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ICHTHYOLOGY

Migrations of Young Fish in Regulated Rivers: Effects of Ecological Filters (Review)

D. S. Pavlov[a], V. N. Mikheev[a, *], and V. V. Kostin[a]

[a]*Severtsov Institute of Ecology and Evolution, Russian Academy Sciences, Moscow, Russia*

**e-mail: vicnikmik@gmail.com*

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Abstract—Unlike in nonregulated rivers, new ecological filters are formed in artificial reservoirs: structures (gradient zones between biotopes) which affect the behavior and distribution of juvenile fish and therefore change parameters of the downstream migration. One distinct feature of such filters is their selective effect on different species and age groups of migrants when they pass boundaries between biotopes. The differential transparency of boundaries considerably affects the composition of migrants and dispersal of juvenile fish over biotopes. These suggestions are confirmed by the data of long-term studies on the downstream migration of juvenile Cyprinidae and Percidae in several reservoirs in Eurasia: Sheksna (Sheksna River), Ivankovo (Volga River), Kapchagay (Ili River), and Sarez (Murghab River) Reservoirs. The formation of ecological filters is shown in the zone of wedging-out backwaters (lotic–limnetic transformation) and in the zone between the littoral (resident) and pelagic (migratory) biotopes in the reservoir and in the near-dam broads. Emigration of juveniles from the reservoir depends on the location of the water intake (deep-water or surface) and overlapping of water intake zones with those of the spatial distribution of juvenile fish. The different selectivity of water intake sites of the hydroelectric power station located not far from each other and of a navigation lock forms different (in species and age composition) complexes of emigrants. The mechanisms and consequences of functioning ecological filters and ecological barriers are considered.

Keywords: juvenile fish, migratory behavior, downstream migration, ecological filters, river continuum, regulated rivers, reservoir, environmental heterogeneity, fragmentation of river system

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The anthropogenic transformation of river systems associated with river regulation significantly changes the conditions for the existence of aquatic organisms, primarily fish. Disturbances in the vital functions of fish such as the interruption of migration routes, the disappearance of spawning grounds, and the formation of suffocation zones are most often in the limelight. It is well known that the peak of mortality in fish populations occurs during the larval period, when fish switch from endogenous to exogenous nutrition and losses from vertebrate and invertebrate predators, as well as from adverse abiotic conditions, are also especially high (Fuiman and Magurran, 1994; May, 1974). During this period, most fish, despite their weak locomotor and orientational capabilities, resettle (downstream migration), which, under the conditions of regulated rivers, creates additional obstacles for migrating juveniles and poses new environmental risks (Pavlov et al., 2019; Kramer et al., 1997; Northcote, 1984). Such risks can also occur as a result of the new hydrological conditions in the rivers (the formation of vast spaces without landmarks and a constant flow, or the appearance of deepwater areas with vertical gradients).

In unregulated rivers, migratory fish juveniles move mainly with the water flow (downstream migration), which significantly reduces the energy costs of migration. Contrary to the recent opinion that downstream migration is a predominantly passive process (Wolter and Sukhodolov, 2008), more and more evidences show the key role of fish behavior in regulating their migration at the very early stages of the life cycle (Lechner et al., 2016; Pavlov and Mikheev, 2017; Schludermann et al., 2012).

For most common fish species in the rivers of Eurasia, migration takes more than one day and, in addition to general downstream movement, includes repeated transitions from littoral (resident) biotopes to a transit stream (migratory biotope) and vice versa. These transitions include the crossing of boundary gradient zones separating biotopes (Lechner et al., 2013; Pavlov and Mikheev, 2017). The boundary zones between biotopes can have different (differential) transparency for juveniles of different fish species, acting as environmental filters that affect migration characteristics. In general, fish migration is not just a movement from the initial to the final point, but a complex process of overcoming a heterogeneous environment consisting of a series of biotopes of different scales separated by physical boundaries/gradients. Overcoming these boundaries depends both on the properties of the borders themselves and on the characteristics of the migrants.

River regulation, a process of dam construction and reservoir formation, dramatically changes the hydrological and biotopic structure of a river (Dynesius and Nilsson, 1994; Regulated Rivers, 1984; Sedell et al., 1990; Zwick, 1992). Dams and reservoirs act as ecological barriers that interfere not only with the spawning migration of adult fishes (Pelicice et al., 2015), but also significantly affect the intensity of downstream migration of juveniles (Pavlov et al., 2019). The main role in the functioning of these barriers is played by the morphological (topographic) complexity of the reservoir and the intensity of water exchange (Pavlov et al., 2019).

The topographic complexity of the regulated waterbody determines the hierarchy of biotopes/environments with boundary zones with different transparency for migrants. Juvenile migrations, the most vivid manifestation of which is downstream migration, are not limited only to movement in the stream. Migration mechanisms include both biological (behavior) and hydrophysical (lateral, vertical drift) elements. The behavior and distribution of migrating juveniles in a water stream (migratory biotope) is the most studied part of migration (Pavlov, 1994; Pavlov and Mikheev, 2017). Much less attention has been paid to the movements of migrating juveniles between biotopes (Pavlov et al., 2019). Migrants can drift both in horizontal and vertical directions, crossing border zones that act as ecological filters. It is possible that, in a regulated water body—a reservoir in which the water outflow is regulated by a dam—such filters are formed in zones with the most pronounced topographic and hydrological gradients. These zones occur primarily on the boundaries between littoral biotopes and the vast water body of the open part of the reservoir, in the dam broad, and also in the area of wedging-out backwaters, where the lotic conditions of the remaining part of the river (or its tributaries) are rather sharply replaced by the limnetic conditions of the reservoir.

We analyze the spatial structure of migration and consider littoral areas to be resident biotopes and the pelagic part of the reservoir to be the migratory biotope (Pavlov et al., 2019). In an unregulated river, their analogues are coastal shallow water and a transit flow of water. New hydrological structures appear in a reservoir, and they have no analogues in a natural river.

The aim of this work is to test the hypothesis that river regulation results in the formation of new ecological filters. We assume that the mechanisms for the formation of ecological filters that appear in the area where the backwater is wedged out, at the boundaries between the migratory and resident biotopes, and in the dam broad are different. To verify these assumptions, we use the results of studies on the downstream migration of juvenile fish species (mainly cyprinids and percids) from reservoirs with different types of drainage withdrawal, as well as data on the spatial distribution and migration behavior of juvenile fishes in a natural river.

Materials and Methods

Data and empirical results on the downstream migration of juvenile fishes and their distribution in regulated rivers which have undergone the necessary processing and initial analysis and are suitable for meta-analysis to identify the functioning patterns and mechanisms of ecological filters are taken from a number of our own publications devoted to the downstream migration of juvenile fish in the most in-depth studied river systems of Eurasia (Pavlov et al., 1981, 1991, 1994, 1999). Thus, the main methodological approach of this work is a new analysis of already published materials.

Field and experimental studies of the spatial and temporal patterns of the downstream migration of river juvenile fish were carried out in the upstream of Volga River and reservoirs of the European part of Russia: Ivankovo (Volga River, 1979–1980 and 1989–1990) and Sheksna (Sheksna River, 1982–1983); as well as in Central Asia: Kapchagay (Ili River, 1972–1975) and Sarez (Murghab River, 1986–1988). The data necessary for assessing the seasonal and diurnal dynamics of downstream migration, the distribution of juvenile fish in migratory and resident biotopes, and the intensity of fish emigration from the reservoir, as well as hydrophysical and topographic characteristics, were obtained on a unitary methodological basis that has been described in detail earlier (Pavlov et al., 1981, 1991, 1994, 1999). Most attention is paid to the quantitative aspects of the migration of juveniles of two groups of river fishes: cyprinids (Cyprinidae) and percids (Percidae). Altogether, we use the data for juveniles of 29 fish species: smelt *Osmerus eperlanus* L., grayling *Thymallus thymallus* L., European weather loach *Misgurnus fossilis* Fatio, European bullhead *Cottus gobio* L., gobies *Rhinogobius cheni* Nichols and s *Rhinogobius brunneus* Temminck et Schlegek, Kessler's loach *Paraschistura kessleri* Günther, eastern crest loach *Paracobitis longicauda* Kessler, Turkmenian crested loach *Metaschistura cristata* Berg, stone loach *Barbatula barbatula* L., Transcaspian marinka *Schizothorax pelzami* Kessler, Ili marinka *Schizothorax pseudaksaiensis* Herzenstein, grass carp *Ctenopharingodon idella* Valenciennes, *Carassius gibelio* Bloch, silver carp *Hypophthalmichthys molitrix* Valenciennes, bream *Abramis brama* L., asp *Aspius aspius* L., dace *Leuciscus leuciscus* L., Aral barbel *Luciobarbus brachycephalus* Kessler, minnow *Phoxinus phoxinus* L., gudgeon *Gobio gobio* L., common nase *Chondrostoma nasus* L., roach *Rutilus rutilus* L., common bleak *Alburnus alburnus* L., common rudd *Scardinius eryth-*

rophthalmus L., zander *Sander lucioperca* L., Volga pikeperch *Sander volgensis* Gmelin, ruffe *Gymnocephalus cernuus* Guldenstadt, common perch *Perca fluviatilis* L., and Balkhash perch *Perca schrenki* Kessler (*Annotirovannyi katalog* ..., 1998; Salnikov, 2014).

Young fish migrating in a water stream were caught with conical nets, which were placed along transverse sections or in a vertical series according to the terms and objectives of the study. The exposure was usually 10–20 min, depending on the abundance of fish and the amount of suspension in the water. The seasonal dynamics of downstream migration was studied year-round (twice a month)—in most detail from May–April to September (four times a month). For the studies of diurnal dynamics of downstream migration, samples were usually taken every 1–2 h. In the pelagic part of the reservoir with a weak runoff, juveniles were caught by trawling using conical nets at different horizons. A detailed description of the volume of material, sampling, fixing, and processing samples of juvenile fish in the river and in the open part, as well in the dam broad and downstream pool of the reservoir, is given in a number of publications (Pavlov et al., 1981, 1991, 1994, 1999). The concentration of migratory fish was expressed by the number of individuals per 1000 m^3.

Ecological Filter in the Upper Part of the Reservoir Determined by the Lotic–Limnetic Transformation

In the upper part of the reservoir, in the backwater zone, the river continuum is disrupted, which leads not only to changes in the living conditions of river fish, but also dramatically changes the situation for migrating juveniles. As examples illustrating the nature and extent of these changes, we choose the wedging-out zone of the backwater of Sarez (Murghab River) (Pavlov et al., 1994) and Kapchagay (Ili River) (Pavlov et al., 1981) reservoirs, a comprehensive study of which were carried out in 1986–1988 and in 1972–1975, respectively. One characteristic feature of these rivers is the increased muddiness of the water, which makes it possible for juvenile fish to migrate all day round, in contrast to rivers with clear water, where juveniles migrate only in the dark. As a result of the round-the-clock drift, the daily duration of downstream migration of juveniles in the Ili River was ~8 times more than, for example, in the Upper Volga, where it lasts only 2.5–3 h a day.

The main features of the backwater wedging-out zone during the transition of the Ili and Murghab rivers to reservoirs indicate a sharp drop in the flow velocity (~3–10 times over 8–9 km), intense sedimentation, and a change in the heterogeneity of the environments according to a number of parameters (depth, bottom topography, flow rate, water transparency (Fig. 1), and the number of juvenile predatory fish).

The combined effect of these factors leads to a significant inhibition of downstream migration of juvenile river fish and an increase in their mortality. The mechanisms of these phenomena are the following: Inhibition of downstream migration occurs not only due to a decrease in the average flow rate, but also due to the release of juveniles from the channel flow into the coastal shallow waters. In shallow waters of the Ili River, where the flow rate is noticeably lower than in the midstream and the water transparency is much higher, migrants (larvae of *Rh. brunneus*, *A. brama*, *L. leuciscus* and other species) become easy prey for predatory fish (*Asp. aspius*, *S. lucioperca*, and perch). Mortality from predators, as well as the death of eggs and larvae in areas of intense sedimentation (Fig. 1), determined the high total death of migrating juveniles of river origin in the backwater wedging-out area. It is impossible to give exact quantitative estimates based on the data, but the abundance of juvenile fish species that accumulate in the shallow part of the backwater wedging-out zone suggests that the inhibition of migration and death from predators are more pronounced for some species than for others. The inhibition of downstream migration in the backwater wedging-out area of the Kapchagay Reservoir is characterized by a delay index (the rank difference in the number of species in the Ili River and in the backwater wedging-out area). The larger the value of this index is, the greater part of the downstream migrants stays in the backwater wedging-out area. Littoral fishes are more likely to stay in this zone than pelagic ones (Fig. 2).

Thus, the backwater wedging-out area acts as an ecological filter which determines differential mortality and reduces the replenishment of the juvenile pool in the reservoir. The effect of this filter affects the formation of the number of juvenile fish in the reservoir. Replenishment sources are spawning grounds of the reservoir itself and juveniles drifting from the river (Pavlov et al., 1981). The filter in the backwater area not only reduces the total number of migrants, but, acting selectively, reduces the number of some species much more than others. Due to siltation of eggs and larvae, as well as predation press, the early juveniles of grass carp, silver carp, and Aral barbel almost do not enter the reservoirs. Obviously, similar processes associated with ecological filters can also be observed at the sites where tributaries flow into the reservoir.

The influence of the lotic–limnetic transformation of the regulated river is associated not only with the wedging-out area of the reservoir backwater. The construction of reservoirs and corresponding sharp change in lotic conditions to limnetic ones lead to an equally sharp change in the quantitative and qualitative composition of the ichthyofauna due to the loss of, first and foremost, stenobiont rheophilous species and pelagophils. Using the example of 13 different types of reservoirs, it was shown that, in the first years after the construction, the number of fish species in reservoirs decreases 14–78% when compared to an unregulated

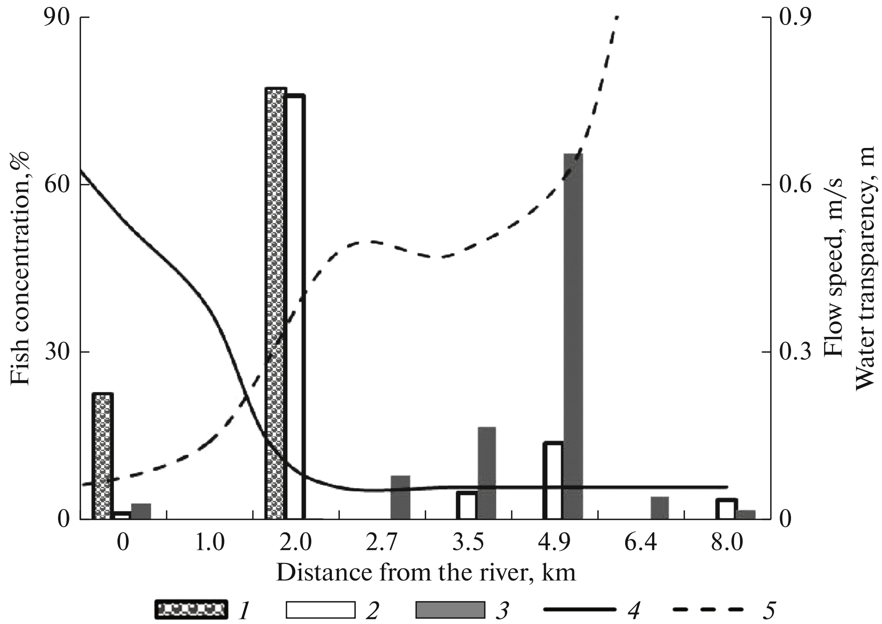

Fig. 1. Distribution of eggs (*1*) and larvae of herbivorous fish (*Ctenopharyngodon idella, Hypophthalmichthys molitrix*) (*2*) and *Rhinogobius cheni* (*3*) in the backwater wedging-out area of the Sarez Reservoir: (*4*) flow velocity, m/s; (*5*) water transparency, m. 100% is the total concentration at all sampling stations. Differences in the shares of downstream migrants at different stations are significant (Kruskell–Wallace test, $p < 0.05$) for all fish species. Sample size, spec.: for herbivorous fish 131 eggs, 53 larvae, for *Rh. cheni* 8290 (according to (Pavlov et al., 1994)).

river (Kamilov, 1973; Kuderskii, 1986; Pavlov et al., 1994). Rheophilous fish species and pelagophils can partially pass through the backwater wedging-out zone, but their fate depends on the presence of habitats for these fish in reservoirs, and the contribution to the number of ichthyofauna sharply decreases compared to the initial one. Some rheophilic species disappear completely from the reservoir. For example, in the basin of the Sarez Reservoir, there are four species that are not found in the reservoir itself (the Transcaspian marinka, Kessler's loach, eastern crest loach, and Turkmenian loach); in the Ivankovo Reservoir basin there are seven such species (*Th. thymallus, B. barbatula, M. fossilis*, *C. gobio*, *Ph. phoxinus, Gob. gobio,* and *Ch. nasus*) (Pavlov et al., 1981, 1994).

Movements between Resident and Migratory Biotopes in a River and a Reservoir

Numerous movements from littoral (resident) biotopes to a transit stream (migratory biotope) and back are associated with the daily rhythm of downstream migration. These migrations are accompanied by the crossing of the boundary gradient zones separating biotopes on the way to the transit stream at evening twilight and at the return to the littoral in the morning (Lechner et al., 2013; Pavlov and Mikheev, 2017). In natural rivers, these zones are, as a rule, rather narrow, which allows even fish larvae to make active selections and drift under sharp gradients (Pavlov and Mikheev, 2017). Although the movements between the resident and transit biotopes during migration are carried out by juveniles of most species of river fish, the parameters of these movements can vary significantly (Pavlov and Mikheev, 2017). In other words, the border zones between biotopes can have different (differential) transparency for juveniles of different fish species, thus acting as ecological filters that affect the characteristics of migration and the composition of the fish population in different biotopes.

In an unregulated river with sufficiently clear water, the downstream migration of juveniles in the channel stream (migratory biotope) occurs predominantly at night (Fig. 3a), which prevents juveniles from being eaten by predators. We observe quite a different picture in the reservoir (Fig. 3b): the concentration of juveniles in the migratory biotope (pelagial of the reservoir) is approximately the same in daylight and dark. This is apparently associated with a significant expansion of the coastal shallow-water zone and the border zone between the littoral and the pelagic zone, which does not allow migrating juveniles to move between these biotopes in the morning and evening twilight. In addition, the orientation of juveniles in the pelagic of the reservoir is complicated by large distances and multidirectional and variable wind currents that do not have a clear structure and direction. Only part of the migrants can leave the pelagic in the daylight and conceal themselves in shallow waters. A significant part of migratory juveniles lacking shelter perishes

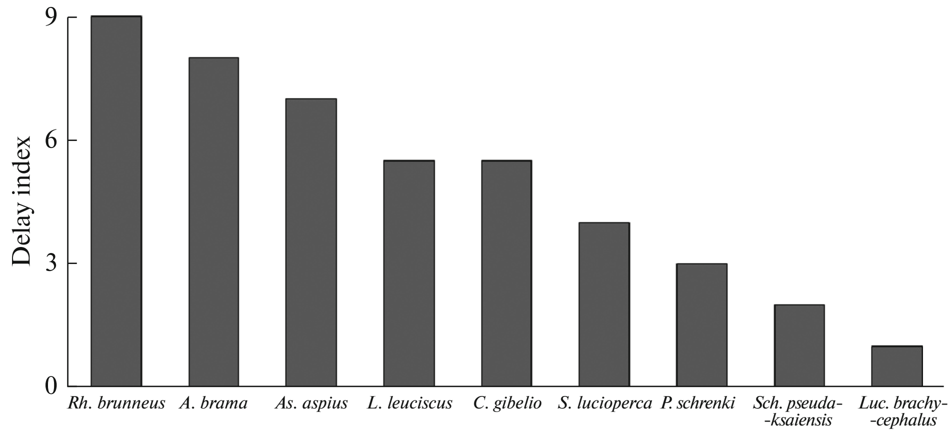

Fig. 2. Delaying stay of migrants from the Ili River in the backwater wedging-out area of the Kapchagay reservoir. Sample size, inds.: *Rhinogobius brunneus* 194; *Abramis brama* 154; *Aspius aspius* 162; *Leuciscus leuciscus* 706; *Carassius gibelio* Bloch 69; *Sander lucioperca* 1626; *Perca schrenki* 504; *Schizothorax pseudaksaiensis* 156; and *Luciobarbus brachycephalus* 1110.

from predators (carnivorous fish and fish-eating birds).

The effect of the ecological filter between the littoral and pelagic biotopes of the reservoir during downstream migration does not affect the entry of different species into the migratory biotope and their further drift to the dam broad. Figure 4 clearly shows that percids (zander and perch) are much more associated with the pelagic part of the reservoir in comparison to cyprinids (*R. rutilus, A. brama, Alb. alburnus*, and *Sc. erythrophthalmus*). It is further shown that the differences between cyprinids and percids, along with the features of their vertical distribution in the dam broad, significantly affect the characteristics of the emigration of these fish groups from the reservoir.

Selective Emigration from the Reservoir with Different Types of Drainage Withdrawal: Hydroelectric Power Station Intake and Navigation Lock

Young fish migrating through the reservoir accumulate in the dam broad (Konobeeva, 1983; Pavlov et al., 2019), from which it emigrates to the downstream pool through the water intakes of the hydroelectric power station or navigation locks. The ratio of species in the migrant complex passes through the hydroelectric station and the gateway of the Sheksna Reservoir varies significantly (Fig. 5). In turn, the abundance ratio of the common fish species emigrating both through hydroelectric power stations and through a navigation lock differs from that in the dam broad pool (Pavlov et al., 1991, 1999).

The basis of the number of migrants through the water intake of the Sheksna reservoir hydroelectric power station comprises smelt and percid fishes (perch, zander, Volga pikeperch, and ruffe). In cyprinids, on the other hand, migration through the navigation lock is more pronounced (Fig. 5). Such significant differences in the patterns of emigration from the reservoir through the water intake of the hydroelectric power station and the navigation lock are determined by (1) parameters of the drainage zones (the deep-water intake of the hydroelectric power station covers the open part of the upstream pool, including, in decreasing order bathypelagial, bathyal, epipelagial and sublittoral; the navigation lock takes water from the surface layers, epipelagial, as well as sublittoral and littoral) and (2) features of fish ecology and behavior.

In a generalized form, the complex of ecological and behavioral properties of species and age groups, primarily the spatial distribution features and their interaction with the zones of water intake, is reflected in the concept of the "ecological zonality of water intakes" (Pavlov et al., 1999). This approach is especially useful for analyzing and comparing the patterns of downstream migration from a large number of water bodies with different conditions of water intakes. In the specific case considered in this work, it is clearly seen that, in the regulation of emigration from the reservoir through different types of water intakes, the environmental zoning of water intake (Fig. 6) and the vertical distribution of fish (Fig. 7), discussed below, dominate.

The prevalence of cyprinids in the littoral zone of the upstream pool and percids in the pelagic zone (Fig. 6b) is naturally reproduced in the ratio of these groups in the relative abundance of migrants through the hydroelectric station and navigation locks (Fig. 6c). Cyprinids predominated among the navigation lock migrants, and percids predominated among the migrants that passed through hydroelectric power stations.

Emigration patterns associated with the features of the vertical distribution of juvenile cyprinids and percids are especially evident when comparing the migration of different age groups, i.e., early and late larvae (Fig. 7). Most of the early larvae of both cyprinids and

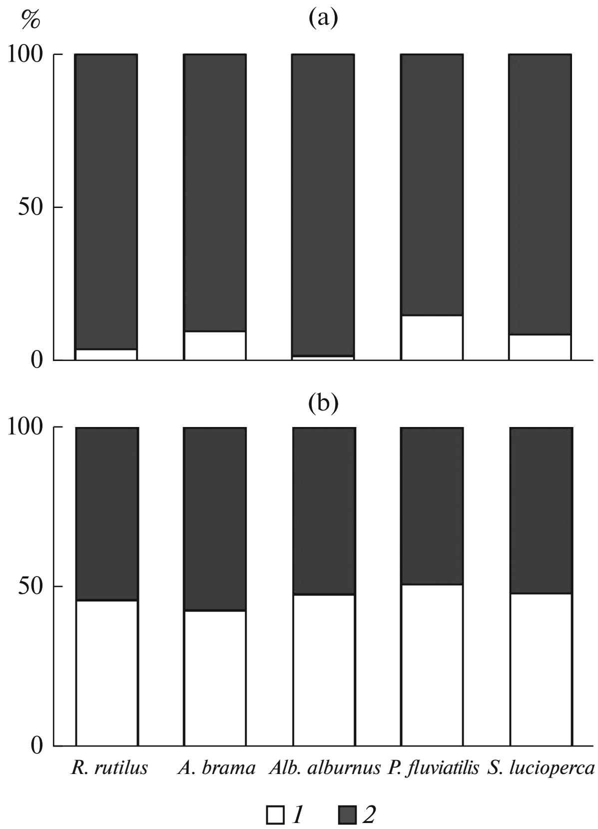

Fig. 3. Average concentration of juvenile fish in the migratory biotope (channel stream) of the Upper Volga (a) and in the Ivankovo Reservoir (pelagial) (b): (*1*) day and (*2*) night. Day and night differences in average juvenile concentrations in the river channel of the river were highly reliable (ratio Student's test, $p < 0.001$), and in the pelagic zone of the reservoir they were unreliable ($p > 0.05$) (according to (Pavlov et al., 2019)).

percids migrated through the navigation lock (Fig. 7b), which is determined by their predominantly littoral and epipelagic distribution. The deepening and drift of late larvae into the open part of the reservoir sharply increased the proportion of migrants through the water intake of the hydroelectric power station when compared with the navigation lock (Fig. 7c).

It should be noted that the total number of percid larvae among migrants is almost an order of magnitude higher than that of cyprinids. The tendency to a greater attraction to the pelagic zone (Fig. 4) and to a greater deepening (Fig. 7a) of percids in ontogenesis creates the preconditions for a more intensive emigration of percid juveniles from the upstream pool of the reservoir. Thus, both ecological filters, the zone between the resident and migratory biotopes of the reservoir and the interaction zone between the water intakes and the biotopes of the dam broad, determine the higher migration activity of juvenile percids compared to juvenile cyprinids in a regulated river.

Fragmentation of the River Continuum during Water-Intake Regulation and a Variety of Ecological Filters

Most rivers create a continuum of geomorphological, physicochemical, and biological characteristics (Sedell et al., 1989; Vannote et al., 1980) which form favorable conditions for the life and migration of juvenile fish. The upstream location of the spawning grounds from the feeding areas of the juveniles for most fish allows larvae and young fish to effectively use the transport capabilities of the water flow during dispersal and when searching for optimal feeding conditions. Representing a continuum in the longitudinal direction, the river is heterogeneous in the transverse direction, which is expressed in the existence of rather sharp topographic, hydrophysical, and hydrobiological gradients that create biotopic heterogeneity for hydrobionts, in particular, for migrating juvenile fish (Wiens, 2002). Since migration is not a monotonous process, but an alternation of flow movements (migratory biotope) and rest/feeding in the littoral (resident biotope), the natural heterogeneity of the river creates the necessary conditions for downstream migration as a stepwise process (Pavlov et al., 2019; Pavlov and Mikheev, 2017). Young river fish are well-adapted to such heterogeneity during its long evolution. In particular, the sharp small-scale hydrophysical gradients between the migratory and resident biotopes allow migrants to leave the resident biotope regularly at evening twilight and return to the littoral by dawn when the night migration ceases in the stream (Pavlov et al., 2019).

Biotopic heterogeneity has a completely different character in a regulated river, and the fish probably have not yet developed the necessary behavioral adaptations. Various environmental filters are added to the new artificial heterogeneity, in addition to ecological barriers (dams and vast reservoir spaces that violate both spawning and downstream migrations). They play the important role of the modifier of downstream migration of juvenile fish.

It is known that environmental heterogeneity is the biotopic basis for the formation of metapopulations (Hanski, 1998; Lima and Zollner, 1996). Migrations are the processes that bind the elements of metapopulations (Burgess et al., 2012; Day et al., 2019). In a natural river, fish are adapted to using the river continuum for all types of migrations (spawning, feeding, and wintering). River regulation changes the nature of heterogeneity. Ecological barriers interrupt migrations and ecological filters change the characteristics of migrations in different ways for different species and age groups of fish. The river continuum breaks up into several partially isolated biotopes separated by ecological barriers and filters with different mechanisms of influence not only on fish migration, but also on the structure of populations and communities.

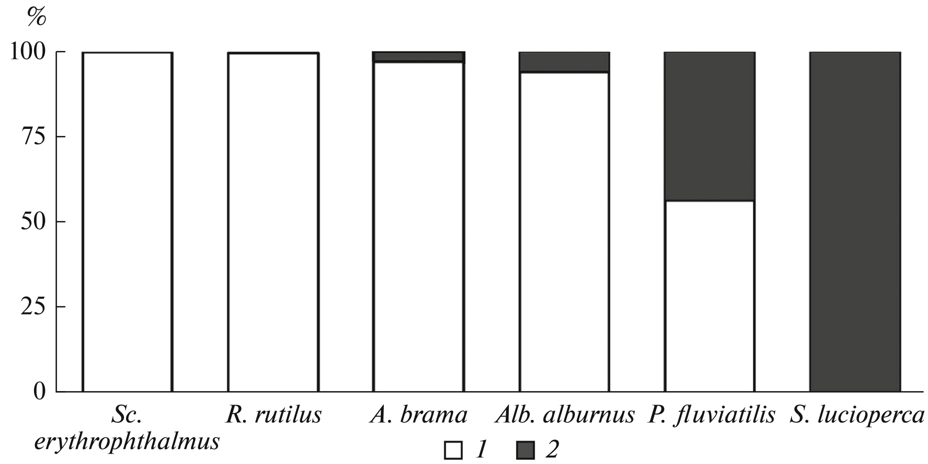

Fig. 4. Average relative concentration (%) of cyprinids and percids during downstream migration in the resident (*1*) and migratory (*2*) biotopes of the Ivankovo reservoir. 100% is the total concentration of a single species. The differences between the species are significant (ratio Student's test, $p < 0.01$) for all pairs of species except for *R. rutilus* with *Sc. erythrophthalmus* ($p = 0.12$).

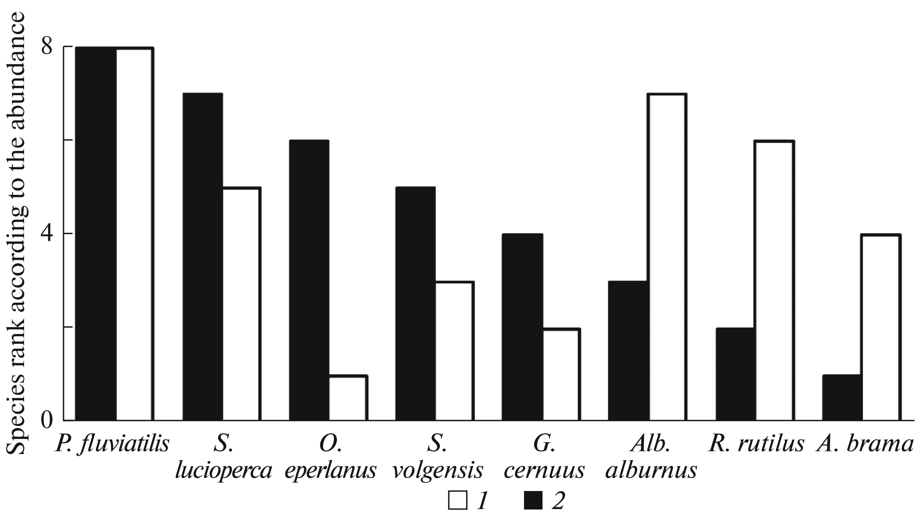

Fig. 5. Relative abundance (ranks) of downstream migrants that pass through the water intakes of the Sheksna hydroelectric station (*1*) and the navigation lock (*2*). Sample size (hydroelectric station/navigation lock), ind.: *P. fluviatilis* 22053/5438, *S. lucioperca* 2469/203, *O. eperlanus* 2221/27, *S. volgensis* 548/79, *G. cernuus* 327/63, *Alb. alburnus* 298/465, *R. rutilus* 79/346, *A. brama* 43/161.

The variety of environmental filters depends primarily on differences in physical structures that determine their different permeability for different species (groups) of migrants (Zollner and Lima, 1999). These include morphological (topography of the bottom and coastline and topographic heterogeneity of the coastal zone) and hydrophysical characteristics (speed and gradient structure of the stream, vectorization and variability of currents, muddiness, and temperature). These characteristics affect not only migration, but also other aspects of fish behavior. In the backwater wedged out area in rivers with high muddiness, the migration of early juveniles can be strongly affected by sedimentation, which leads to the death of pelagic eggs and early larvae. The vast volumes of water in reservoirs with a lack of landmarks and a variable current structure significantly reduce the rate of downstream migration (Fahrig, 2007).

The mechanisms that reduce downstream migration in the reservoir are associated not only with the difficult movement of juveniles between the resident and migratory biotopes, but also with the complex and variable structure of the currents, often without a clearly distinguishable stream flow. On the scale of the entire reservoir, the slow of the downstream migration may be due to the high level of morphological (topographic) complexity of the reservoir (Pavlov et al., 2019). The selective emigration of juveniles from the

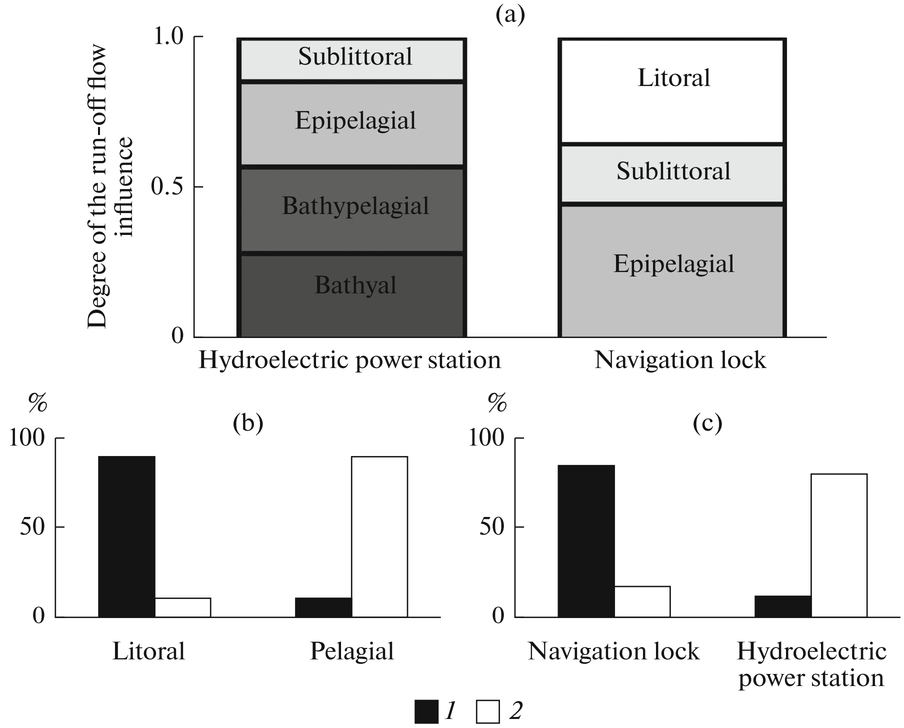

Fig. 6. Scheme of ecological zoning of the water intake (a) and relative abundance (%) of juvenile cyprinids (*1*) and percids (*2*) that inhabit the Sheksna Reservoir (b) and emigrate from it (c). 100% is the total number of fish of the family in all ecological zones or in the migration through both water intakes. Sample size, ind.: cyprinids 7327 and percids 51774. Differences in the ratios of cyprinids and percids in various ecological zones and during migration through different water intakes are significant (ratio Student's test, $p < 0.01$).

reservoir through the dams mostly depends on the nature of the water intake (deep or surface) and the interaction of the runoff currents with the biotopes of the upstream pool (littoral, bathyal, and epipelagial). In addition, in the zones of ecological filters that occur during the regulation of rivers, the characteristics of migrations (speed, direction, and synchronism) change significantly; they are often characterized by increased migrant mortality.

Ecological filters result in a sharp three-time modification of the species and quantitative composition of migrants in the river—reservoir—downstream pool section. The first modification is determined by the different transparency of the filter associated with the lotic—limnetic transformation, primarily in the backwater wedging-out area and, for some rheophilic species, in the whole reservoir. The second modification is related to the conditions of fish migration through the reservoir, both on the scale of the entire reservoir (water exchange and topographic complexity of the reservoir) and during the transition from a resident to a migratory biotope and vice versa. The third modification depends on the coincidences/mismatches of two spatiotemporal structures, the distribution structure of fish in the dam part and the hydraulic structure of the water intake. These migration modifications result in significant changes in the quantitative, species, and age composition of the migrants. For example, of the six species of common migrants in the Ili river upstream of the Kapchagay Reservoir (zander, barbel, dace, grass carp, Balkhash perch, and Ili marinka), only one species rolls from the reservoir itself, the zander.

CONCLUSIONS

In a heterogeneous environment, differences between populations or communities can be formed not only due to differences in abiotic and biotic conditions between habitats, but also due to the influence of ecological barriers and filters that modify the migratory activity of animals. Ecological barriers interrupting/aggravating migration or ecological filters providing a selective transition from one biotope to another for different fish species affect the formation of populations and communities.

In an unregulated river, the interaction between different intrapopulation groups of fish can, to some extent, be disrupted by a large distance, sometimes by natural barriers (waterfalls and lakes), but, in general, movements of different lengths, including long migrations, occur along the entire length of the river continuum. In a regulated river, on the contrary, several biotopes partially isolated from each other appear: the

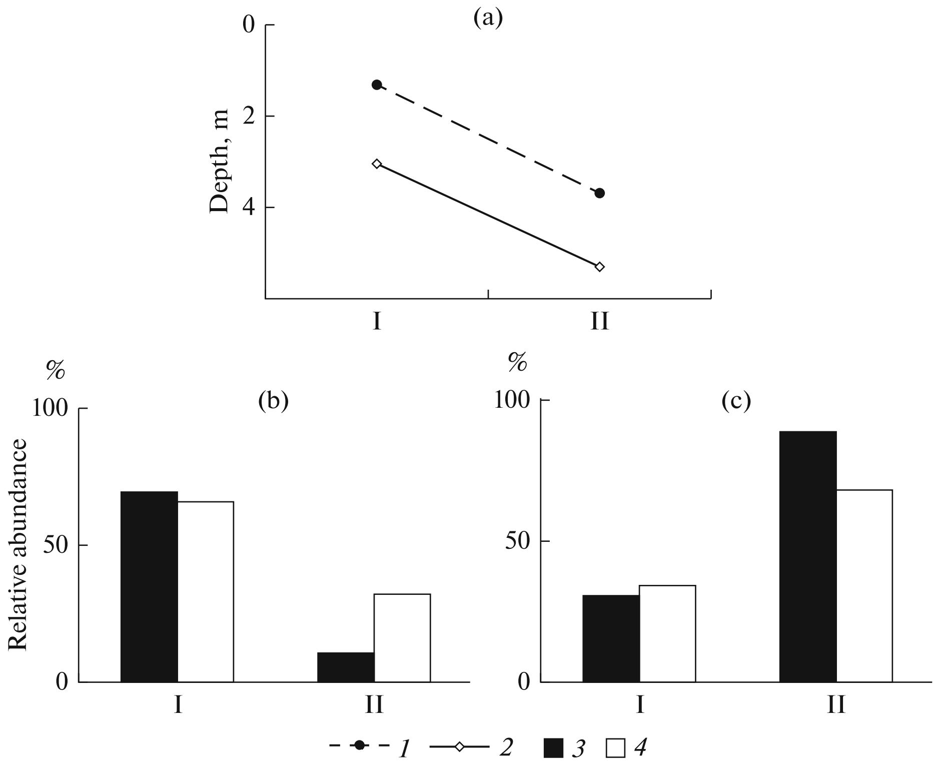

Fig. 7. Average depth of the habitat of the early (I) and late (II) larvae of cyprinids (*1*) and percids (*2*) in the upstream pool of the Sheksna reservoir (a) and the relative abundance of cyprinids (*3*) and percids (*4*) migrants that pass through the water intakes of the navigation lock (b) and hydroelectric power station (c). 100% is the total number of fish of the family in the migration through both water intakes. Sample size, spec.: cyprinids 6595 and percids 47632. All differences in the rations of downstream migrants (by age in one intake and by water intake for the same age) are significant (ratio Student's test, $p < 0.01$).

remaining unregulated part of the river upstream to the reservoir, the reservoir itself, tributaries of the reservoir, and the river downstream to the dam. Ecological barriers and filters interrupt or aggravate the movement of adult and juvenile fish between these biotopes, partially or completely isolating individual parts of the population. These barriers and filters are not just physical structures that modify migration. Their influence on migration is manifested as a result of interactions between the behavior of migrants and physical structures (gradients and obstacles). The existence and functioning of ecological barriers and filters are assessed by a comprehensive study of the physical and biological processes and patterns that form the nature of migration. Among mechanisms of different levels that affect the migration characteristics of juvenile fish (Pavlov, 1994), environmental filters can be especially important modifiers of downstream migration in regulated rivers. Their selective influence is determined not only by the changes in the intensity and duration of migration into the reservoir when compared to the river, but also by the increased mortality of migrants (primarily from predators) in the gradient zones that separate the biotopes. The selectivity of the influence of filters is manifested to various extents for different species and age groups.

Ecological barriers and filters should not be opposed to each other. These concepts can be associated with the same physical structures and reflect their influence on different sides of the same process: fish migration. Both ecological barriers and filters, by their nature, are a dynamic interaction of two spatiotemporal structures: the structure of the morphological, hydrophysical, and hydrochemical parameters of the reservoir and the distribution structure of migratory fish. The ecological barrier acts as an obstacle aggravating or completely interrupting migration. The ecological filter acts selectively, preventing the migration of some species to a greater extent than others.

The concepts of ecological barriers and filters and ideas about the mechanisms of their functioning can be useful in modeling and predicting the dynamics of populations and successions in natural and regulated river ecosystems. Understanding the functioning features of the ecological filters is important in developing measures to manage migration and protect fish, as well as to achieve the processes of formation of the fish population in partially isolated biotopes of regulated rivers (upper river, reservoir, upstream pool, and downstream pool). For example, in addition to fish-passing facilities for fish migrating to the upper reaches of a river to spawn, the consideration of spatiotemporal patterns of migration of juveniles through dams with different types of water intakes will allow one to predict and influence the selective emigration of juveniles to the downstream pool. In regulated water bodies, management capabilities are especially great near dams and water intakes (regulation of time and place of water intake) (Pavlov et al., 1999).

The role of environmental filters can include not only the species-selective passage of migrants from one biotope to another. In this case, the filter acts as an environmental factor affecting the structure of communities in neighboring biotopes. Another, microevolutionary role that determines the operation of the filter as an intraspecific-selection factor may be no less important (Bonte et al., 2010; Chapman et al., 2011). This selection may result in an over-time decrease of the migration activity of that part of the population that remains "upstream." However, there is an alternative hypothesis: polymorphism in terms of migrancy—residency is constantly reproduced, despite the emigration (removal) of more active migrants. These hypotheses require verification on regulated river systems of different ages.

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COMPLIANCE WITH ETHICAL STANDARDS

The authors declare that they have no conflict of interest. This article does not contain any studies involving animals or human participants performed by any of the authors.

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