

Review

Migrations of Young Fish in Anthropogenically Transformed Rivers: Responses of Cyprinids and Percids to Ecological Filters and Barriers

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Abstract: Downstream migration (DSM) of larvae and fry is an important phase of the life cycle of fish as it allows them to disperse, and it increases the size and diversity of the populations via them extending rearing grounds, exchanging genes, and avoiding competition and cannibalism. Two numerous and diverse fish families of the Eurasian rivers, Cyprinidae and Percidae, are well adapted to the conditions of the riverine continuum. Having said that, the regulation of rivers (construction of dams and water reservoirs) drastically changes their hydrology and topography. In this work, we argued that novel conditions of transformed river habitats influence the DSM of young cyprinids and percids in different ways. The published results on fish DSM and spatial distribution in nine European reservoirs (Russia, Kazakhstan, Czech Republic, Bulgaria) in comparison with untransformed rivers were reanalyzed from the viewpoint of this argument. Changes in the major characteristics of DSM of young cyprinids and percids, i.e., intensity, diel (24-h period), and seasonal patterns of migrations, as caused by anthropogenic transformation of the rivers, were revealed. We found that the novel ecological barriers and filters associated with different parts of water reservoirs differently influence the lateral and longitudinal movements, and the diel and seasonal dynamics of DSM of cyprinids and percids. These effects result in significantly more intensive emigration of young percids compared to cyprinids from reservoirs with deep-water intakes. At the scale of the whole regulated river, the morphological complexity (topography) of the reservoir plays a pivotal role in controlling the intensity of the DSM of young fish. Measures for the conservation and restoration of percid and cyprinid populations should be different.



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Keywords: young fish; cyprinids; percids; dispersal; downstream migration; regulated rivers

1. Introduction

Most organisms disperse from a natal/breeding site, which enables the exploitation of spatially and temporally variable resources in continually changing natural habitats [1,2]. Downstream migration (DSM), or downstream drift, is an important phase of the life cycle of fish that allows young fish to disperse, and it increases the size and diversity of fish populations [3,4]. DSM allows young fish to use flowing water to extend the range of the fish population, exploit increased trophic resources [5–7], exchange genes [8], avoid cannibalism and competition at spawning grounds [9], and enhance habitat connectivity and community stability [7,10].

The DSM of young fish is not only a passive dispersal by water flows but a structured process controlled by hydraulic and behavioral drivers [11]. In natural rivers, fish are well adapted to the topography and hydraulic structure of the river, and they efficiently use the main channel as a migratory habitat and the inshore zone as a resting habitat [11]. During migrations, which usually last for days, young fish repeatedly leave the inshore zone and enter the main channel on a diel (i.e., 24-h period) basis [3,12,13]. Ecological barriers for downstream migrating young fish are related to the longitudinal heterogeneity

of the riverine continuum [14,15]. Fish usually overcome such barriers. The entire process of DSM comprises a sequence of active and passive components. Short periods of decision making when migrants enter the drift at dusk and return to the inshore retention zone at dawn are of particular importance in the control of DSM. In a previous study, we showed that such key events are associated with high gradient zones (e.g., interfaces between habitats of residence and migration habitats) [11].

The transformed habitat structure in regulated rivers may influence the role of fish behavior in DSM [6,16]. Novel physical objects create ecological barriers [17,18] and filters [19], which substantially change conditions for DSM. Ecological barriers, which hamper and modify migrations of young fish, are associated with physical–chemical gradients (marginal zones of habitats, frontal zones). The permeability of a particular barrier for different species or age groups may be different. In this case, we consider this to be an ecological filter, one that differentially influences different groups of migrants [19]. A question to pose here is, do these barriers and filters exert similar impacts on the most abundant and diverse downstream migrants, cyprinids and percids, which usually form the core of fish communities?

In European Russia, cyprinid and percid fishes are the most common and abundant inhabitants of both natural and regulated rivers [20]. Their spawning periods and spawning grounds partially overlap [21]. In natural rivers, the most intensive DSM of the larvae of common cyprinids (roach, *Rutilus rutilus* (Linnaeus, 1758); bream, *Abramis brama* (Linnaeus, 1758); bleak, *Alburnus alburnus* (Linnaeus, 1758)) and percids (perch, *Perca fluviatilis* Linnaeus, 1758; zander, *Sander lucioperca* (Linnaeus, 1758); ruff, *Gymnocephalus cernuus* (Linnaeus, 1758)) occurs in June. On a diel scale, the DSM of both cyprinids and percids reaches its highest intensity during the night and twilight [21]. It appears that the ability of young percids and cyprinids to efficiently use structured habitats of natural rivers and migrate freely along the whole river continuum is similar. With this in mind, does their migratory behavior change in regulated rivers where fish should overcome vast open water and dams? A large number of publications has covered various aspects of the fish ecology in regulated rivers. Most of them concern studies on the three families: Salmonidae, Cyprinidae, and Percidae [22]. However, downstream migrations are not among the main topics of such studies, especially for cyprinids and percids.

The construction of dams and water reservoirs leads to a variety of serious transformations of the river continuum. This large-scale discontinuity creates abrupt lotic–lentic (river–lake) transitions, which radically modify conditions for DSM [4,20,23]. These modifications change not only the flow patterns that provide downstream movement, but the whole complex of contiguous habitats where migrating fish undertake repeating diel moves between migratory and resting habitats. The emigration (leaving a habitat) of young fish from the water reservoir through the passages associated with dams is especially important because of the high mortality, damage, and irrevocable withdrawal of fish from the reservoir. Because of the similarity of the main characteristics of the DSM of young cyprinids and percids in natural rivers, we may expect similar patterns of their migration both within water reservoirs and downstream of dams. However, the intensive emigration through dams has thus far been found in young percids but not in cyprinids [4,21]. Is this difference typical and consistent? If so, what ecological and behavioral mechanisms are responsible for this difference between cyprinids and percids in regulated rivers?

Modifications of downstream migrations caused by transformations of habitat structure and hydraulic regime in regulated rivers were analyzed and discussed mainly at the level of “total ichthyoplankton” (all larval fish) without emphasizing the biological (ecological and behavioral) specificity of particular categories of migrating fish [5,11,18,19]. Generally, similar patterns of downstream migrations of the two most abundant groups of European riverine fish, cyprinids and percids, differ in the spatial distribution of migrating larvae [11]. We expect that such differences, which under conditions of natural rivers do not lead to differences in the main patterns of DSM of cyprinids and percids, may cause a significant differentiation under the conditions of regulated rivers. To study this argument,

we compare data on DSM of young cyprinids and percids obtained at diel and seasonal scales in nine regulated rivers in Russia, Kazakhstan, Bulgaria, and the Czech Republic [21,24]. We reanalyze this information to reveal changes in the major characteristics of DSM of young cyprinids and percids (intensity, diel, and seasonal patterns of migrations) caused by anthropogenic transformation of the rivers. The most abundant field data on the temporal and spatial patterns of downstream migrations of young cyprinids and percids are obtained for the Volga and Sheksna rivers in European Russia from the 1970s until the 2000s (Figure 1).

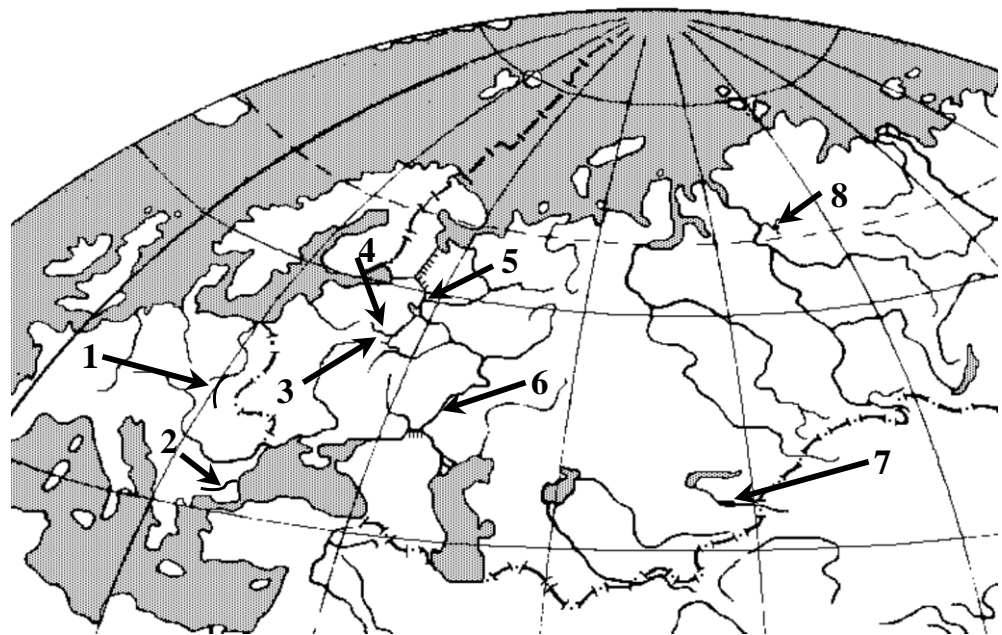


Figure 1. Locations of the studied reservoirs. 1—Mostishte, Czech Republic; 2—Al. Stamboliiskii, Bulgaria; 3—Ozerninskoe, Moscow Region, Russia; 4—Ivan’kovskoe, Upper Volga, Russia; 5—Sheksninskoe, Vologda Region, Russia; 6—Volgogradskoe, Lower Volga, Russia; 7—Kapchagaiskoe, Kazakhstan; 8—Ust’-Khantaiskoe, Russia.

Our study aims to compare the modifications of downstream migrations in young cyprinids and percids in regulated rivers. More specifically, we study (1) the changes of the spatiotemporal structure of the downstream migration of the two fish groups within water reservoirs in comparison with natural rivers; (2) the difference in spatiotemporal patterns of emigration between young cyprinids and percids from water reservoirs; and (3) the role of ecological barriers and filters as modifiers of the downstream migration in anthropogenically transformed rivers.

2. Spatiotemporal Structure of the Downstream Migration in Natural Rivers and Water Reservoirs

River regulation due to the construction of dams and spacious water reservoirs causes multiple changes in hydrology and in the habitat structure of riverine continuum. Lotic-limnetic transformations, large water bodies with varying depth and currents, and modified transition zones between habitats of residence and migration habitats radically change conditions of the downstream migration for young fish, creating ecological barriers of different permeability [18,19]. Considering the influence of these barriers on the downstream migrations of fish in rivers of European Russia and Central Asia, we discovered that novel ecological barriers are associated with physical structures of different scales. Locally, fish migrating in a reservoir face extended transition zones between the migratory habitat (open part of the reservoir) and the habitat of residence (shallow-water inshore zone). Compared with natural rivers, the extended transition zone makes repeated lateral diel movements

between the habitats more difficult. Another strongly modified area within a reservoir is associated with the dam, which controls downstream water flows and thus influences the downstream migration of young fish. On the scale of the whole reservoir, vast bodies of water with changeable flow patterns may function as a large-scale ecological barrier disturbing the unidirectional migratory route of drifting fish. The spatiotemporal structure of the downstream migration is controlled by the interaction between the behavior of migrating fish and their biotic and abiotic environment [5,6].

2.1. Diel Changes of Downstream Migrations

The diel rhythms in the behavior of migrating fish and their interactions with small-scale hydrological gradients and topography can shape the temporal patterns of downstream migration in young fish [3,4,6,21]. The exact behavioral and ecological mechanisms driving diel patterns in downstream migration are not clearly understood. However, the intensity of illumination, water turbidity, and avoidance of predation pressure are among the key factors controlling the circadian rhythm of drift [5,11]. Peak densities of migrating fish in unregulated rivers are usually recorded during the night. During the day, the migration habitat (main channel) is virtually free of downstream migrants (Figure 2a). Migration habitats in regulated rivers (open water of reservoirs) contain larval cyprinids and percids both day and night (Figure 2b). Comparing these two contrasting patterns, we argue that riverine migrants, both cyprinids and percids, easily leave the migratory habitat at dawn and enter the shallow-water inshore zone. Lateral movements allow them to cross a narrow flow gradient (interface) between the habitats. This task seems significantly more difficult for larvae, which migrate in the reservoir of a regulated river; the spreading of the interface (gradient zone) between migratory and residence habitats creates a barrier, which functions as a hardly permeable obstacle for migrants. A large number of migrants stay in the open water during both day and night, and they drift either downstream towards the dam or in other directions, depending on the prevailing currents, the main flow, and wind-induced currents.

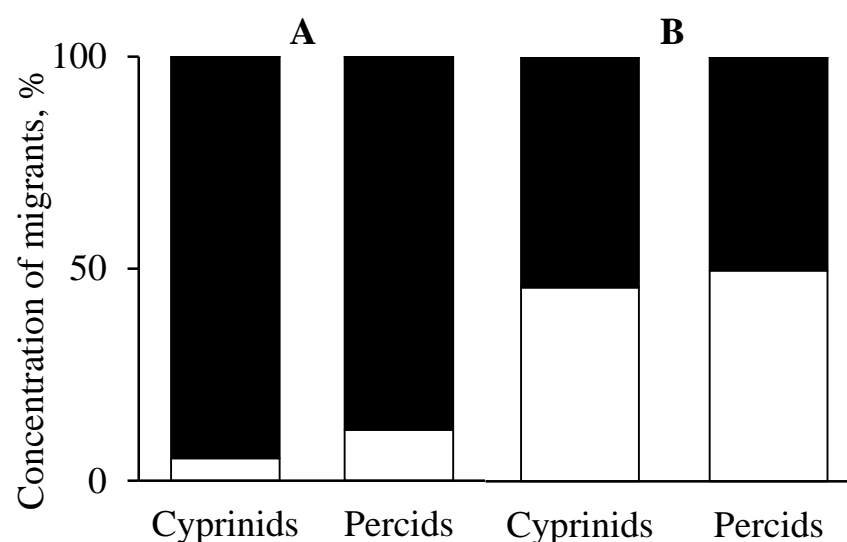


Figure 2. Mean relative concentration of young cyprinids and percids in migration habitats of the Upper Volga (A) and Ivan'kovskoe Reservoir (B) during the day (light) and night (dark part of the bars). Differences between the day and night values are significant in the river and nonsignificant in the reservoir (chi-squared test: $p < 0.001$ and $p > 0.05$, respectively). Number of fish sampled: cyprinids—2120 ind., percids—3810 ind. Data from Pavlov et al. [21,24]. See Supplement 1 for more details.

2.2. Seasonal Changes of Downstream Migrations

Seasonal patterns of the downstream migration are influenced by a variety of biotic and abiotic factors, such as the timing and success of reproduction, water discharge, and temperature. Depending on the species richness, the uni-, bi- and multimodal seasonal patterns are characteristic of different rivers [7,11,21,25].

Larvae of riverine cyprinids and percids migrate most intensively in June (Figure 3). In the Ivan'kovskoe Reservoir of the Volga River, the period of downstream migration is more prolonged than in the river (Figure 4). As seen in Figure 4b, within this period, i.e., June–September, a much higher concentration of young percids was recorded in the open water (migration habitat) than in shallow water (habitat of residence). The opposite pattern was observed in cyprinids—they were much more abundant in the inshore zone of residence (Figure 4a). During the period of downstream migration in the reservoir, consistently more than 50% of the young percids were recorded in the migration habitat in comparison with those in the habitat of residence; usually less than 5% of cyprinids were recorded in the migration habitat (see Supplement 1 for more detail).

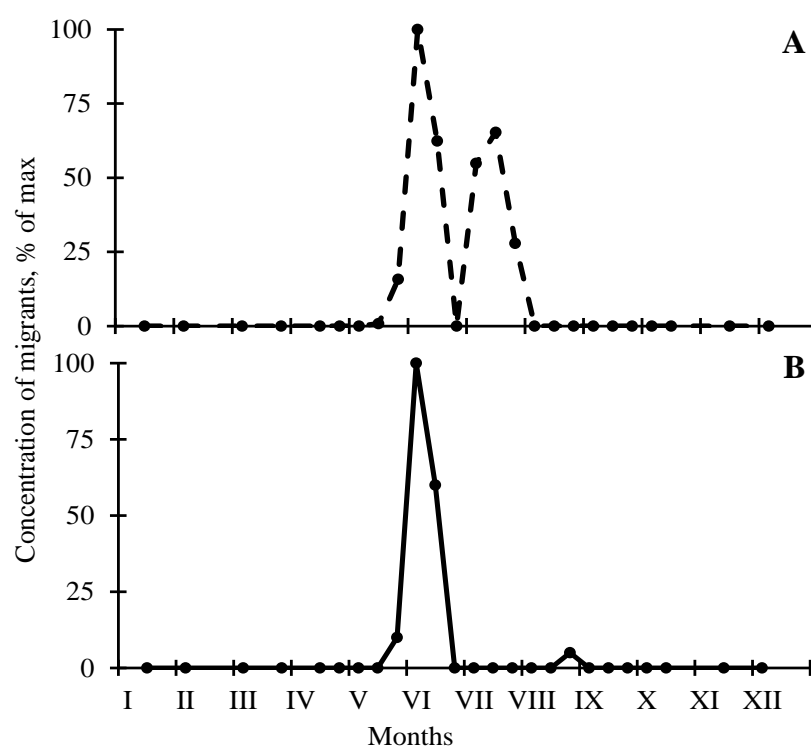


Figure 3. Seasonal patterns of the downstream migration of cyprinids (A) and percids (B) in the Upper Volga. Concentrations are expressed as percentages of the maximum value. No significant difference between cyprinids and percids. Kolmogorov–Smirnov test: $p > 0.01$. Data from Pavlov et al. [21].

This difference produces a prerequisite for more intensive drift of the young percids than cyprinids towards the dam. The functioning of ecological barriers at different scales, which hamper both the lateral and longitudinal movements of migrants, could be one of the reasons prolonging the period of migration. We argue that the whole water body of the reservoir, working as a macroscale barrier, restricts the intensity and efficiency of the downstream migration through the lowering of its speed and change of direction. This is primarily caused by highly variable and unpredictable flow regimes [22,26], which in turn is influenced by the variability of the wind-induced currents [27] and the topography of reservoirs [18]. Within morphologically complex reservoirs, numerous bays of various sizes may operate as a sort of ecological trap, which accumulates migrating fish [28]. As a result of the differences between young cyprinids and percids in their characteristics of

migration through the water reservoir, more percids than cyprinids are usually transported towards the dam.

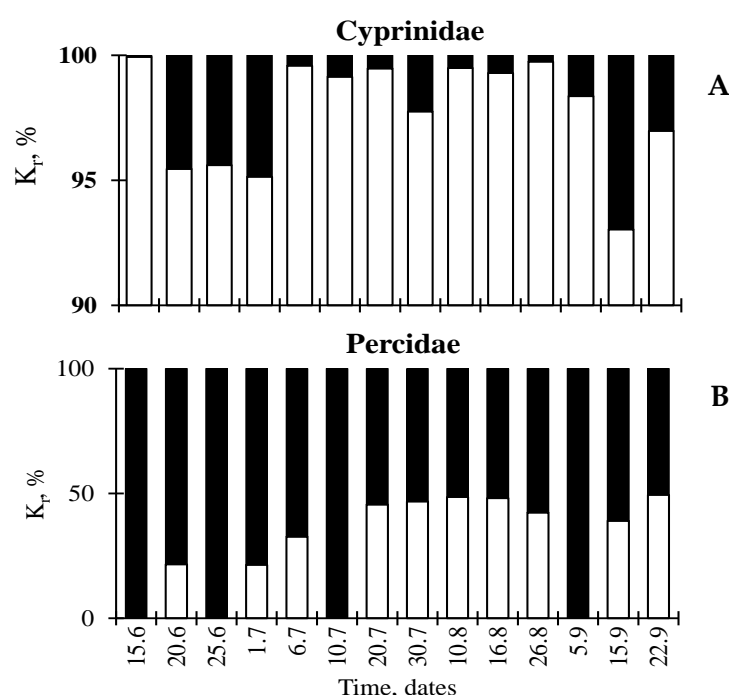


Figure 4. Relative abundance of the young cyprinids (A) and percids (B) measured in mean concentration (K_r , in %) for the whole day–night period of each date in both migration (dark) and residential (light part of each bar) habitats of the Ivan’kovskoe reservoir in June–September 1992. Much more percids were observed in the migration habitat. Differences between cyprinids and percids are significant (Wilcoxon matched pairs test, $p = 0.001$) in both migration habitat and habitat of residence. Number of fish sampled: cyprinids—1317 ind., percids—1732 ind. Both vertical axis scales have different scales. Data from Pavlov et al. [24].

3. Emigration of Young Cyprinids and Percids from Water Reservoirs

In the lower part of the reservoir, hydraulic conditions for the downstream drift of young fish are drastically changed. Fish may be entrapped by the strong unidirectional water flow, which carries them downstream through the dam.

The studied power plants on the regulated rivers were equipped with deep (25–40 m) water intakes, which produce a funnel-like water flow structure that influences different layers of the water column, particularly in the near-bottom layers [24]. In contrast to the downstream migration in an unregulated river, where fish are involved in the main channel due to horizontal lateral movements (between the inshore zone and the main channel), drift with the water intake flow is associated primarily with the vertical distribution of fish [24].

3.1. Diel Dynamics of the Downstream Emigration

The pronounced diel patterns of the downstream migration, which are relatively similar in percids and cyprinids migrating along the channel of the unregulated river, are different in the case of the drift with the water intake induced flow (Figure 5). The main peaks of the concentration of migrants were recorded at dusk and at night. For cyprinids, this was the only peak in the diel rhythm, similar to the drift in natural rivers. For percids, in addition to the largest nocturnal peak, a considerable concentration of migrants was also recorded during the day (Figure 5b). We argue that the main drivers governing the diel pattern of the drift downstream of dams are the diel vertical movements and distribution of fish. We should emphasize that most of the young fish in the area near the dam resided

in the upper layers, but the main bulk of percid larvae were located significantly deeper than that of the cyprinids [19].

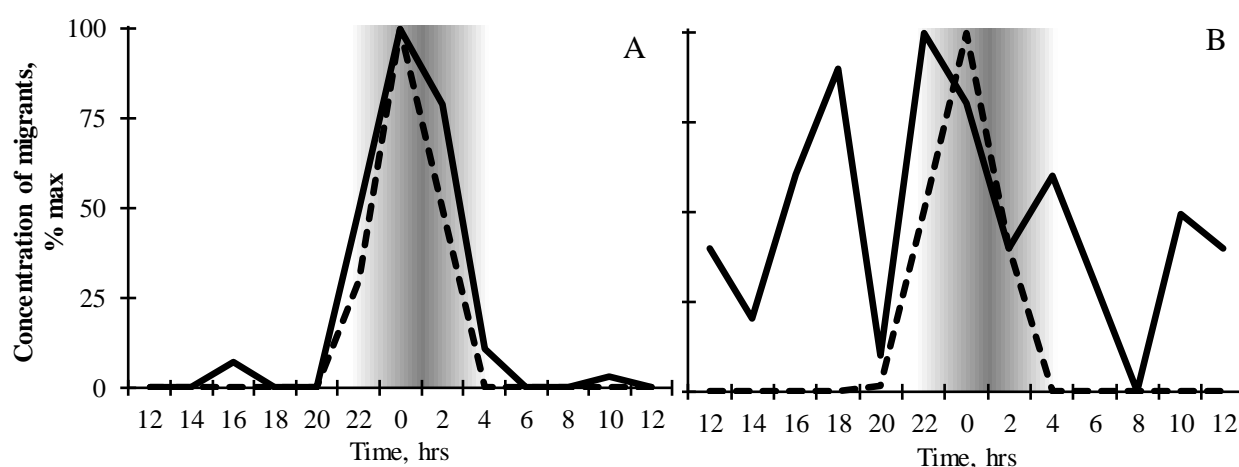


Figure 5. Diel patterns of the downstream migration of larval cyprinids (A) and percids (B) in the nonregulated part of the Upper Volga (dashed lines) and through the water intake of the Ivan'kovskaya Power Plant (solid lines). Diel patterns in the river and reservoir are similar in cyprinids (Kolmogorov–Smirnov test: $p > 0.05$) and different in percids ($p < 0.05$). Number of fish sampled: cyprinids—222 ind. (river), 166 (reservoir); percids—263 ind. (river), 532 (reservoir). Data from Pavlov et al. [21,24].

When young percids and cyprinids migrate in the natural river, they show no difference in the diel patterns of the downstream migration, despite the difference in spatial distribution across the river channel (usually, migrating percids were found further from the shore than cyprinids) [11]. In the river, a narrow flow gradient between the inshore zone and main channel is a permeable structure for both categories of migrants. In the water reservoir near the dam, a 3D flow “funnel” produced by the deep-water intake creates a vertical flow gradient, which acts as an ecological barrier for both cyprinids and percids. Both groups of the larvae undertake diel vertical movements, but the ranges of their movements were found to be different [19,24]. Most cyprinids were located above the flow “funnel” during the day, and only at night, they sank deeper and entered the water flow, which conveyed them downstream through the dam. Percids stayed within the zone of water intake flow even during the day; during the night, they descended deeper, and their concentration in the outflow was even higher.

3.2. Seasonal Dynamics of the Downstream Emigration

In contrast to the seasonal patterns of the concentration of migrants in the natural river, where the only pronounced peak was observed in June and smaller peak for cyprinids in July (Figure 3), in regulated rivers, broader main seasonal peaks (June–July) were recorded in both families of fish (Figure 6). Moreover, a lower but still considerable concentration of migrants was recorded during the rest of the year, especially for percids (Figure 6). A significant amount of migrating YOY grown percids was recorded during the autumn–winter period. This may lead to a substantial loss of a valuable portion of percid populations.

3.3. Emigration through the Power Plants and Shipping Locks

In addition to the main deep-water intake of the power plant, other intakes may be associated with the dam. Amongst the most common constructions are shipping locks, which periodically create a downstream water flow conveying young fish downstream. Such water intakes are situated close to the bank and predominantly influence the upper water layers. We monitored the intensity of the downstream migration of the young fish through the power plant (throughout the year) and the shipping lock (from May to October)

intakes located at the middle part of the Sheksna River (Vologda Region, European Russia). The intensity of emigration from the reservoir was by an order of magnitude higher for the percids (Figure 7b) than for cyprinids (Figure 7a). Significantly more percid larvae drifted through the power plant water intake than through the shipping lock; conversely, the migration of cyprinid larvae was more intensive through the shipping lock (Figure 7a). These obtained results showed that the emigration of larval percids from the reservoir stock was much higher than the emigration of cyprinids. The difference between the two fish families is especially pronounced when the main discharge of water flows through the deep-water intake of the power plant.

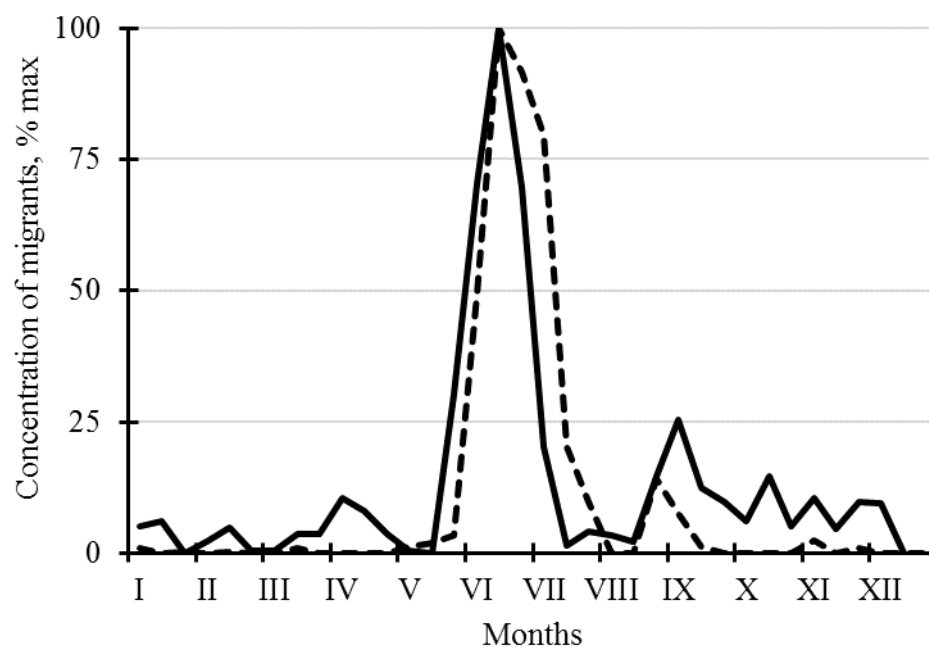


Figure 6. Seasonal patterns of the downstream migration of cyprinids (dashed line) and percids (solid line) from the Ivan'kovskoe Reservoir. The patterns significantly differ (Wilcoxon matched pairs test, $p = 0.018$). Number of fish sampled: 4100 ind. See Supplement 2 for more detail; data from Pavlov et al. [21,24].

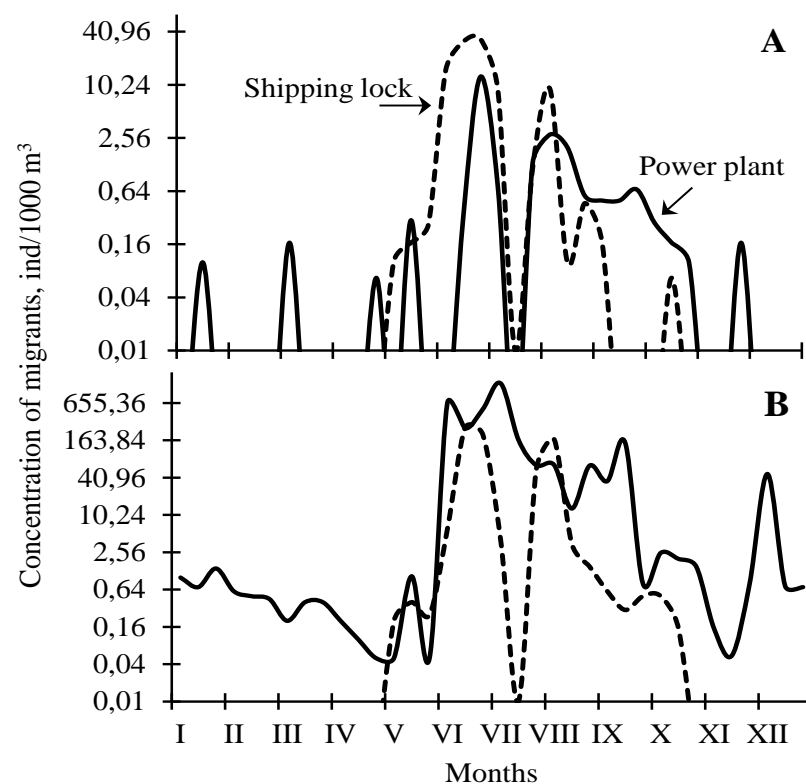


Figure 7. Seasonal patterns of emigration of cyprinids (A) and percids (B) through the shipping lock (dashed lines) and power plant (solid lines) passages on the Sheksninskoe Reservoir. Mean concentrations of both percids and cyprinids are higher when drifting through the power plant (Wilcoxon matched pairs test, $p < 0.023$; see Supplement 3 for more details). Number of fish sampled: cyprinids—1298 ind.; percids—30,169 ind. Data from Pavlov et al. [24]). Note that different irregular Y-axes used.

4. Ecological Barriers and Filters as Modifiers of the Downstream Migration in Transformed Rivers

In contrast to the downstream migration in unregulated rivers, in which the main patterns (diel and seasonal) are relatively similar in cyprinids and percids, the modified structure of regulated rivers drastically enhances differences in the temporal and spatial patterns of the downstream migrations between these groups of migrants. We showed that a set of novel ecological barriers influences the spatiotemporal characteristics of migrating larvae of both families. These differences are distinct at the local scale and at the scale of the whole reservoir. The barriers work as ecological filters exerting a selective impact on the two most abundant and diverse groups of fish inhabiting lowland water reservoirs.

The resulting effect of behavioral responses of migrating fish to these barriers can be estimated via a comparison of the number of fish emigrating from the reservoir. A correct comparison should take into account the population numbers of different fishes inhabiting the impoundment. An index of migration intensity (MI), which reflects the relative number of fish of a particular species (group) leaving a reservoir, was previously proposed [24]. Using the data on the intensity of drift from eight reservoirs and the abundance of young fish in these reservoirs, we calculated MI indices for cyprinids and percids (Figure 8). A tendency to migrate downstream from reservoirs was much more pronounced in percids than in cyprinids (Mann–Whitney U test: $p < 0.001$).

Considering the mechanisms underlying the striking difference between cyprinids and percids in terms of the intensity of the downstream migration, the role of ecological barriers influencing their spatial distribution and migration at different scales should be emphasized. Within a reservoir, the following hydrological barriers can be distinguished:

- The extended gradient zone between the migration habitat and habitat of residence which hampers movements of young fish between the open water area (migration habitat) and inshore zone (habitat of residence);
- A vast water body with a changeable flow structure, which slows and hampers the drift of young fish downstream towards the dam;
- A transformed hydrological structure with a deep-water downstream flow near the dam, as the probability of being entrapped by the deep-water intake flow and conveyed downstream is higher for fish inhabiting deeper layers further from the in-shore zone.

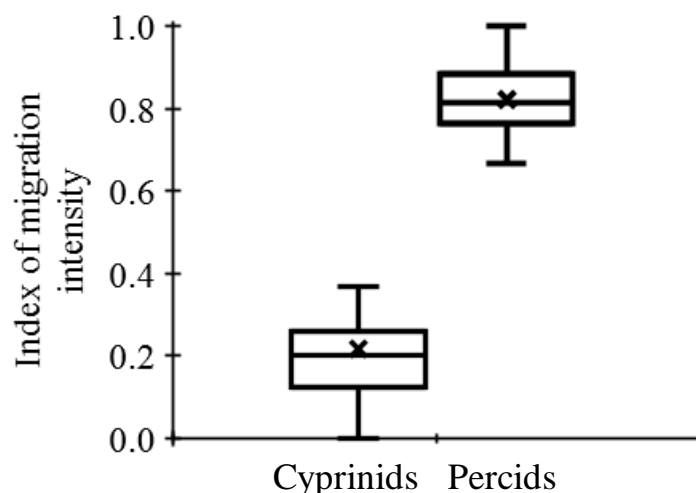


Figure 8. Mean indices of migration intensity of cyprinids and percids from eight water reservoirs. These indices are consistently higher in percid species than in cyprinid species (Mann–Whitney U test, $p < 0.001$). See Supplement 4 for more detail. Data from Pavlov et al. [24].

At the scale of the whole regulated river, the morphological complexity (topography) of the reservoir plays a pivotal role in the control of the intensity of the downstream drift of young fish. The whole reservoir works as a large-scale ecological barrier or trap that hampers the downstream migration [18,28]. The impact of the morphological complexity of the reservoir overrides the impact of the water turnover (discharge) rate [18]. We compared the total number of fish emigrating from two reservoirs of similar surface area but different complexity (the ratio of the shore line length to the length of the longitudinal axis), both located on the Volga River—i.e., Volgogradskoe (turnover rate, 8.0; index of morphological complexity, 0.03) and Ivan’kovskoe (12.9 and 1.83, respectively), measured throughout the year. We found that the number of young fish emigrating from the first reservoir was 3000 times more than from the second. The main bulk of the emigrants from the both reservoirs were young percids [18].

Certain ecological and behavioral traits of percids make them more subject to the impact of the downstream transportation under conditions of regulated rivers. Common riverine percids (perch, zander, ruff) occupy similar habitats to cyprinids (roach, bream, bleak) in natural rivers. They are generally similar in their timing and spatial distribution, at least in early ontogeny [21,29,30]. However, there are some differences in their spatial distribution, which under riverine conditions do not markedly influence patterns of their downstream migration [11]. Spawning grounds of percids are usually located further offshore than those of cyprinids [21,24,31,32]. In water reservoirs, their early larvae cannot maintain a steady position among inshore vegetation, and they are much more vulnerable to wind-induced currents than cyprinid larvae. Such currents disperse percid larvae in all directions [33–36]. Young percids are able to inhabit a wide range of depths [37,38]; cyprinids, in contrast to percids, inhabit predominantly inshore zone and upper layers. Both cyprinids and percids undertake horizontal and vertical diel movements [39–41].

Spatial distribution and diel movements make young percids more vulnerable to water currents, which in water reservoirs often direct them to the water intakes of power plants and emigration from the reservoir.

5. Conclusions

The obtained results suggest that patterns of downstream migration of cyprinid and percid fishes are strongly influenced by a novel physical template created by river regulation. Novel ecological barriers associated with different parts of water reservoirs differently affect patterns of migration of cyprinids and percids. These differences result in significantly more intensive emigration of young percids than of cyprinids from reservoirs with deep-water intakes. The loss of percids from reservoirs differs from cyprinids not only in terms of the higher total number but also in age (size) structure of the migrants. The highest number of percid larvae emigrating from reservoirs is found at mid-summer (June–July), but, unlike cyprinids, young percids continue a rather intensive downstream migration from reservoirs during autumn and winter. This leads to the loss of grown YOY percids, which could constitute a significant and important portion of the overwintering stock. Such disproportional removal may be one of the important factors controlling the ratio of cyprinids/percids in the fish stock of reservoirs with deep-water intakes, in turn influencing the structure of the fish fauna of the reservoirs. Other large-scale factors are related to the morphology of reservoir. Reservoirs that are morphologically more complex can prevent the emigration of young fish more efficiently than channel-like reservoirs [18]. Dispersal ability is not simply an attribute of a species (group of species), but it varies strongly with landscape structure; thus, landscape change due to human activities may be more influential for one group of animal than for another [42].

Various approaches exist for managing reservoir fish fauna and stock [23,43–47]. Usually, reservoir managers want to create a fish stock most suitable for the purposes for which the reservoir was built. Ensuring a high production of cyprinids by designing eulittoral ecotones is one strategy for reservoirs where these fast-growing fish are to be exploited for human or animal food [20]. The intensive removal of young percids from reservoirs with deep-water intakes should also facilitate conditions in favor of cyprinids by reducing competition for resources. To promote populations of percids in a reservoir, we should not only adjust diel and seasonal regimes of hydropower water intakes but also optimize water intake location to minimize the withdrawal of young percids.

Supplementary Materials: The following are available online at <https://www.mdpi.com/article/10.3390/w13091291/s1>, Supplement 1—Table S1: Mean relative concentrations of migrants during the day and night; Table S2: Seasonal patterns of the downstream migration of cyprinids and percids in the Upper Volga; Table S3: Statistics for the seasonal dynamics of the concentration of migrants in the Upper Volga River; Table S4: Relative concentrations (%) of the young Cyprinidae and Percidae in the migration habitats and habitats of residence in the Ivan'kovskoe Reservoir in June–September 1992; Table S5: Significance of differences between relative concentrations of Cyprinidae and Percidae in the migration habitats and habitats of residence. Supplement 2—Table S6: Diel changes of the relative concentration (% max) of the early larvae of Cyprinidae and Percidae migrating in the Upper Volga and from Ivan'kovskoe Reservoir; Table S7: Diel changes in the concentration of Cyprinidae and Percidae migrants in the Upper Volga and Ivan'kovskoe Reservoir; Table S8: Number of caught fish (ind., according to species) in the Upper Volga and Ivan'kovskoe reservoir; Table S9: Seasonal changes of the relative concentrations (% max) of Cyprinidae and Percidae emigrating from the Ivan'kovskoe Reservoir; Table S10: Comparison of seasonal changes of the Cyprinidae and Percidae emigration from the Ivan'kovskoe Reservoir; Table S11: Sample sizes (ind.) for the main species of Cyprinidae and Percidae. Supplement 3—Table S12: Concentrations (ind./1000 m³) of Cyprinidae and Percidae migrants through the power plant water intake and shipping lock of the Sheksninskoe Reservoir; Table S13: Difference between concentrations of cyprinids and percids migrating through the power plant and shipping lock; Table S14: Number of sampled fish (by species of cyprinids and percids) emigrating through the power plant and shipping lock. Supplement 4—Table S15: Migration

index for common and frequently found fishes in reservoirs; Table S16: Comparison of the indices of migration in cyprinids and percids.

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