riverbed depression – 12.58 times, compared to the lotic part and the mouth of the Konda River (4.12 and 7.12 times respectively). This pattern is due to the temporary aggregation of fish in the water body with the absence of intense currents (lentic part) until the required temperature and water level indicators, which is beneficial for the fish in terms of energy costs and reduced competition for spawning sites (Brönmark et al., 2014; Krabbenhoft et al., 2014). Subsequently, the migration of fish in the floodplain through the Konda River occurred without the formation of their aggregations in the lentic part of the riverbed depression. That is, the lentic part of the riverbed depression during the spring flood, as well as the lotic part perform the role of a temporary station of fish until the necessary conditions are met. Statistically significant differences in the dynamics of the structure and abundance of fish in the conjugate lotic and lentic sections of the floodplain-channel complex, as well as the spatial-temporal differences in the same areas, are also noted by other researchers (Hurd et al., 2016, Wang et al., 2019).

In the lotic part of the riverbed depression and the mouth of the Konda River, during the observation period, the density of larger fish decreased and the proportion of smaller individuals increased, in the lentic part, on the contrary, during the observation period the proportion of smaller fish decreased and the proportion of larger individuals increased. This pattern is explained by the initial entry into the floodplains of larger specimens of mature fish to spawn, and then smaller ones for feeding (Reshetnikov, 2003). On the other hand, from the perspective of fish relations in the predator-prey system, there is a "shelter" of prey in turbulent areas (lotic part of the riverbed depression and Konda River), due to the increase in the proportion of predators in the water area with a low mixing intensity of water masses and corresponding turbulence (the lentic part) (Vanderpham et al., 2013), because it has been shown that with increasing flow velocity predators are less successful in capturing prey (Bozeman et al., 2019).

For migrant fish, low water temperature also "signals" the absence of flooded floodplain areas due to low water levels (Rakowitz et al., 2008), which in turn implies increased competition for spawning areas and food resources. (Krabbenhoft et al., 2014; Winemiller et al., 2014), because for successful spawning of cyprinids, percids fish and pike, flooded terrestrial vegetation is necessary (Grift et al., 2003; Janáč et al., 2010; Górski et al., 2011), which then becomes an important habitat for the larvae and young fish of these species (Grift et al., 2003, Janáč et al., 2010). At the same time, the correlation between the factors of temperature and water level is very high ($R = 0.96$, $P < 0.05$). It should be noted that for predatory fish species, the most likely overlap of trophic niches is noted in the spring and autumn periods (Raborn et al., 2004). Movement of fish into the floodplain reduces the density of their aggregations in the main river, which in turn allows them to level out the competition for food and the risk of predation arising from the high density of fish (Baumgartner et al., 2018), as a result of their redistribution in the floodplain, thus ensuring higher survival rates and growth of fish (Welcomme, 1979; Lucas & Baras, 2001).

In turn, it was shown (Górski et al., 2011) that when flooding is synchronized with an increase in temperature, the success of replenishment of populations of river fish species is enhanced, which is noted in our study as a highly dynamic decrease of the density of fish in the conjugated water bodies, which correlates with the main factors of the aquatic environment during the spring flood period – temperature and water level. The difference in the physical parameters of conjugated water bodies, including the hydrological regime (Vítek et al., 2012; Granzotti et al., 2019) formed on the intensity and direction of flow, the depth (Reinhold et al., 2016; Granzotti et al., 2019), flood levels (Espínola et al., 2016, Jin et al., 2019), temperatures, and the presence of macrophytes (Granzotti et al., 2019) are the determining factors for fish numbers, their distribution, species diversity and size structure (Górski et al., 2012; Vítek et al., 2012; Espínola et al., 2016; Reinhold et al., 2016). In our study, the maximum density of fish was observed in the hydrological complex high-turbulent water environment of the lotic part of the riverbed depression.

Thus, the dynamics and differences of the taxonomic and size structure of the ichthyofauna in the conjugate water bodies of the floodplain-channel complex in the period under consideration are explained by the combination of environmental conditions, which in turn cause behavioural responses of fish of the Irtysh River, at the same time, the complex of conditions of the areas under consideration ultimately determines their role in the fish life cycle.

Conclusion

As a result of this work, we enlarged the understanding of the regularities of the distribution of the size and taxonomic groups of the fish population from non-salmon families in floodplain-channel complexes, on the example of the large Ob-Irtysh river basin in the boreal zone. It has been shown that in spring the larger fish first leave their wintering places due to the transit to the floodplain, then the smaller fish, thereby securing a more successful spawning selection. We established the ecological role of various, by degree of turbulence and hydrology, features of conjugated water bodies within the floodplain-channel complex of the Irtysh River during the spring flood: the lentic part of the riverbed depression and the mouth of the tributary (Konda River) are transit migration sections. At the same time, the lentic part of the riverbed depression additionally performs the role of a temporary station that is advantageous from an energy point of view for fish before the onset of the necessary indicators of level and temperature factors. We established a statistically significant high inverse correlation between the dynamics of fish density in the water area of transit migration sites: the mouth of the Konda River and the lentic part of the riverbed depression, depending on temperature and water level, which in turn reflects the importance of these factors. The value of their effect on reducing the density of fish at the wintering place is ≈40%. It is worth noting that the considered factors are synchronized, because they have a very high direct correlation. The constructed acceptable regression models make it possible to adequately predict the dynamics of density and, accordingly, the number of fish in the initial location (wintering places) of their spring migration depending on the factors of temperature and water level during the spring flood.

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