Downstream migration and mechanisms of dispersal of young fish in rivers

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19 **Running head:** Downstream migration of young fish

20 **Keywords:** young fish, drift, migration, dispersal, aggregation, heterogeneity, rivers

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Abstract

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28 Downstream migration (DSM) of young fish has traditionally been considered a passive
29 process. A review of studies of the patterns and mechanisms of DSM showed that it met the
30 main criterion for migration: that animals move between well-defined habitats according to a
31 predictable schedule. During DSM, fish often leave the habitat in which they reside (inshore
32 zone) and enter a migratory habitat (main channel). DSM is manifested at a seasonal or diel
33 scale and in species-specific spatial distribution patterns. According to our “dispersal with
34 low dilution” hypothesis, the supposed adaptive value of DSM is due not only to dispersal but
35 also maintenance of aggregations and synchronisation of migratory activity. Temporal and
36 spatial peaks of migration promote efficient intra-specific interactions, such as shoaling, and
37 the integrity of populations. We conclude that migratory behaviour is most successful in
38 habitats with optimum complexity and that the influence of behaviour on DSM is most
39 important at key periods and sites (twilight windows and interfaces between habitats).

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50 Introduction

51 Downstream migration (DSM) is an important phase of the life cycle of fish that
52 allows young fish to disperse and increases the size and diversity of fish populations (Harden
53 Jones 1968; Northcote 1984; Pavlov et al. 2008). The intensity and timing of DSM, size
54 distribution of migrants and proportion of migrating fish in the population is variable
55 (Keckeis and Schiemer 2001; Humphries et al. 2002; Reichard and Jurajda 2007; Pavlov and
56 Skorobogatov 2014).

57 We aim to answer the following questions: What are the major determinants and
58 controlling mechanisms of DSM? Is DSM passive dispersal influenced by only external and
59 primarily physical factors, or does the behaviour of migrating fish significantly influence
60 DSM?

61 Biologists studying the migration of adult fish consider DSM differently from those
62 who study the migration of young fish. Contrary to the spawning migrations of freshwater
63 fish (e.g. Brönmark et al. 2014), the DSM of young fish was considered to be *passive drift*,
64 *dispersal* or *flow- driven transportation*, with negligible active behaviour influencing the
65 direction of movement and distance travelled by the fish (e.g. Pavlov 1979). However, the
66 influence of behaviour on DSM is receiving increasing attention (e.g. Pavlov et al. 2008;
67 Schludermann et al. 2012; Lechner et al. 2016).

68 Most organisms disperse from a natal/breeding site, which enables the exploitation of
69 spatially and temporally variable resources in ever-changing natural habitats (Clobert et al.
70 2004; Clobert et al. 2009; Ronce 2007). DSM allows young fish to use flowing water to
71 extend the range of the fish population, exploit increased trophic resources (Schmidt 1947;
72 Pavlov 1994; Janac et al. 2013), exchange genes (Fuiman and Cowan 2003), avoid
73 cannibalism and competition at spawning grounds (Humphries, 2005) and enhance habitat
74 connectivity and community stability (Janac et al. 2013; Roberts et al. 2013).

75 During dispersal, the local densities of migrating fish may become very low. This
76 could prevent vital intraspecific interactions, such as group formation. Solitary individuals
77 lose the benefits of cooperation, such as defence against predators and parasites, improved
78 ability to search for food and navigate (Pitcher and Parrish 1993; Krause and Ruxton 2002;
79 Mikheev et al. 2013). Such negative consequences are especially probable in large
80 homogenous habitats like water reservoirs, in which the shortage of landmarks makes
81 interactions among migrating fish difficult. Therefore, it is important that we understand
82 which behavioural and ecological characteristics of DSM and habitats help maintain high
83 local densities of migrating fish.

84 Both field and experimental studies could be useful for analysing the role of fish
85 behaviour as a determinant of the patterns and mechanisms of DSM. However, there have
86 been few such experimental studies, and most of those that do exist focus on protecting
87 migrating fish from injury in power plant turbines and water abstraction systems (Pavlov
88 1979, 1989; Larinier and Travade 2002). Only a few field studies examining DSM in rivers
89 are useful for comparing passive (physical) and active (behavioural) influences on DSM.

90 Individual tagging, although widely used in studies of adult fish, is of limited use for
91 investigating DSM of early fish stages. Despite the existence of methods based on
92 geochemical signatures and otolith structures (e.g. Thorrold et al. 2007; Sponaugle 2010),
93 drift net sampling is the most widely used method in studies of the patterns and mechanisms
94 of DSM. This method prioritises long-term (seasonal) and diel sampling along vertical and
95 horizontal transects. To analyse the role of fish behaviour in controlling DSM, we need to
96 obtain datasets regarding the variability of DSM traits on small temporal (diel) and spatial
97 (tens of centimetres to tens of meters) scales.

98 Unlike passive dispersal, migration requires that individuals or populations (or parts
99 of populations) move between two well-defined habitats on a temporally predictable basis

(Baker 1978; Dingle 2006; Brönmark et al. 2014). Additionally, migration has species-specific spatial and temporal patterns. In early ontogenesis, most fluvial fish are similar in size, shape and density/buoyancy. If their movement in the flow is predominantly passive (physically driven), then the spatio-temporal characteristics of DSM should be similar for most species. Species-specific and intraspecific variations of these characteristics could prove that behaviour has an effect on DSM. Thus, it is important to perform detailed, small-scale field and experimental studies of DSM. Our review is based on published and unpublished information about the patterns and mechanisms of DSM of young fish mainly in rivers in European Russia and the Far East.

Our primary goal was to determine whether the behaviour of young fish influences their DSM and whether the role of behaviour varies depending on biotic and abiotic factors. In a broad sense, we consider patterns and processes related to the dispersal of young fish in rivers, which have been extensively reviewed (Lechner et al. 2016). In our review, we focus mainly on aspects of the ecology of DSM that have received little attention in the review by Lechner et al. (2016), such as variations caused by topographical and hydrological habitat heterogeneity, inter- and intraspecific differences in fish behaviour and the ratio of dispersal to cohesion among migrating fish. More specifically, we consider the spatial and temporal patterns of DSM at different scales, the ratio of active to passive processes during fish ontogeny and ways in which this ratio changes depending on a habitat's complexity and scale. The "dispersal with low dilution" hypothesis, which relates to mechanisms and factors that maintain high local densities of migrating fish and synchronization of DSM, is proposed and discussed.

The paper is divided into four sections. In the first section, we consider the results of field studies of riverine fish drift that reveal the spatio-temporal patterns and variability of DSM. Based on these patterns, we will discuss hypotheses regarding the effect of behaviour

on DSM and maintenance of aggregations of migrating fish. In the second section, we highlight the importance of heterogeneity (both topographical and hydraulic) in habitats at different scales for establishment and control of DSM. In the third section, we consider the association between the intra-population variability of DSM, habitat heterogeneity and the physiological state of fish. A brief overview of the main concepts and hypotheses regarding the behavioural and ecological mechanisms associated with multilevel control of DSM is provided in the fourth section.

Spatial and temporal patterns and variability of DSM

Most riverine fishes engage in DSM, but the timing, duration and intensity of such migration vary greatly depending on species, age and habitat (Nikolsky 1963; Northcote 1984; Zitek et al. 2004; Pavlov et al. 2008; Lechner et al. 2016). Field studies of DSM either record DSM at the community level (total ichthyoplankton drift) or at the species/population level (species/stage-specific drift). The second approach is much more informative and suitable for studying the patterns and mechanisms related to the active-passive conundrum (Lechner et al. 2016).

To understand the factors and mechanisms controlling DSM, we need to know not only the duration and magnitude (concentration of drifting fish) of the process but also the temporal and spatial patterns of variations in migration. This knowledge is important for understanding the role of DSM in the dispersal of young fish in different taxonomic groups as well as for planning practical measures to conserve and restore populations of riverine and anadromous fishes. We have to take into account not only the taxonomy and ecology of fish populations but also the scaling of DSM.

Scaling DSM as an ecological process is not an easy task due to the variability in the traits of migrating fish populations and their habitats. Previous field and experimental studies distinguish seasonal and diel changes in the migrant concentration and macro- and micro-scale spatial variations.

Temporal changes to DSM

DSM dynamics depend on various interactions between biotic (species-specific and age-related traits regarding fish biology, nutrition, defence and social interaction) and abiotic (illumination, temperature, hydrological regime, etc.) factors (Northcote 1984; Zitek et al. 2004; Reichard and Jurajda 2007; Pavlov et al. 2008). Cyclic changes in DSM, primarily seasonal and diel, are related to the natural cyclic processes in ecosystems. Seasonal changes are related to ontogenetic and demographic processes in fish populations, while diel changes are primarily related to individual and behavioural processes (such as trophic and defence interactions), which do not result in any noticeable changes in population. Sensory adaptations, primarily those related to vision, are very important for controlling diel changes to DSM (Girsa 1981; Guthrie et al. 1993, Reichard et al. 2002).

DSM is most typical in the early stages of fish development (during the free embryo and early larval stages), but in some species of fish, the migratory window lasts for a year or more (Northcote 1984; Humphries et al. 2002; Pavlov et al. 2008). Free embryos and the larvae of some fishes migrate *en masse* within a short period during their first summer (Table 1). For predominantly non-migratory riverine fishes like northern pike (*Esox lucius*), gudgeon (*Gobio gobio*) and freshwater sculpin (*Cottus gobio*), DSM occurs during a single stage of their development. The DSM of the YOY fish may cover several stages of its early development (eggs, free embryos, larvae, fries). The longest DSM period is observed in

174 pelagophilous fish, such as black-backed shad (*Alosa kessleri*), Caspian barbel (*Barbus*
175 *brachycephalus*), grass carp (*Ctenopharyngodon idella*) and silver carp (*Hypophthalmichthys*
176 *molitrix*).

177 Some species of fish and lampreys may be engaged in two or more waves of
178 migratory activity, first in the YOY and then in older fish (Table 2). Between the consecutive
179 ontogenetic migratory windows, they spend one to five years in a river. Active or active-
180 passive migration is typical of older fish migrating either from tributaries to a main river or
181 from a river system to the sea.

182 **The seasonal patterns of young fish DSM in rivers** are extremely irregular – sharp
183 peaks of activity are interspersed with periods of very low intensity. In predominantly non-
184 migratory species, which live in near-bottom habitats (*B. barbatula*, *C. gobio*, *G. gobio*),
185 short-term primary dispersal occurs very soon after hatching (Fig. 1 A, B). Larvae of other
186 fish species, like perch (*Perca fluviatilis*) and roach (*Rutilus rutilus*), migrate over longer
187 periods with two or more peaks of intensity occurring consecutively (Fig. 1 C, D). This
188 pattern differs from that of salmonids, which demonstrate peaks of primary and secondary
189 dispersal in different years (Fig. 1 E, F). We suggest that the first temporal peak of DSM (the
190 only one for *B. barbatula*, *C. gobio* and *G. gobio*) occurs in all three patterns of DSM (Fig.
191 1): continuous migration with one short peak (Fig. 1 A, B), continuous migration with two
192 peaks (Fig. 1 C, D) and interrupted migration (Fig. 1 E, F). The first peak, primary dispersal,
193 is the most predictable aspect of DSM. It involves the dispersal of larvae from spawning
194 grounds. The following peak/peaks of DSM are related to secondary dispersal from the
195 nursery grounds when the habitat becomes unfavourable. The magnitude of the peaks and
196 duration of intervals between them depend on many factors. Additionally, field evidence
197 suggests that secondary dispersal is a much more variable component of DSM dynamics than
198 primary dispersal (Pavlov et al. 1981; Pavlov and Skorobogatov 2014).

199 If DSM is a passive process predominantly controlled by hydraulic factors, its
200 seasonal patterns should be similar in fishes with similar ecology and biology at early
201 developmental stages. A comparison of the seasonal dynamics of the DSM of the most
202 numerous fish species in the same river (Fig. 1 C, D) shows pronounced inter-species
203 dissimilarity in terms of both the timing and magnitude of the main peaks of DSM. These
204 differences suggest that the biology of larvae, primarily their behaviour, has a significant
205 influence on DSM.

206 The variability and diversity of seasonal patterns of DSM seem to be connected to the
207 spawning and nursery grounds' relative distances from one another. For instance, the
208 spawning and nursery grounds of fish species with a short period of primary dispersal, like *B.*
209 *barbatula* and *C. gobio* (Fig. 1 A, B), are usually located very close to each other. In contrast,
210 river-spawning cyprinids and percids undertake longer, potamodromous migrations, moving
211 downstream to more productive habitats. The spawning and nursery grounds of salmonids are
212 even more separated, and young salmonids undertake the longest DSM of the mentioned
213 fishes (Fig. 1 E, F).

214 **Diel changes to DSM** are usually linked to cyclic changes in illumination that also
215 substantially influence the foraging and defence behaviour of young fish (e.g. Blaxter 1966;
216 Girsu 1981; Clark and Levy 1988; Wanzenböck et al. 2006). DSM typically reaches its
217 highest intensity during the night or twilight (Fig. 2 A, B, C). This pattern can be modified by
218 significant shifts in illumination, such as a polar day (Fig. 2 D), or in turbid water (Fig. 2 E,
219 F). The dependence of DSM on illumination and turbidity suggests the important role of
220 behaviour in controlling DSM on a diel scale.

221 Larvae about 10–15 mm in length demonstrate regular diel periods of DSM, with the
222 highest intensity occurring during darkness (Fig. 3). However, smaller larvae demonstrated

irregular diel dynamics. This difference could be observed in larvae from four families of riverine fish with DSM during the first summer of life (Fig. 3).

More regular diel patterns of DSM synchronised with cyclic changes in illumination arise during the larval period of the development of fish. The ontogenetic formation of more regular and consistent behavioural patterns typical of early fish development (Kieffer and Colgan 1992; Stoll and Beeck 2012) could be responsible for this trend. Such ontogenetic changes, which were observed in four families of fish, may support the hypothesis that behaviour plays an increased role in DSM during the ontogeny of fish. At first glance, however, data regarding the diel patterns of DSM in young salmonids contradict this tendency (Fig. 4).

YOY salmonids typically experience the highest intensity of DSM during the darkness. Younger salmonids' higher threat of predation causes them to migrate synchronously and only in the darkness. However, this pattern becomes more diverse and variable in fish one year or older (Fig. 4); the DSM of older fish may be triggered by various factors, not only threat of predation.

Diversity in seasonal patterns of DSM is caused not only by differences in the time at which fish reproduce and the distribution of spawning grounds in a river (Lechner et al. 2013b; Humphries 2005) but also by the behaviour of the migrating fish (Leis 2007; Pavlov et al. 2008). However, analyzing only the seasonal patterns of DSM makes it difficult to assess the influence of active and passive processes on DSM; analysis of diel changes seems to be more promising. The close association between intensive DSM and darkness suggests that migratory behaviour is activated when the threat of predation is at a minimum. However, field data allow an alternative hypothesis: fish that are disoriented in darkness are 'washed out' by the transient flow (Pavlov 1966, 1979). Experimental evidence that fish have active responses to heterogeneous flow within a diel cycle will be considered later.

Surprisingly, the diel dynamics of DSM are similar in different fishes. At first glance, a consistent response to darkness supports the hypothesis that loss of orientation affects DSM. However, DSM also takes place during the polar day (Fig. 2 D), when illumination allows orientation for twenty-four hours. This fact suggests that behavioural mechanisms are at play. Thus, we ask the following question: Why is species-specific variability in DSM common seasonally, yet far less common on a diel basis? We suggest that threat of predation is a major determinant of the behaviour of young fish on a diel scale. Its impact could be so strong that it overrides other factors and synchronizes the DSM patterns of different species.

Spatial variability of DSM

The spatial structure of DSM depends on distribution of spawning grounds (Lechner et al. 2013b; Humphries 2005), size and morphology of the riverbed (Pavlov et al. 1995), hydraulic structure of the flow (Lechner et al. 2013a) and other biotic and abiotic factors. Below, we consider the spatial distribution patterns of migrating fish to show how these patterns are influenced by interactions between hydraulic and biological factors. We emphasise species-specific heterogeneity and consistent spatial distribution.

The vertical distribution of young fish engaging in DSM differs depending on the species and stage of ontogeny of the fish in question (Pavlov and Skorobogatov 2014). It is influenced by a number of factors, like the buoyancy and photoreactions of migrating fish, the vertical distribution of available prey and the hydraulic structure of the flow (Pavlov and Skorobogatov 2014). Additionally, vertical distribution is significantly modified at river channel bends (Fig. 5).

The cross-river distribution of migrating fish depends on the hydraulic structure of the flow, which in turn depends on morphology of the river channel (Pavlov et al. 1981). The

active component of distribution of migrating larvae is controlled by innate reactions (photo-, rheo-, baric and tactile reactions) and acquired behaviour (feeding and defence) (Northcote 1984; Pavlov et al. 2008; Pavlov and Skorobogatov 2014).

Active mechanisms of spatial distribution play a more important role at the straight parts of the river channel, where the hydraulic flow structure is less complex than at curved parts due to reduced lateral circulation. The behavioural responses of migrants are probably more pronounced near interfaces (bottom, shallow areas near river banks), where topography and hydraulic structure are more heterogeneous (Pavlov et al. 2008; Mikheev et al. 2010). Species-specific characteristics of the spatial distribution of migrating fish are most pronounced along the straight parts of the river. Roach (*R. rutilus*) and perch (*P. fluviatilis*) larvae migrate closer to the riverbanks, while smelt (*O. eperlanus*) and zander (*Sander lucioperca*) migrate in the centre (Fig. 6). In parts of the river with more complex morphologies and hydraulic structures, the influence of physical factors probably overrides that of behaviour.

The influence of habitat complexity on DSM: topographical and hydrological habitat heterogeneity

Downstream migration, a part of the migratory cycle, is a rather long process, lasting for days or months, during which the behaviour of migrants (Zitek et al. 2004; Reichard and Jurajda 2007; Pavlov and Skorobogatov 2014) and surrounding habitats (Wintersberger 1996; Wiens 2002) change. DSM is influenced by the behaviour of fish that are drifting in the flow (migratory habitat), located in near-shore or near-bottom habitats (habitat of residence) and shifting between the two habitats. All these behaviours occur within the diel cycle. A

sequence of these cycles comprises the seasonal cycle of DSM, which is part of the migratory (life) cycle.

Migratory habitats and habitats of residence differ in terms of size, structure/heterogeneity at different scales and spatial and temporal variability. These characteristics are related to both mobile (water flow) and stable (water–substrate interface) parts of the habitat. Together, hydraulic parameters and topographical characteristics of habitats influence the orientation, locomotion and trophic and defence interactions of fish. High flow velocity and a shortage of landmarks in the migratory habitat hamper the orientation and locomotion of migrants. In the habitat of residence, conditions are more favourable for fish behaviour due to more heterogeneous surroundings, which influence fish behaviour directly or through modification of the flow.

Habitat scaling and DSM: distribution and behaviour of migrants in the water flow

The behaviour of young fish, including orientation, locomotion and decision making, should match the spatio-temporal scale of the habitat in which they migrate. During the period of most intensive nocturnal migration, drifting larvae are not able to actively respond to a target site from a distance of more than several meters. At present, we are not able to predict the spatial distribution of drifting larvae, even if we know their swimming and orientation abilities. Laboratory experiments in flow-through tanks are suitable for studying small-scale patterns (tens of centimetres or meters), but to study large-scale patterns (10–100 metres), *in situ* experiments are needed.

At a scale of 100 meters, the spatial distribution of migrating larvae does not differ from that of passively drifting particles (Fig. 7). This suggests that hydrophysical processes play a primary role in DSM at this scale. However, *in situ* observations of the spatial

distribution of drifting larval nase (*Chondrostoma nasus*) have shown that larvae disperse unlike passive particles (Lechner et al. this issue). The contradiction with our results is presumably related to differences in the ecology of fish larvae (our results are mainly based on clupeids, while Lechner et al. used nase) and scale of observations. Drifting larval nase had been sampled in the shallow-water inshore zone (Lechner et al.), and clupeids across the Volga River (Pavlov et al. 1995).

To investigate the role of fish behaviour at a smaller scale, we recorded the spatial distribution of live and dead cyprinid larvae (*R. rutilus* and *Leuciscus leuciscus*) in a flow-through tank with a gradient flow at a mean velocity of 20 cm/c (Fig. 8). The experimental flow, in which velocity varies by a factor of four within one meter (Fig. 8), may be considered a model of the hydraulic interface between habitats of residence and migratory habitats. In such a flow, fish larvae with the appropriate internal state (“migrants”) choose an optimum velocity depending on illumination (Pavlov and Shtaf 1981). In the darkness, migrants choose zones with higher velocity, thus entering the drift, while at dawn, the number of fish and flow velocity is oppositely correlated, indicating that the fish are leaving the drift. This change in distribution within a heterogeneous flow shows that diel cycles of illumination affect the DSM of migrating larvae. No correlation between the number of dead larvae and flow velocity was observed (Fig. 8). Transitions between habitats of residence and migratory habitats can be also influenced by the lateral aspects of water flow (Lechner et al. 2013a, 2013b). We believe that the major temporal and spatial parameters of DSM are influenced by fish behaviour (locomotion, orientation, decision making), 3-D flow structure and diel cycles of illumination. Further studies examining the interactions between these factors and DSM should include laboratory and *in situ* experiments as well as mathematical modelling.

Habitat heterogeneity and cohesiveness of migrants. Transitions between habitats of residence and migratory habitats

To understand the relative influence of biotic and abiotic factors on the patterns and mechanisms of DSM, we have to consider the characteristics of not only migratory habitats but also habitats of residence and the transition zone (interface) between these two types of habitats. The structure, topography and flow parameters of the transition zone are especially important for fish undertaking DSM (Wolter and Sukhodolov 2008; Lechner et al. 2013 a, 2013b).

Throughout DSM, migrating fish move across the transition zone many times when they enter the drift and return to the shore. Thus, this directional movement is the important part of DSM. According to the simplified view of the DSM of young larvae as a passive process (Pavlov 1966, 1979), the behaviour is due to a lack of orientation in the dark and washing out from the inshore zone to the main stream. If their transition to the flow is completely passive, the relative abundance of larvae of different species has to be similar in both habitats of residence and migratory habitats. We tested this hypothesis with the larvae of two cyprinid species, *R. rutilus* and *Phoxinus phoxinus*, which are common in the Bolshaya Kosha, one of the tributaries of the Volga River (Pavlov et al. 1981) (Fig. 9). Despite having a lower concentration in the habitat of residence, roach larvae were the most common migrants (Fig. 9). An increase in the number of roach larvae in the migratory habitat compared to the number in the inshore zone can be explained only by behaviour.

Habitat heterogeneity in rivers (Palmer et al. 2000; Wiens 2002) influences not only the spatial distribution of migrating fish but also the seasonal dynamics of their DSM. We compared the seasonal patterns of DSM of roach larvae in two tributaries of the Upper Volga, which are similar in size but differ in habitat complexity. Bolshaya Kosha is a river with

more complex topography and higher habitat diversity than the channel-like T'ma River. Two seasonal peaks of DSM were observed in both rivers, but the peak in secondary dispersal was recorded much later in the more heterogeneous Bolshaya Kosha (Pavlov et al. 1981). We suggest that the higher ecological capacity of a more heterogeneous river delays DSM from nursery grounds and increases the period between peaks of DSM. The important role of riverbed morphology, especially in the inshore zone, and the hydraulic heterogeneity of the flow were demonstrated in experiments *in situ* (Lechner et al. 2013b; Schludermann et al. 2012) and by mathematical models (Wolter and Sukhodolov 2008).

Uneven spatial distribution of fish larvae and patches of high local concentration are typical of inshore zones of rivers, even during intensive DSM (e.g. Pavlov et al. 1981; Keckeis et al. 1997; Price and Humphries 2010). In habitats of residence in inshore zones, aggregation is promoted by landmarks, shelter, prey and heterogeneous water flow with low average velocity. It is much more difficult to maintain the cohesiveness of larvae drifting at night in a main stream with high flow velocity and turbulence. Bearing this in mind, we can expect expanded/diluted patterns of spatial distribution of fish drifting in the rather narrow section (less than 100 m) of the Upper Volga, like those observed in the channels of the Lower Volga (Fig. 7). In the Lower Volga, the drift of total ichthyoplankton was recorded, while in the Upper Volga, the distribution of drifting larvae was recorded separately for each species (Fig. 6). In the latter case, pronounced species-specific peaks of concentration were observed either at the edge of the inshore zone (roach, perch) or in the main stream (zander, smelt) (Fig. 6). These differences between species were maintained for many days. Thus we ask the following question: What factors are responsible for maintaining peaks in the concentration of drifting fish larvae? This question should be addressed by both *in situ* and laboratory studies.

Maintenance of rather dense local aggregations is necessary for efficient intra-specific interactions, particularly group formation and shoaling behaviour (Pitcher and Parrish 1993; Krause and Ruxton 2002). In habitats in the inshore zone, where fish spend much more time than in the transit flow, even during intensive DSM, heterogeneity and hydrological regime affect the concentration of fish populations (e.g. Wintersberger 1996; Pavlov et al. 2008; Mikheev et al. 2010). Sites within inshore zones at which the level of habitat heterogeneity is optimal, and thus may contain more food, may attract migrants leaving the transit flow at dawn. Additionally, the local concentration of migrating fish should counterbalance the dilution of fish larvae drifting in the dark. The increased concentration of migrating fish is associated with heterogeneous riverine habitats in which lateral flows and local eddies may transport drifting fish to inshore retention sites/zones with high local productivity and food availability (Hildrew 1991; Reynolds and Descy 1996; Schiemer et al. 2001).

The enhanced probability of entering retention sites may allow not only local aggregation but also synchronisation of the migratory behaviour of larvae (e.g. their transition from a habitat of residence to the migratory habitat at dusk). Synchronisation may result from the similarity between individual responses to changes in illumination and/or could be related to shoaling behaviour, which is typical of late-stage larvae and fry (Radakov 1973; Pitcher and Parrish 1993; Krause and Ruxton 2002). The more synchronised responses of older larvae to diel changes in illumination (Fig. 3) support the concept of interactive responses.

Most studies on the patterns and mechanisms controlling DSM have focused on integral factors, such as species composition, average concentration of migrants, duration of DSM and so on (e.g. Pavlov et al. 1981; Northcote 1984; Reichard and Jurajda 2007). Despite the increase in research on the various ecological effects of habitat heterogeneity (e.g. Wiens et al. 1986; Shurin et al. 2009; Mikheev et al. 2010), local and short-term effects of heterogeneity are very rarely considered in studies of the patterns and mechanisms of DSM

(Schiemer et al. 2001; Pavlov et al. 2008). We believe that small-scale habitat heterogeneity, which is related to both topography and hydrology, influences all phases of DSM, including transitioning from a habitat of residence to a migratory habitat, drifting in the transit flow and entering the next residency site.

The overall success of DSM depends not only on the behaviour of fish in the transit flow but also on other vital activities, such as foraging, defence and grouping, in both habitats of residence and migratory habitats (Mikheev 2006; Pavlov et al. 2008; Mikheev et al. 2010). Migrating fish both drifting in the transit flow and moving from one inshore site to another constantly find themselves in new habitats. The micro-scale heterogeneity and local aggregation of fish in these habitats seem to have a significant influence on the synchronisation and DSM of the migrating fish. However, this suggestion needs to be confirmed by more field and experimental studies.

Migration polymorphism: variability of behaviour associated with DSM

Do fish larvae of the same species behave similarly when engaging in DSM? Differences in the individual responses of fish observed in the gradient flow (Fig. 8) suggest that behaviours associated with DSM are variable. To investigate the heterogeneity of a population in terms of propensity for migration, we tested a group of roach larvae 10–15 mm length during intensive DSM. In a flow-through tank, fish could choose between compartments with high or low flow velocity (Fig. 10) (Pavlov et al. 2005).

Differential responses of roach larvae to flow velocity were observed only in darkness. The most intensive response lasted for a short time within the period with no illumination (Fig. 10). This finding supports the hypothesis that synchronised DSM could

promote local aggregation of migrating fish. Such a difference in responses, which was observed in both laboratory tests and *in situ* experiments (Pavlov et al., 2005), was correlated with differences in the concentration of catecholamine hormones between migrants and residents (Fig. 11). A much higher concentration was observed in migrants in both laboratory and field tests.

Experiments regarding the behaviour of cyprinid larvae in gradient flows in habitats with small-scale heterogeneity can be considered models of the beginning of DSM. At the onset of darkness, fish choose either rapid flow (migratory tactic) or low velocity/stagnant zones (residency tactic). It should be emphasised that differences between roach larvae (residents and migrants) were observed during primary dispersal (first peaks of DSM in Fig. 1). Are behavioural differences between residents and migrants consistent throughout DSM? Further shaping of migration behaviour and spatial segregation is influenced by small-scale habitat heterogeneity and biotic interactions. The role of genetic and epigenetic mechanisms controlling DSM as factors affecting migration polymorphism (partial migration) is not yet clear.

Salmonids demonstrate intrapopulation migration polymorphism (groups of migrants and residents) at various spatial and temporal scales. Diversity in behavioural tactics, including differences in migration behaviour, as well as differences in physiological and biochemical traits lead to a variety of life cycle strategies within a single population. Part of the population employs an anadromous strategy, migrating from a river to the sea, while others employ a potamodromous strategy, spending their lives in fresh water. We found that the relative abundance of anadromous and potamodromous fish within a river depends on habitat complexity. After comparing two rivers on the west coast of the Kamchatka Peninsula, we found that in the Kol River, which features high habitat complexity and high biological productivity, more than 80% of *Parasalmo (O.) mykiss* fish were potamodromous,

while in the less complex and less productive Kekhta River, anadromous fish prevailed (Fig. 12).

In summary, the heterogeneity of both habitats and fish populations could play an important role in adaptations associated with the migration behaviour of young fish. A variety of migratory tactics within a population not only influences dispersal and the availability of foraging grounds but also distributes risks in a heterogeneous and changeable environment (Taylor and Warren 2001; Brodersen et al. 2008; Chapman et al. 2011).

Controlling mechanisms and adaptive significance of DSM

It is generally accepted that the adaptive significance of DSM is mainly related to the dispersal of larvae from overcrowded spawning grounds to more productive nursery/foraging grounds (e.g. Northcote 1984; Pavlov 1994). Behavioural and ecological factors, which are responsible for the variability in the DSM of young fish, occur at three levels and provide stimuli, triggers and control over migrations (Pavlov 1994; Pavlov et al. 2008; Lechner et al. 2016).

First-level mechanisms influence the onset of DSM. They enhance the activity of fish and ensure their distribution in open water by exposing them to currents. Behaviours provoking DSM can be either specific or nonspecific. Nonspecific responses are innate behaviours related to feeding, respiration, defence and primary dispersion from the spawning grounds. Specific responses work only in the presence of currents and direct fish towards the flow. In the upper reaches of the Volga River, roach larvae, *Rutilus rutilus*, which have the highest concentrations of catecholamin hormones, demonstrated more pronounced migratory behaviour than their resident conspecifics (Pavlov et al. 2005). In the Lower Volga, juvenile migratory roach, *R. rutilus caspicus*, and white bream, *Blicca bjoerkna*, changed their

buoyancy from negative to positive in the evening when they started DSM (Pavlov et al. 1995). No such changes were observed in non-migrating juvenile rudd, *Scardinius erythrophthalmus*. Ontogenetic changes due to photoreaction can also modify the responses of fish to water flow and DSM (Pavlov et al. 1981).

Second-level mechanisms are associated with rheoreaction—the major behavioural complex controlling the activity of fish in a flow. This complex consists of two types of behaviours, those related to locomotion and those related to orientation. Rheoreaction could fail when the velocity of a current is higher than the critical swimming speed of a given fish; adverse factors could impair a fish's orientation and ability to resist water flow.

Third-level mechanisms influence the spatial distribution and temporal characteristics of migrating fish. These mechanisms include hydrodynamic factors (flow gradients and turbulence) and the attraction or repulsion of migrating fish to various environmental cues. Horizontal distribution of migrating larvae in rivers is mainly determined by turbulent mixing of the water flow. The emerging patterns of distribution are strongly dependent on the width of the river. In addition, vertical distribution is determined by both turbulence and the buoyancy of drifting fish (Pavlov et al. 1995). Locomotion and active choice of microhabitats become more important as the fish grow and develop.

The concept of mechanisms that control over DSM is mainly based on generalised patterns and trends and does not include the effects of micro- and meso-scale habitat heterogeneity and migration polymorphism. Recently, aspects of migrations related to habitat complexity, hydraulic heterogeneity (Pavlov et al. 2008; Wolter and Sukhodolov 2008; Schludermann et al. 2012; Lechner et al. 2016) and intra-population polymorphism (Brodersen et al. 2008; Clobert et al. 2009) have been of increased interest.

As previously mentioned, DSM has usually been considered a mechanism of dispersal and expansion of fish foraging grounds (e.g. Northcote 1984; Pavlov 1994). We aimed to

answer the following question: How do young fish, which strongly rely on grouping behaviour, maintain local aggregation and do not become overly diluted during DSM? We believe that the mechanisms of aggregative behaviour as well as the effects of habitat heterogeneity should be taken into account when developing the concept of multilevel control of DSM.

The risk of dilution is great for migrating populations of young fish. The limitations of biotic interactions with low-density populations and positive density dependence are termed the “Allee effect” (Allee 1938; Odum 1953; Stephens et al. 1999). This effect seems to be especially important for young fish, which have high feeding demands, vulnerability to predators and a tendency to group. Excessive dilution for young fish can be even more dangerous than overcrowding and high competition for resources. Without shoaling, which is impossible at a low local population density, young fish are not able to efficiently avoid predators, search for food and navigate (Pitcher and Parrish 1993; Krause and Ruxton 2002). Thus, we suggest that DSM is adaptive if dispersal and widening of nursery grounds work together with mechanisms for maintenance of local aggregations to ensure efficient intraspecific interactions, termed the “dispersal with low dilution” hypothesis.

In homogeneous environments with few landmarks and highly variable flow structure (wide rivers, lakes, reservoirs), the risk of overdilution during dispersal is high. It seems to be much easier to retain local aggregations in heterogeneous habitats in smaller rivers if migrants’ activity is synchronized. Much data on the seasonal and diel dynamics of DSM support the concept of synchronisation and show that many fish experience sharp and short-term peaks of DSM. Extended and rather even migrations were observed in turbid water or under constant illumination. Early fish larvae, which are not able to synchronise their activity, exhibited primary asynchronousness, while salmonids aged a year or older exhibited secondary asynchronousness as a result of nonsynchronised movements.

We suggest that the effects of spatial and temporal heterogeneity of DSM patterns allow local aggregation and dispersal of migrants. These conflicting outcomes can be obtained given the conditions of heterogeneous habitats and significant involvement of fish behaviour. Maintenance of local aggregations is important not only for fish in habitats of residence in the inshore zone but also for drifting fish, as drifting is the most risky part of migration behaviour. Increased density of migrant conspecifics dramatically improved the survival rate of sockeye salmon (*Oncorhynchus nerka*) smolts (Furey et al. 2016). If the risk is too high, a significant part of the population may stay in the inshore zone as a retention strategy. Together with heterogeneous spatial distribution, the functional heterogeneity of the population (migration polymorphism or partial migration) may be considered an adaptation to changeable environments.

Patterns and mechanisms of intraspecific interactions and migrants' interactions with heterogeneous water flow and riverbeds should be intensively studied both empirically and with biophysical models (Christensen et al. 2007; Leis 2007; Staaterman and Paris 2014; Lechner et al. 2016).

The data and concepts discussed here show that the widely accepted view of DSM as a passive process dominated by dispersal and drift and controlled primarily by hydrophysical factors is untrue. Adaptive temporal and spatial variations of DSM and migrants' species-specific responses to changeable and heterogeneous environments make the role of behaviour at this stage of migration just as important as during adult migration.

Most researchers agree that migration requires individuals or populations (or parts of populations) to move between two well-defined habitats on a temporally predictable basis. Hence, migration differs from dispersal in that individuals return to the initial habitat. The other generally accepted feature of migration is that it is, to some degree, temporally predictable (Northcote 1984; Brönmark et al. 2014). The information reviewed in this paper

suggests that the DSM of young riverine fishes meets these criteria beginning from the early larval stages. The role of behaviour increases as fish develop, and the rate of increase is especially pronounced at early stages of development.

Although we emphasise the importance of behaviour in the control of DSM, we do not ignore passive drift. The whole process of DSM is comprised of 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 controlling of DSM. We suggest that such key events are associated with high gradient zones (e.g. interfaces between habitats of residence and migration habitats). It seems that the significant attention researchers have paid to passive drift resulted from the understanding of DSM as a process associated only with high-velocity transient flow. Further studies should be focused more on other aspects of DSM—entering the drift, returning to the inshore zone, maintaining local aggregations and synchronising of fish activity. For synchronisation, both coordinated activity of migrants and appropriate habitat heterogeneity are needed. An optimum level of heterogeneity (topography and hydraulics) is important in both habitats of residence and migratory habitats.

The reduced habitat heterogeneity in regulated rivers (which have straight sides and large homogeneous reservoirs) with unfavourable conditions for orientation and navigation may substantially influence the role of fish behaviour in DSM. These negative effects, together with impairments regarding spawning migrations and spawning grounds, may significantly reduce the survival rate of young fish and recruitment of populations in regulated rivers. Purposeful investigations are needed to understand and assess these negative effects and migrants' adaptations to transformed habitats.

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767 Table 1. Single phase downstream migration of young-of-the-year riverine fishes associated

768 with different stages of their development. - not found; * rare; ** common.

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Fish species	Developmental stages				
	Eggs	Free embryos	Larvae	Fry	1+ and older
<i>Acipenser ruthenus</i>	-	**	-	-	-
<i>A. stellatus</i>	-	**	**	**	-
<i>A. gueldenstaedtii</i>	-	**	**	**	*
<i>Huso huso</i>	-	**	**	**	-
<i>Alosa kessleri</i>	**	**	**	**	-
<i>Oncorhynchus gorbusha</i>	-		**	*	-
<i>O. keta</i>	-		**	**	-
<i>Thymallus thymallus</i>	-		**	-	*
<i>Osmerus eperlanus eperlanus</i>	-	**	**	**	-
<i>Esox lucius</i>	-		-	*	-
<i>Abramis brama</i>	-	**	**	**	-
<i>Barbus brachycephalus</i>	**	**	**	*	-
<i>Ctenopharyngodon idella</i>	**	**	**	*	-
<i>Gobio gobio</i>	-	*	-	-	-
<i>Hypophthalmichthys molitrix</i>	**	**	**	*	-
<i>Phoxinus phoxinus</i>	-	**	*	-	-
<i>Rutilus rutilus</i>	-	**	**	**	-
<i>Barbatula barbatula</i>	-	*	-	-	-

<i>Lota lota</i>	**?	**	**	-	-
<i>Cottus gobio</i>	-	-	-	*	-
<i>Gasterosteus spp., Pungitius spp.</i>	-	-	*	**	-
<i>Perca fluviatilis</i>	-	**	**	**	-

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Table 2. Two-waves downstream migration of young-of-the-year and smolts of anadromous fish and lampreys. - not found; * rare; ** common.

Fish species	Developmental stages				
	Eggs	Free embryos	Larvae	Fry	1+ and older
<i>Lethenteron camtschaticum</i>	-	-	**	-	**
<i>Lampetra fluviatilis</i>	-	-	**	-	**
<i>Oncorhynchus kisutch</i>	-	-	**	**	**
<i>O. masou</i>	-	-	*	**	**
<i>O. nerka</i>	-	-	**	**	**
<i>Parasalmo (O.) mykiss</i>	-	-	**	**	**
<i>Salmo salar</i>	-	-	**	*	**
<i>S. trutta</i>	-	-	*	-	**
<i>Salvelinus leucomaenis</i>	-	-	**	**	**
<i>S. malma</i>	-	-	**	**	**

804 **Figure captions**

805 **Fig. 1.** Seasonal changes of the DSM intensity. A, B – fishes with short period of dispersal.
806 Only primary dispersal from spawning grounds was observed in the *Cottus gobio* (A) and
807 *Barbatula barbatula* (B) - a tributary of the Upper Volga. Longer period of DSM is typical of
808 *Rutilus rutilus* (C) and *Perca fluviatilis* (D) – Upper Volga. Primary dispersal was followed
809 by the peak of dispersal from the nursery grounds. Secondary dispersal of young salmonids in
810 the rivers of Western Kamchatka was observed in the 1+ fish: E - *Oncorhynchus kisutch*, F -
811 *Parasalmo (O.) mykiss*.

812 **Fig. 2.** Diel changes of the DSM intensity of the YOY fish under normal illumination (A –
813 Upper Volga 56° 27' N, B – Lower Volga 46° 05' N, C – Ethiopia 10° 00' N), under
814 conditions of the polar day (D – Northern Russia 61° 55' N) and in turbid water (E – Kuban
815 River 45° 16' N, F – Ili River 43° 00' N).

816 **Fig. 3.** Diel changes in DSM of the larvae of percids (A – 4-11 mm, A' – 21-25 mm),
817 cyprinids (B – 6-11, B' – 16-25 mm), clupeids (C – 6-10, C' – 16-20 mm), and osmerids (D –
818 11-15, D' – 16-25 mm). Strong association of the DSM peak with the dark period, which is
819 typical of the late larvae, was not observed in the early larvae.

820 **Fig. 4.** Diel changes of DSM in YOY (A – *Parasalmo mykiss*, D – *Oncorhynchus kisutch*)
821 and 1+ (B, C – *P. mykiss*; E, F – *O. kisutch*) salmonids in a river of Western Kamchatka.

822 **Fig. 5.** In the bended parts of the river channel, modified flow structure differently influences
823 spatial distribution of migrating larvae in different layers. A schematized example from a part
824 of the Upper Volga of 60-80 m wide and 5-8 m deep. Flow velocity at the surface: 0.5 – 1.1
825 m s⁻¹. A – vertical profiles of lateral velocity at the upstream transect (left transect on B, C
826 panels). Horizontal arrows indicate velocity vectors (1 cm – 10 cm s⁻¹) directed to either left
827 or right river bank. B – distribution of cyprinid larvae migrating in the surface layer. C – the
828 same in the near-bottom layer. Arrows on B and C indicate flow direction.

Fig. 6. Cross river distribution of migrating larvae of cyprinids, percids and osmerids (Upper Volga, width 80-100 m). Average distance between sampling sites (numbered from 1 to 6) is about 15 m. Roach: A – 11-15, A' -16-20 mm; perch: B – 11-15, B' - 16-20 mm; zander: C – 11-15, C' – 16-20 mm; smelt: D – 11-15, D' – 16-20 mm.

Fig. 7. Distribution of migrating fish larvae – A, A', and distribution of suspended matter – B, B' across the narrow (200 m) (A, B) and wide (860 m) (A', B') river channels in the Lower Volga. Concentration of migrants (mainly clupeid, cyprinid and percid larvae) and suspended matter were recorded along the transects located 1500 m downstream the release sites (black dots).

Fig. 8. Concentration of migrating and dead cyprinid larvae along a gradient of flow velocity. A – live larvae in the dark; $R_S = 0.807$, $p < 0.0001$; B – dead larvae; $R_S = -0.227$, $p = 0.3813$; C – live larvae in the light; $R_S = -0.813$, $p < 0.0001$.

Fig. 9. Relative abundance (%) of the roach (*R. rutilus*) and minnow (*P. phoxinus*) early larvae in the residency – A and migratory – B habitats. Bolshaya Kosha – a tributary of the Upper Volga. Data from a four years sampling program are used. Differences between concentration of the roach and minnow are significant (Xi-square test, $p = 0.02$) for both residency and migratory habitats.

Fig. 10. Choice of the compartment with high flow velocity (solid line) and low velocity (dashed line) by the roach larvae in the period of intensive DSM. Tests were done in the flow-through tanks submerged in a tributary of the Upper Volga.

Fig. 11. Hormonal state (relative content of the catecholamine hormones) of the roach larvae tested in a laboratory flow-through tank (A) and sampled in the river (B) from high velocity flow (migrants) and low velocity inshore (residents) zones.

852 **Fig. 12.** Proportion of *Parasalmo (O.) mykiss* that use anadromous startegy (black area on the
853 diagram A, Kehta River) and potamodromous strategy (white area on the diagram B, Kol'
854 River). Potamodromous fish prevailed in the more complex and productive Kol' River.

Draft

Fig. 1

Fig. 2

Fig. 3

Fig. 4

Fig. 5

129x205mm (300 x 300 DPI)

Fig. 6

Fig. 7

Fig. 8

Fig. 9

Fig. 10

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Fig. 11

Fig. 12

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