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especially *Chondrostoma nasus* (L.), in running waters”

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1. Preface

This cumulative dissertation, on the dispersal patterns of young fishes in rivers, is composed of four publications that were either published in or have been submitted to peer-reviewed journals. The work begins with a general introduction on movement ecology and dispersal, leading over to special features of larval fish drift. This is followed by my first-author publications (chapter by chapter) that were co-authored (in varying combinations) by my supervisor Hubert Keckeis and a number of colleagues: Reinhard Krusch, Franz Lumesberger-Loisl, Elisabeth Schludermann, Bernhard Zens (University of Vienna; Department of Limnology and Bio-Oceanography), Martin Glas, Helmut Habersack, Michael Tritthart (BOKU-University of Natural Sciences, Vienna; Christian Doppler Laboratory for Advanced Methods in River Monitoring, Modelling and Engineering) and Paul Humphries (Charles Sturt University, Australia; School of Environmental Sciences). With regard to all publications, I did most of the writing and the statistical analyses. In the last section of the thesis, I provide a short concluding discussion.

The major part of the work was performed within the project MODI (*Modelling dispersal patterns of fish larvae in a large river*), financed by the Austrian Science Fund (FWF, project no. P 22631-21 B17). It was conceptualized by Keckeis, Habersack, Humphries and Schludermann. One publication contains data from a former project (*Quantitative Erfassung von Plastikgranulat in der Schwechat und Donau*, project no. FA 572016), initiated by Keckeis and financed by the Borealis Polyfine GmbH.

All animal experiments were performed to the best of our knowledge and beliefs, and according to applicable regulations. I hope the sacrifice of numerous individuals during my studies will ultimately be of value and promote the conservation of fish populations in the Danube River.



2. General Introduction

Movement is a unifying characteristic in the life-cycle of virtually all living organisms (Nathan et al., 2008a). It ranges from the migration of bacteria (Klausen et al., 2003) and whales (Mate & Lagerquist, 1999) to the fall of plant seeds (Bullock & Clarke, 2000). Changes in position, at varying spatial and temporal scales, can directly influence the survival and fitness of individuals and thereby population and community structure (Matthysen, 2012). Due to its relevance, movement research is a hot topic in biology and ecology, featuring dispersal as one of its key words (Holyoak et al., 2008).

Dispersal is a versatile term, essentially describing the movement of organisms away from source locations such as the place of birth (i.e. natal dispersal; Dingemanse et al., 2003), a breeding site (i.e. breeding dispersal; Berteaux & Boutin, 2000), unsuitable habitat patches (Massot et al., 2002; Bates et al., 2006) or a point of release (Schludermann et al., 2012), towards areas where they might reproduce, establish and grow (Nathan et al., 2008b). In many cases, dispersal implies a potential gene flow across space (Ronce, 2007), making it a crucial parameter in (meta-) population concepts (Olivieri et al., 1995; Hill et al., 1996).

Dispersal is described as a three-stage process with clearly discriminable phases of *departure*, *transience* and *settlement* (Clobert et al., 2001). The inherent processes and dynamics of each phase primarily depend on the mode of dispersal. A rough differentiation can be made between *active* and *passive* dispersal. The passive dispersal of organisms, with limited or no self-propulsion, is for the most part governed by environmental forces. The observed distribution patterns are then based on the strength of the external drivers and on morphological attributes of the individual (weight, density, body shape etc.) (Andersen, 1993; Renner, 2004; Vikebo et al., 2010). Active dispersers predominantly control their own movement. Accordingly, distribution patterns often result from a complex set of species-specific behavior-environment interactions and physiological performances (swimming, flying etc.) in all three stages of dispersal (Fisher et al., 2000; Levin, 2006; Travis et al., 2012).

In aquatic ecology, dispersal commonly refers to the water current-mediated movements of propagules (seeds, spores, eggs, embryos, larvae) (Economou, 1991; Stella et al., 2006; Price & Humphries, 2010; Schwalb et al., 2010). Especially in marine habitats, major scientific efforts have been made to unravel the process of larval fish dispersal (of economically interesting species) from spawning grounds to adequate nursery habitats, which strongly regulates recruitment success and year-class strength (Fox et al., 2006; Peck & Hufnagel, 2012; Rochette et al., 2012). Individual-based studies on the internal state (Armsworth et al., 2001), navigation capacity (Staaterman et al., 2012), motion capacity (Fisher, 2005) and the movement paths (Paris et al., 2013) of dispersing larvae, frequently including the influencing external factors (Gerlach et al., 2007), are leading to a growing holistic understanding. The consistent message

of these studies is: (marine) fish larvae are by no means solely passive dispersers (but see Leis, 2007). This has considerable implications for the designation of marine protected areas (MPAs), which should preferably be located along dispersal paths (Planes et al., 2009).

Such information in running freshwaters are scarce, although dispersal is of comparable importance and has multiple functions in the life-cycle of many riverine fish species. The downstream dispersal of the early developmental stages (eggs, larvae), usually termed drift, is an effective connectivity vector between the patchily distributed key habitats in rivers (i.e. spawning, nursery, shelter, feeding) (Pavlov, 1994; Araujo-Lima & Oliveira, 1998; Braaten et al., 2008). These movements are associated with fitness costs and benefits for the individual. Among the benefits of leaving a certain area is the avoidance of (kin) competition (Humphries, 2005), the escape from local adverse conditions (Gale & Mohr, 1978) or/and the exploitation of the most advantageous feeding grounds (Pavlov et al., 2008). Costs result when small fish move because they are more vulnerable to physiological stress and predation when negotiating the intervening (and often hostile) matrix between habitats (Harvey, 1987; Reeves & Galat, 2010). As mentioned above, these processes may impinge on the population level, therefore being substantial for species conservation and river management issues (Carter & Reader, 2000; Ellsworth et al., 2010).

To date, studies on larval fish drift in rivers have focused on the more obvious characteristics such as seasonal, diurnal, spatial and developmental stage-specific patterns as well as associated differences between species (Peñáz et al., 1992; Reichard et al., 2002; Zitek et al., 2004; Johnson & McKenna, 2007). Nonetheless, many open questions remain relating to the single phases of a drift event (departure, transience, settlement) hindering integrated assumptions on the process.

This doctoral thesis addresses a number of under-investigated aspects in drift research. It is organized in 4 chapters (i.e. articles published in, or submitted to scientific journals) which are briefly outlined below:

- 1.) The first chapter (**Lechner et al., 2016a**: *Patterns and processes in the drift of early developmental stages of fish in rivers: a review*) serves as an introduction to the topic. It reviews most of the available literature on larval dispersal in rivers, summarizes the existing knowledge on several drift features and identifies deficits therein. Inspired by a general model for organismic movement (Nathan et al., 2008) and current advances in marine dispersal research, we call for holistic studies in running waters designed to help answer the questions *why?*, *how?*, *where?*, and *when?* young fish drift.

The next sections (chapters 2+3) refer to drift experiments with larval nase carps (*Chondrostoma nasus*), conducted in consecutive years (2011, 2012) within a free-flowing stretch of the Austrian Danube east of Vienna. This work is a key part of an interdisciplinary project aiming at developing the first individual-based model of larval dispersal in rivers (ILAM, see Glas et al., 2016). A rough overview on the methodological approach is provided in Figure 1, detailed information can be found in the respective publications.

2.) The second chapter (**Lechner et al., 2016b**: *The influence of discharge, current speed and development on the downstream dispersal of larval nase (Chondrostoma nasus) in the River Danube*) highlights the drift mode of larvae. The principle debate is whether the downstream movements of young fish are an active or passive process (Corbett & Powles, 1986; Copp & Faulkner, 2002; Lechner et al., 2014c; Janáč et al., 2013). By observing the simultaneous downstream dispersal of nase larvae and floating passive particles away from a point of release, we investigate the activity level of drifting fish and identify the influencing environmental factors.

3.) The third chapter (**Lechner et al., 2014a**: *Shoreline configurations affect dispersal patterns of fish larvae in a large river*) deals with the influence of shoreline morphology, and the associated hydraulics, on the spatio-temporal drift and settlement patterns of larval nase. We compare a near-natural gravel bar and an artificial rip-rap with groynes with respect to their *accessibility* for drifters, their inherent *connectivity* between habitat patches and their *retention potential* for settling individuals. We point out negative effects of bank reinforcement and discuss the effectiveness of taken restoration measures.

The last section is (thematically) somewhat separated from the rest. It relates to an issue that unexpectedly appeared during the field sampling but is potentially of crucial importance for drifting larvae.

4.) The fourth chapter (**Lechner et al., 2014b**: *The Danube so colourful: A potpourri of plastic litter outnumber fish larvae in Europe's second largest river*) deals with the observed pollution of the Danube River. Beside larvae, we found high numbers of tiny plastic particles ("microplastics") in our fine-meshed, stationary drift nets. On the one hand, we thereby demonstrate a potent method in rivers for detecting what is described as one of the key pollutants in aquatic systems (Thompson et al., 2009). On the other hand, we reveal a potential source of larval mortality: small (drifting) fish might mistake such particles for food and ingest them, possibly with fatal consequences (Wright et al., 2013).

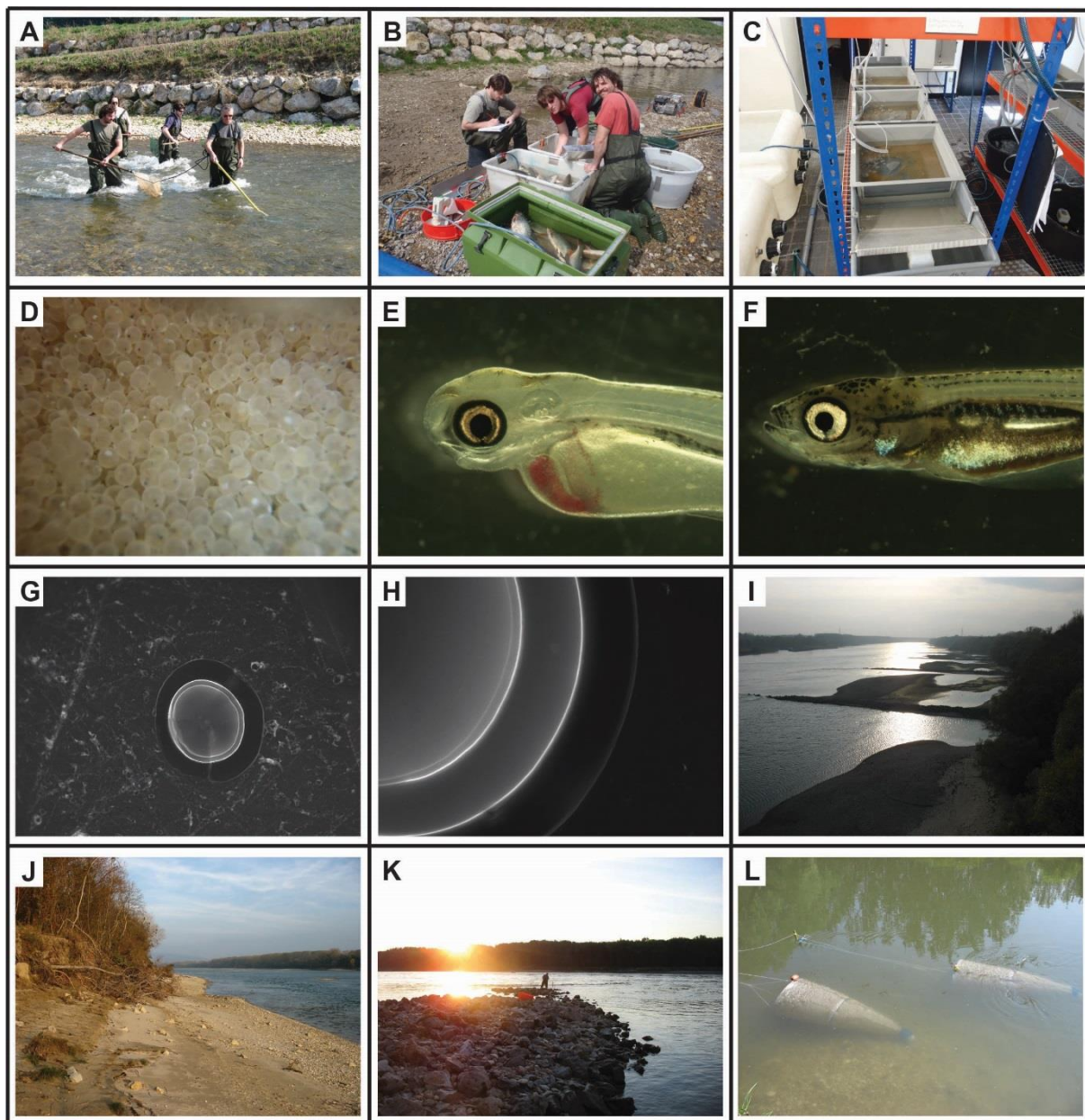


Figure 1. Ripe adult nose carps (♀+♂) were taken from a natural spawning population in a Danube tributary (Schwechat River) by electro-fishing (A, B). The obtained gametes were mixed by hand in our water lab; fertilized eggs were transferred to well oxygenated rearing flumes (C, D). After hatching, free embryos briefly feed on their yolk reserve (E) until they start exogenous feeding at the beginning of the larval phase (F). At certain points, the otoliths (osseous structures of the inner ear) of young nose were stained with a chemical marker (Alizarin Red). The resulting marking sequences, visible under certain wave-lengths with an epifluorescence-light microscope (G, H), contained information (e.g. place of release, stage at release) crucial for the mark-recapture experiment in the field. All tagged larvae were released at predefined locations in the Danube section east of Vienna, situated within the national park “Donau-Auen” (I). Those locations were a near natural gravel bar along the left shore (J) and an artificial rip-rap with boulder embankments at the right shore (K). Released larvae were caught with stationary drift nets (L). Knowing the place of release and the place of recapture enabled certain conclusions on the movement of larvae between these sites (©Hubert Keckeis).

Please note that there are two separate numbering schemas for figures and tables within this thesis. First, the peer reviewed publications each have their self-contained schema, and second, all other figures and tables are continuously numbered throughout the different chapters.

3. Publications

Chapter 1: Drift of young fishes in rivers: a detailed introduction to the topic

REVIEWS

Patterns and processes in the drift of early developmental stages of fish in rivers: a review

Aaron Lechner · Hubert Keckeis ·
Paul Humphries

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Abstract Current-mediated downstream dispersal by the early developmental stages of fish in rivers is a common phenomenon. Knowledge of patterns and processes in the dispersal, or ‘drift’, of young fishes provides important information on spawning location and spawning success, habitat use, movement paths and flow-ecology relationships more generally, all of which are critical for effective river conservation and management. But despite the importance of such information, our understanding of the patterns and processes of the drift of the early life stages of riverine fishes is limited. Furthermore, riverine fish drift research has tended to occur in isolation from movement studies of other organisms, limiting its integration with higher level concepts and theory. This manuscript reviews the literature on the dispersal of young fishes in running waters. Relevant studies from all climatic zones and geographical regions are investigated, with particular attention given to the

types and life history stages of fishes that drift and the seasonal and diel patterns of drifting. We then consider how fish enter the drift and their mode of drifting, attempting to reconcile a long-running discussion, under what we call the ‘active–passive conundrum’. We argue that, aside from eggs, the early stages of fish are not exclusively either passive or active drifters, but usually a mixture of the two, which we term ‘actipassive’ drift. Finally, we evaluate existing knowledge in the context of a general conceptual framework for movement ecology, identifying gaps in our understanding of the roles of internal state, navigation capacity, motion capacity, external factors and internal factors in influencing the dispersal process.

Keywords Fish larvae · Free embryos · Drift · Dispersal · Rivers

Introduction

Placing a fine-mesh net in a river in spring or early summer will usually catch the eggs, free embryos and larvae of fishes moving downstream, sometimes in vast numbers. These early developmental stages of fishes are participating in the first mass movement of their lives, dispersing from spawning or nursery sites to what are presumed appropriate rearing habitats (Pavlov, 1994). This group includes individuals that seem deliberately to use the current to help them move (Braaten et al. 2012), and others that are apparently accidentally entrained (Harvey 1987; Wolter and Sukhodolov 2008). Whatever the mechanism, current-mediated dispersal – or ‘drift’ – of the young stages of fish is an integral part of the life cycle of many

riverine species (Muth and Schmulbach 1984; Bujold et al. 2004; Humphries 2005). It enhances habitat connectivity and gene flow, promotes community stability and extends the range of populations (Janáč et al. 2013; Roberts et al. 2013).

While drifting, eggs, free embryos and larvae are relatively simple to collect, and these collections can provide much information on the dynamics of early life. This information can elucidate patterns and processes associated with spawning and larval production (Zitek et al. 2004a; King et al. 2005; Braaten et al. 2010; Borchering et al. 2014), it may allow forecasting of future year-class-strength (Johnston et al. 1995) and provide estimates of stock size of spawning adults (Usvyatsov et al. 2013). It also assists in understanding how fishes and their environment – especially the flow environment – interact. This is vital for effective river management, because the presence of drifting fishes provides evidence of in situ reproduction of native and alien species, common and rare species, and species important for recreational and commercial fisheries (Humphries and Lake 2000; Jiang et al. 2010).

This sort of information is also critical if we are to assess, and perhaps counter, the impact of flow alteration and other anthropogenic disturbances (Pavlov et al. 2008; Bracken and Lucas 2013; Lechner et al. 2014a). But despite the importance of such information, our understanding of the patterns and processes of the drift of the free embryos and larvae of riverine fishes is limited (Corbett and Powles 1986; Flecker et al. 1991; Schmutz and Jungwirth 1999). There are many studies from around the world that have described temporal and spatial patterns of drift of the larvae of riverine fishes (e.g. Gadomski and Barfoot 1998; Oesmann 2003; Zitek et al. 2004b). These include a range of temporal scales, from diel, daily to seasonal (e.g. de Graaf et al. 1999; Copp and Faulkner 2002; Araujo-Lima and Oliveira 1998). But what catalyzes fish larvae to drift in the first place, how far they drift, how they navigate to settlement sites, how they detect these sites, how they exit the current, how they avoid predation and other hazards *en route*, and how significant this dispersal is to population dynamics, are largely unknown (but see Johnston 1997; Robinson et al. 1998; Schludermann et al. 2012).

Here we review the literature on the patterns and processes associated with the dispersal of the free embryos larvae and juveniles of riverine fishes, with the overall aim of understanding why, how and where fish drift and how drifting fish interact with the riverine environment. We searched a range of scientific databases (Google Scholar, Web of Science, Scopus) and employed the search terms *fish larvae + drift + dispersal + rivers*.

The review is divided into three sections. In the first, we consider species-, stage- and location-specific characteristics of fish drift, and discuss drift patterns at different temporal scales. In the second section, we highlight processes associated with the downstream movement of young fish; i.e. the entry into the current and the subsequent behavior in the flow. We discuss established classifications and introduce new approaches based upon recent insights. In the

third section, the existing literature on fish drift is analyzed in the context of the unifying organismal movement model of Nathan et al. (2008), by evaluating the state of knowledge relating to the *internal state*, *motion capacity* and *navigation capacity* of drifting fish. Knowledge gaps are identified and suggestions for future research, towards an integrated approach in drift studies, are made.

What types of fishes drift?

The intensity of drift, its governing mechanisms and the importance of the process in the life cycle of fishes is species-specific (Johnston et al. 1995; D'Amours et al. 2001). For example, Reichard et al. (2001) discriminated between taxa that continuously appeared in the flow of a Czech lowland river and others that were exclusively found during elevated discharge. Humphries and King (2004) classified species based on the relevance of drift to their life history. Species were categorized as *obligate*- (high abundance in drift, low abundance in other habitats), *facultative*- (occur in similar abundance in the drift and in low-flow habitats) or *non-drifters* (low abundance in the drift, drift entrance is likely accidental). The assignation to a specific group appears independent of velocity preference of the adults of particular species: some normally limnophilic species as adults (e.g. *Rhodeus sericeus*, Cyprinidae) drift as larvae and utilize the flow for dispersal (Jurajda 1998), whereas the larvae of some normally rheophilic species as adults (e.g. *Squalius cephalus*, *Gobio spp.*, Cyprinidae) avoid drifting (Brown and Armstrong 1985; Reichard et al. 2001).

Species-specific patterns in initial drifting patterns greatly depend on the spawning mode of the fish in question (Pavlov 1994). Pelagophilous fish release buoyant or semi-buoyant eggs that immediately enter the flow and, apart from the influence of buoyancy and shape, drift passively (Araujo-Lima and Oliveira 1998; Jiang et al. 2010; Widmer et al. 2012). Embryos and larvae successively develop in the water column during transport (Wootton 1998). By contrast, the early embryogenesis of salmonids (brood hiders) and many rheophilous cyprinids (open-substrate spawners) is characterized by an extended below-gravel period (Persat and Olivier 1995; Bardonnnet 2001). Here, the first dispersers are free embryos or well-developed larvae that enter the current after the yolk sac is depleted. The influence of the spawning mode on subsequent drift events weakens as the fish grow and develop specific phenotypes and behaviors, resulting in variable drift patterns within the same reproductive guild (Pavlov 1994).

Other factors affecting patterns of drift are related to the migratory behavior of the adults. In some amphidromous species, for example, larval drift is a continuous downstream movement, with a distinct spatial goal: the ocean (Iguchi and Mizuno 1990; Maeda and Tachihara 2010). Movement between freshwater and the sea is, in this case, an obligate part of the life history, and so it is unsurprising that drift is deliberate and controlled (Bell and Brown 1995). Wholly freshwater fishes, however, tend to show more diverse drift patterns (Pavlov et al. 1978). For

example, whereas larvae of the anadromous smelt (*Osmerus eperlanus*, Osmeridae) use strong currents in the mid-channel of the River Elbe as a vehicle for swift downstream movements, potamodromous cyprinids instead drift in moderate currents along the shoreline (Oesmann 2003). Likewise, while larvae of some amphidromous sculpins (*Cottus aleuticus*, *Cottus asper*, Cottidae) in Smith and Van Duzen rivers, Northern California, expedite their dispersal to estuaries by drifting at elevated river flows, the potamodromous fish community here apparently has evolved life histories that minimize the risk of transport into saltwater (White and Harvey 2003).

However, comprehensive drift models for potamodromous fish are, with a few exceptions, largely absent or theoretical. Apparently, the larvae of long migratory, potamodromous sturgeon species feature a continuous drift over several days and hundreds of kilometers (see Online Resource). Drift distance and duration are highly variable among species, and may be genetically coded in order to reach distinct nursery habitats and to compensate for the long upstream migrations of the adults (D'Amours et al. 2001; Kynard et al. 2002; Kynard et al. 2007a; Kynard et al. 2007b; Braaten et al. 2008; Braaten et al. 2012). Instead of a continuous downstream movement, the early dispersal of other potamodromous species potentially includes a sequence of drifting phases (primarily during night), interspersed with periods of inshore settlement in nursery habitats (primarily during day) (Carter et al. 1986; Gadomski and Barfoot 1998). The cumulative distance covered during this pattern is not known and needs more research.

At what life history stage do fishes drift?

Drifting typically occurs during defined intervals of ontogeny and at certain body lengths for particular species. A narrow size range of drifting individuals, for example, has been observed in two invasive benthic species (*Neogobius melanostomus*, *Proterorhinus semilunaris*, Gobiidae) in the River Dyje, Czech Republic (Janáč et al. 2013), catfish alevins (*Ictalurus punctatus*, *Pylodictus olivaris*, Ictaluridae) in the Illinois River, Arkansas (Brown and Armstrong 1985), and particular native fishes (*Catostomus latipinnis*, *Catostomus discobolus*, Catostomidae; *Gila robusta*, *Rhinichthys osculus*, Cyprinidae) in the Colorado River, Colorado (Carter et al. 1986). The Murray cod (*Maccullochella peelii*, Percichthyidae) in the Murray River, Australia (Humphries 2005), and pumpkinseeds (*Lepomis gibbosus*, Centrarchidae) in the River Rhone, France (Copp and Cellot 1988), predominantly drift as free embryos. Cyprinids, on the other hand, mostly disperse during their early larval development (larval stages L1-L4; Copp and Faulkner 2002; Zitek et al. 2004a; Sonny et al. 2006) or at the transition between the larval and the juvenile period (stages L6/J1; Reichard and Jurajda 2007; Lechner et al. 2014b). But the former generality, that downstream dispersal is most intensive during early embryogenesis and sharply decreases upon the achieving of the juvenile period

(Pavlov 1994), does not always apply: e.g., the drift in two Czech rivers, Morava and Kyjovka, and in a bypass section of the River Rhone was dominated by juvenile cyprinids, percids and cobitids (Peňáz 1992; Reichard et al. 2001).

Drifting by fishes at particular sizes and developmental stages may be an adaptation to coping with, or taking advantage of, riverine conditions. Behavioral and physiological changes during development may enable certain stages to actively react to their environment and to temporally and spatially regulate their drift (Pavlov et al. 2008). Developmental stage, for instance, was found to correlate with change in swimming ability and habitat or diet shifts among seven drifting cyprinid species (Reichard and Jurajda 2007) and swimming ability of several Murray-Darling Basin fishes (Kopf et al. 2014). Alternatively, the size-structure of drifting cyprinids in the diel cycle might instead relate to an altered reaction to light during ontogeny. It may only be older, more-developed larvae that respond to the transition from day to night by moving into the current (Reichard et al. 2002a; Zitek et al. 2004b).

In fact, stage-specific drift patterns have also been observed in non-riverine species (*Rhodeus sericeus*, Cyprinidae; *Lepomis gibbosus*, Centrarchidae) inhabiting running waters (Copp and Cellot 1988; Jurajda 1998), suggesting that stage-dependency could merely reflect susceptibility to entrainment in the current. Ontogenetic changes in morphology (i.e. filling of the swim bladder) and behavior, as well as deficits (i.e. low visual acuity and swimming ability), or even improvements (i.e. enhanced swimming capacity and activity) in physical capabilities, may increase chance encounters with high currents, thereby inducing washouts and accidental drift (Harvey 1987; Persat and Olivier 1995). It must be borne in mind, however, that the stage and size distributions of larvae collected in a drift net may be an artefact of the spatial distribution of drifting larvae and how larvae are collected. For example, catch composition will be affected substantially by the spatial (e.g., distance from shore [Reichard et al. 2004], distance from hatching sites [Sonny et al. 2006] or vertical position in the water column [Pavlov et al. 1978]) and temporal (e.g., diel or seasonal [Carter and Reader 2000]) design of the sampling program or the used sampling gear (Tonkin et al. 2007).

At what time of the year do fishes drift?

The timing of drift is directly linked to that of reproduction (Brown and Armstrong, 1985). The peak in spawning- and hence drift activity is presumably adaptive and initiated by environmental cues that promise favorable conditions for the progeny (Somarakis et al. 2000). The most important factors, in this respect, are water temperature (Carter et al. 1986; Johnston 1997; D'Amours et al. 2001; Reichard et al. 2002b; Hay et al. 2008) and discharge (Johnston et al. 1995; Robinson et al. 1998; Araujo-Lima and Oliveira 1998; Auer and Baker 2002). Either because fish do not spawn or produce viable eggs and larvae (i.e. *reproductive effects*; Zitek et al. 2004a) or because larvae do not survive (i.e. *recruitment effects*; Schiemer et al. 2001;

Humphries et al. 2013), temperature and discharge not only govern the timing, but also the spawning success and hence the subsequent intensity of larval drift (Reichard et al. 2002b; Durham and Wilde 2008; Ellsworth et al. 2010b). Intra- and inter-annual variation in drift densities, for instance, may be attributed to fluctuations in water temperature and the related variability in egg mortality during incubation (Busch et al. 1975; Sonny et al. 2006). Rising discharge levels during certain periods may inundate breeding grounds, and ensure efficient oxygenation of the eggs, thereby increasing larval density and inducing seasonal drift peaks (Johnston et al. 1995; de Graaf et al. 1999; Martin and Paller 2008).

The time-density curves of larval drift are often location- or river-specific and can be informative about the composition of the resident fish assemblage (Humphries and Lake 2000; Reichard et al. 2002b). Bi- and multi-modal seasonal patterns are characteristic of taxa-rich waters and reflect time-staggered spawning and drifting of species (Jiang et al. 2010). Additionally, multiple spawning events throughout the season of frequently drifting species may contribute to these patterns (Zitek et al. 2004b; Janáč et al. 2013). Unimodal drift patterns can occur when single species dominate in the drift, or peak drift densities of different species overlap in the seasonal course (Lechner et al. 2014b).

At what time of the day do fishes drift?

The pronounced circadian rhythm of drift, with peak densities during the night, is a unifying pattern that applies for virtually all fishes and fish-like organisms. For example, drifting lamprey ammocoetes (superclass: Agnatha) show a nocturnal increase in abundance (Johnston 1997; White and Harvey 2003; Bracken and Lucas 2013), as do some sturgeon species (superclass: Gnathostomata, infraclass: Chondrostei) (D'Amours et al. 2001; Kynard and Parker 2006) and many teleost fishes (superclass: Gnathostomata, infraclass: Teleostei) (Johnson and McKenna 2007; Durham and Wilde 2008; Jiang et al. 2010). Day-night ratios of drifting fish vary between 1:1.3 (Peñáz et al. 1992) and 1:190 (Reichard et al. 2004). The diurnal differences in downstream dispersal are most likely related to the light level and its influence on drift entrance (see next section). Different species and ontogenetic stages of fish respond to different levels of light, apparently resulting in time-staggered density peaks of species (dusk, night and dawn; Pavlov et al. 1978; Brown and Armstrong 1985; Janáč et al. 2013), and sizes of larvae throughout the course of the night (Zitek et al. 2004b; Sonny et al. 2006). Similarly, varying light conditions not only induce intra-specific differences in drifting patterns among rivers (Johnson and McKenna 2007), but also along the course of the same river (Iguchi and Mizuno 1991). Low illumination or water transparency during the day (e.g. high turbidity during flood events) can cause a cessation of diel periodicity in drifting (but see review by Reeves and Galat 2010). Nevertheless, the mechanisms driving diel patterns in drift are uncertain, and results far from unequivocal: for example, some drift studies have not detected

temporal patterns (Muth and Schmulbach 1984; Robinson et al. 1998; Braaten et al. 2012; Borcharding et al. 2014) or the influence of water turbidity (Jurajda 1998).

The Active-Passive-Conundrum (APC)

There has been a long-standing debate about the active or passive nature of fish drift (Pavlov 1994; Reichard and Jurajda 2004; Copp and Faulkner 2002; Schludermann et al. 2012). Entry into the current and the subsequent downstream movement may be deliberate, with the ultimate aim of efficient dispersal. Presumably, this behavior occurs in response to particular environmental cues, and evolved to expedite the process of downstream dispersal (Robinson et al. 1998; Lechner et al. 2014b). If this is the case, drift should be considered a predominantly *active process*. The alternative explanation is that drift primarily occurs accidentally, and environmental factors, such as current and light, override the physical capabilities - swimming capacity and orientation - of small fish (Corbett and Powles, 1986; Wolter and Sukhodolov 2008). In that case, drift should be considered a predominantly *passive process*.

In reality, knowledge about larval behavior is still fragmentary (Reichard and Jurajda 2007; Pavlov et al. 2008), and many authors discuss both active and passive explanatory models; but typically they offer no resolution or integration (Gadomski and Barfoot 1998; Bardonnnet 2001; Humphries and King 2004; Reichard et al. 2004; Sonny et al. 2006). An analysis of what we call the “Active-Passive-Conundrum” (APC), based on empirical studies, is outlined in the next sections. Specifically, we assess what we know about how fish larvae enter the drift and how they behave while drifting and contrast the internal and external factors involved. In our review, the work of Dmitry Pavlov is pivotal (Pavlov et al. 1978; Pavlov 1994; Pavlov et al. 1995; Pavlov et al. 2008; Pavlov et al. 2011). His concepts on the nature of fish drift are briefly summarized at the beginning of each of the following sections. We then offer a classification of drift entrance modes and suggest modifications to Pavlov’s model of active/passive drift, based upon our review of the drift literature.

Drift entrance and its reasons

According to Pavlov (1994), drift entrance incorporates mechanisms of different orders. *First order* mechanisms enhance fish activity and distribute them in the open water. They constitute the prerequisite for drift entrance, and include behavioral responses that either can be related (*specific behavioral responses*) or unrelated (*non-specific responses*) to the current (Pavlov et al. 2008). *Second order* mechanisms inhibit rheoreaction, the fish’s inherent behavior to move against a current (Pavlov 1994). In the following, we use Pavlov’s work, substantiated by other significant research in the field, to introduce three scenarios for how young fish can enter the current.

Entry into the drift can be: a) accidental, caused by environmental conditions that exceed and inhibit the individual's ability to maintain position, and flushes them away from nursery or hatching sites (*passive drift entry*); b) partly behavioral, when unrelated factors (e.g., feeding movements, flight responses) cause young fish in the open water to be exposed to strong currents and they are entrained (*coincidental drift entry*); or c) deliberate, as an adaption to fluvial conditions, and relying on innate species- and stage-specific behavioral responses that are aimed at leaving or reaching specific habitats (*active drift entry*). Discriminating between these alternative explanations is largely speculative. We can only guess at what initiates, and the ultimate goal of, drifting behavior. And mechanisms may change during ontogeny for the same species, where the probability of a passive entry could decrease with increasing physical and behavioral abilities (Pavlov 1994; Kynard et al. 2007b). In the following, we consider each mode of drift entry in turn.

Passive drift entry

In passive drift entry, elimination of rheoreaction is triggered by the loss of visual cues at low illumination and in swift flows, or by the inability of fishes to resist overcritical current speeds (Pavlov 1994). In this respect, small fish are particularly vulnerable, because both swimming capacity and visual acuity increase with size, and are limited in embryos and larvae (Wanzenböck and Schiemer 1989; Flore et al. 2000).

The loss of visual orientation and the ensuing displacement from refuges is a common explanation for the increase in drift density of fish larvae with the onset of darkness and in highly turbid waters (Northcote 1962; Corbett and Powles 1986; Gadomski and Barfoot 1998; Peñáz et al. 1992; Reichard et al. 2001; Oesmann 2003; Reeves and Galat 2010). In this context, Bardonnnet (1993) demonstrated that phosphorescent landmarks lessened the nocturnal drift peak of emerging brown trout (*Salmo trutta*, Salmonidae). Additionally, experiments by Pavlov et al. (1972) on various teleost species showed that the critical current velocities that young fish could resist were markedly higher in light than in darkness.

Other studies highlight the effect of high current velocities during flood events on influencing larvae to enter the drift (Reichard et al. 2001). The larvae of usually non-drifting species were frequently detected in the flow during rising water levels in two Australian rivers (Humphries and King 2004). The authors concluded that these individuals were flushed from backwaters and other still-water habitats. Harvey (1987) observed a taxon- and size-specific susceptibility of downstream displacement by flooding in Brier Creek, Oklahoma, where smaller fish (5-10 mm) were at greater risk of being entrained than larger ones (10-25 mm). Likewise, washouts of mainly eurytopic 0+ cyprinids during a summer flood in the river Oder, Germany, caused a drastic decline in fish densities in different mesohabitats (Bischoff and Wolter 2001). Drifting during flood events can lead to substantial mortality, likely caused by gill damage from

suspended sediment (Mion et al. 1998). Notably, moderate variation in discharge does not appear to affect the abundance or taxonomic and size composition of drifting larvae (Corbett and Powles 1986; Robinson et al. 1998; Copp et al. 2002; Reichard and Jurajda 2004; Zitek et al. 2004b; Humphries 2005).

Coincidental drift entry

Drift entry may be initiated by behaviors which are not targeted deliberately at dispersal, but expose young fish to strong currents (*sensu non-specific behavioral responses*; Pavlov et al. 2008). In that case, individuals inadvertently enter the flow while emerging from substrate, or during feeding activities and flight responses.

The directional movements of larvae in response to a light stimulus (=phototaxis) are considered crucial for the coincidental entrance of young fish into the water column (Pavlov 1994). Positive and negative photoreactions are species-specific, unconditioned reflexes to certain levels of illumination (Pavlov et al. 1978). They *inter alia* mediate the emergence of recently hatched larvae from the spawning substrate in order to fill the swim bladder and start exogenous feeding (Persat and Olivier 1995, Zitek et al. 2004b). Photoreactions are supposed to be important determinants of temporal drift patterns. Observations by Iguchi and Mizuno (1990), for example, indicate that diel drift patterns in the Japanese common goby (*Rhinogobius brunneus*, Gobiidae) depend on light preferences of the free embryos and changes in the ambient light conditions along a river course.

Armstrong and Brown (1983) and Brown and Armstrong (1985) concluded that coincidental drift entry relates to a higher risk of colliding with fast currents after initiation of feeding activities, because they detected only a few pro-larvae (with yolk sac), and mainly uniform-sized post-larvae (without yolk sac), in the Illinois River. Encounter rates with currents can also increase during exploratory behavior and may depend on visual habitat heterogeneity. For example, in experiments with *Cichlasoma octofasciatum*, Cichlidae, Pavlov et al. (2008) discovered that motor activity during habituation in novel surroundings is higher when visual landmarks are missing.

Active drift entry

Young fish commonly leave a specific area in order to escape unfavorable conditions or to reach the most advantageous habitats. Active drift entry, together with the utilization of the river current as means of transport, may have evolved to facilitate these movements (Gadomski and Barfoot 1998; Ellsworth et al. 2010a; Braaten et al. 2012). There are several reasons for relocations during early life-history. One of the most important may be the matching of larval requirements and environmental conditions at certain points of ontogeny. Mismatches in these two can arise immediately after hatching, when vulnerable embryos and early larvae

face the swift-flowing, nutrient-poor spawning grounds chosen by their parents (Bardonnnet 2001; Keckeis 2001). And they can occur later, when food or physico-chemical requirements change (Corbett and Powles 1986; Bardonnnet et al. 2001; Schiemer et al. 2003). Consequently, the initial drift entry at the spawning site, along with a rapid transport to suitable near-shore feeding areas and subsequent movements between these nurseries, are crucial for maximizing energy gain and survival (Jonsson 1991; Usvyatsov et al. 2013). By diluting the naturally high aggregation of individuals at spawning sites and nurseries, drift entry and dispersal also reduce the attraction of predators, the risk of cannibalism and competition for food and space (Copp et al. 2002; Humphries 2005). Population density effects, by way of example, are the main dispersal drivers in salmonid fry: downstream movement of territorial young brown trout (*Salmo trutta*, Salmonidae) ceased, independent of current speeds, after a constant final proportion of fish had been displaced (Daufresne et al. 2005). The smaller and lighter fry component of steelhead (*Oncorhynchus mykiss*, Salmonidae) and Atlantic salmon (*Salmon salar*, Salmonidae) left their hatching sites, because they were out-competed by larger conspecifics in establishing and holding territories (Johnston 1997; Bujold et al. 2004; Johnson et al. 2013).

Although drift entry is often linked to illumination and current velocity, lack of correlation between these variables and abundance of drifting individuals may provide evidence for the deliberate nature of the process. For example, there was no relationship between light intensity and body length of drifting cyprinids in the River Morava (Reichard et al. 2002a). A negative correlation was expected if drift entrance was catastrophic and solely attributed to a size-dependent loss of visual orientation and neutralization of rheoreaction. The conclusion that entry into the drift is a time-dependent behavioral decision is supported by other studies: Sonny et al. (2006) ascribed the observed differences in the diurnal size range of drifting chub (*Squalius cephalus*) and roach (*Rutilus rutilus*, Cyprinidae) in the River Meuse, Belgium, to diverging dispersal strategies of both species; Pavlov (1994) watched roach larvae actively entering the flow of a hydrodynamic channel during the night; in experiments with brown trout, Roussel and Bardonnnet (1999) showed that upstream movements were predominantly nocturnal, indicating that darkness might instead of inhibiting a fish's orientation, in fact allow it the freedom to disperse. Irrespective of why fish choose to enter the current, doing so during the night or at high levels of turbidity may be beneficial, and be a way of avoiding visual predators (Clark and Pearson 1980; Johnston 1997; Copp et al., 2002; Usvyatsov et al., 2013). Another hypothesis, that adaptive night-time drift entrance of young fish corresponds to the feeding on synchronously drifting invertebrates (Elouard and Leveque 1977), is rather implausible: capture success and consumption rate of larvae sharply decrease with increasing velocity (Flore and Keckeis, 1998) and decreasing light (Blaxter 1986), making it difficult for

drifting fish to locate and eat prey. Most larvae are caught with empty guts at night (Shepherd and Mills 1996).

Other results suggest that rising water levels and current speeds do not necessarily trigger a passive displacement, but an active movement of young fish. Increasing current speeds, during elevated discharge, neither affected abundance nor size and age of drifting young-of-the-year cyprinids (Reichard and Jurajda 2004). In a similar way to the effects of light, young fish may enter the drift only under particular hydraulic conditions (Johnston et al. 1995; Araujo-Lima and Oliveira 1998). Studies on Kootenai white sturgeon larvae (*Acipenser transmontanus*, Acipenseridae) in artificial streams concluded that there is a threshold velocity needed to trigger larval dispersal (Kynard et al. 2007b). Daufresne et al. (2005) deduced that drift entry is not only attributed to swimming abilities, because greater displacement rates of brown trout were observed at lower *and* higher velocities.

Other abiotic factors than light and current can provoke an active drift entry: Gale and Mohr (1978) interpreted the high densities of drifting larvae downstream of an acid mine drainage as escape from heavily polluted waters; and the negative correlation of drift density and suspended particular matter in the main channel of the Elbe has been attributed to active drift avoidance (Oesmann 2003).

Drift control and orientation

Pavlov's classification of larval drift modes has served as a basis for almost all the work that has been carried out on this topic (but see his review papers: Pavlov 1994 and Pavlov et al. 2008). He cites the most common drift mode as constituting *passive drift*: non-oriented individuals are transported downstream at the same rate as the current speed. Passive drift mode likely corresponds to accidental drift entry, typical of the early larval stages and usually observed in the dark. The opposite, *active drift*, logically follows a deliberate entry into the current. Here, oriented individuals move faster downstream than the current, primarily during daytime. A hybrid form, *active-passive drift*, is characterized by upstream oriented fish, moving downstream at lower rates than the mean current speed. This mode, originally attributed to impaired swimming ability at decreased water temperatures and during starvation (Pavlov et al. 2008), is now considered as one manifestation of negative rheoreaction; i.e. an oriented, active downstream movement (Pavlov et al. 2011)

Below, we review the evidence for active and passive drift in the literature. We suggest that recent work indicates that classification into discrete drift modes may not be the best model of what happens in the wild, and instead, we offer an alternative approach.

Passive drift

A solely passive downstream transport of larvae is mostly ascribed to a combination of poor swimming abilities with highly variable flow conditions in rivers (Corbett and Powles 1986; Gadomski and Barfoot 1998; de Graaf et al. 1999). Average current speeds in rivers often exceed swimming speeds of recently hatched larvae (Wolter and Sukhodolov 2008). Additionally, turbulent flows make maintaining position or direction of swimming extremely difficult if not impossible for many larvae (Webb and Cotel 2011), increase the energetic costs of locomotion (Liao 2007) and reduce the critical swimming velocities young fish can maintain (Lupandin 2005).

If passive transport is the norm, vertical and lateral distributions of drifting fish larvae depend on the location of upstream spawning sites (Brown and Armstrong 1985; D'Amours et al. 2001) and a subsequent exposure to hydraulic forces (e.g. average current speeds, transverse flow circulations, rheogadients, turbulent mixing; Pavlov 1994; Pavlov et al. 2008). Therefore, passively drifting individuals should become redistributed according to their body shape and buoyancy (Copp et al. 2002). They should end up in depositional habitats (e.g. groyne fields; Lechner et al. 2014a) or be concentrated in dead zones, slackwater habitats (Wolter and Sukhodolov 2008; Kopf et al. 2014) and concave riverbanks (Pavlov et al., 2008). Depending on discharge levels, hydraulic forces may concentrate young fish in areas with high current speeds, such as the thalweg (Braaten et al. 2010; Ellsworth et al. 2010a). If larvae are kept in suspension under high discharges, this may considerably increase drift distance and influence longitudinal distribution patterns (Corbett and Powles 1986).

However, a growing number of studies, documenting behavioral, sensorial and physical abilities of young fish (Garner 1999; Hogan and Mora 2005; Stoll and Beeck. 2012), refute the model of a solely passive drift. Specifically, it has been shown that the spatio-temporal dispersal patterns of fish larvae differ from those of virtual (Schludermann et al. 2012) and physical (Lechner et al. 2014a) passive particles, and that passive transport models overestimate drift distance by far (Braaten et al. 2012).

Active drift

The drifting free embryos and larvae of some species are well developed and are active swimmers, able to determine their location in the water column (Peñáz et al. 1992; Humphries 2005). Even at low light levels and overcritical currents, they may respond to hydraulic gradients and drift under certain conditions (Kaminskas 2011; Schludermann et al. 2012). Experiments on zebrafish larvae (*Danio rerio*, Cyprinidae), for instance, showed that rheoreaction is mediated by neuromasts of the lateral line, which enables young fish to sense water flows and orient in currents at night (Olszewski et al. 2012; Stewart et al. 2013).

If active transport is the norm, the spatial distribution of drifting larvae depends on deliberate swimming behavior and the ability to locate preferred hydraulic habitat, or at least to orientate along gradients which lead to these (Robinson et al. 1998). Vertical positioning of drifting larvae may reflect an effort to avoid benthic predators and collisions with the substrate (Brown and Armstrong 1985; Gadomski and Barfoot 1998). Lateral positioning of drifting larvae, however, is thought to be a result of specific dispersal strategies; e.g., drifting near-shore to enhance the probability of being able to move into suitable habitat when coming close to it (Araujo-Lima and Oliveira 1998), or drifting offshore to accelerate transport and thereby minimize mortality (Reichard et al. 2004). The distance covered during active drifting will clearly vary depending if larvae choose to drift at low (Lechner et al. 2014b), intermediate (Schludermann et al. 2012) or high currents (Oesmann 2003) and whether they drift low or high in the water column (Kynard et al. 2007a)

A continuum mode of dispersal: *actipassive* drift

We argue that, aside from eggs, the early developmental stages of fish are not exclusively either passive or active drifters. On the one hand, the hydraulic forces can exceed the swimming capabilities of free embryos and larvae (Wolter and Arlinghaus 2003). On the other hand, even tiny larvae display orientation in the dark at over-critical currents and can, to a degree, regulate their dispersal (Zens et al. 2015). Therefore, a strict separation of drift modes, as applied in the majority of studies (*active*: Peñáz et al. 1992; Robinson et al. 1998; Humphries 2005; Braaten et al. 2012; *passive*: Armstrong and Brown 1983; Harvey 1987; de Graaf et al. 1999; Wolter and Sukhodolov 2008; Ellsworth et al. 2010a; Janáč et al. 2013) appears inappropriate. Although, it may appear reasonable to evaluate the ratio of active and passive components for single dispersal events along a continuum (Fig. 1), this ratio must result from the strength of hydraulic forces and species- or stage-specific capabilities (behavioral, physical).

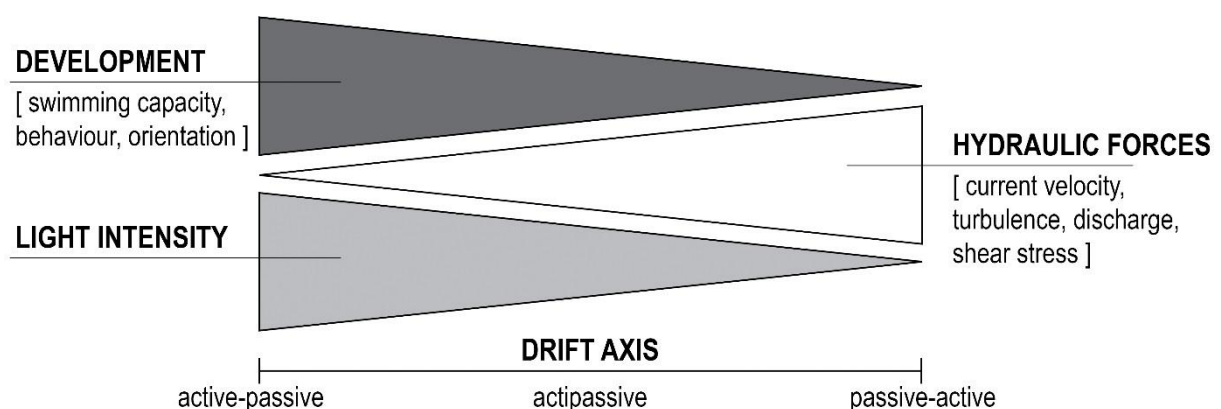


Figure 1. Illustration of the continuum drift mode. Triangles represent the range of parameters with low values for hydraulic forces and rudimentary developmental state at the apexes.

A profound knowledge of larval skills (i.e. swimming performance, orientation ability, drift behavior) and the limiting environmental conditions is required, if one wants to assess the proportion of each component. As a theoretical model we suggest instead, that the drift of larvae, free embryos and juveniles should be referred to as an *actipassive* process. Provided there is detailed information on the ratio, the terms *active-passive* - for a predominantly controlled mode of downstream movement - and *passive-active* - for a primary externally vectored transport - might be used.

An integrated approach to the drift of early life stages of riverine fishes

The state of knowledge in research on the drift of early life stages of riverine fishes was reviewed, based on peer-reviewed publications between 1972 and 2014 (see Online Resource). Of the 60 publications, 89% were field studies, and of these, 85% used stationary drift nets (Fig. 2).

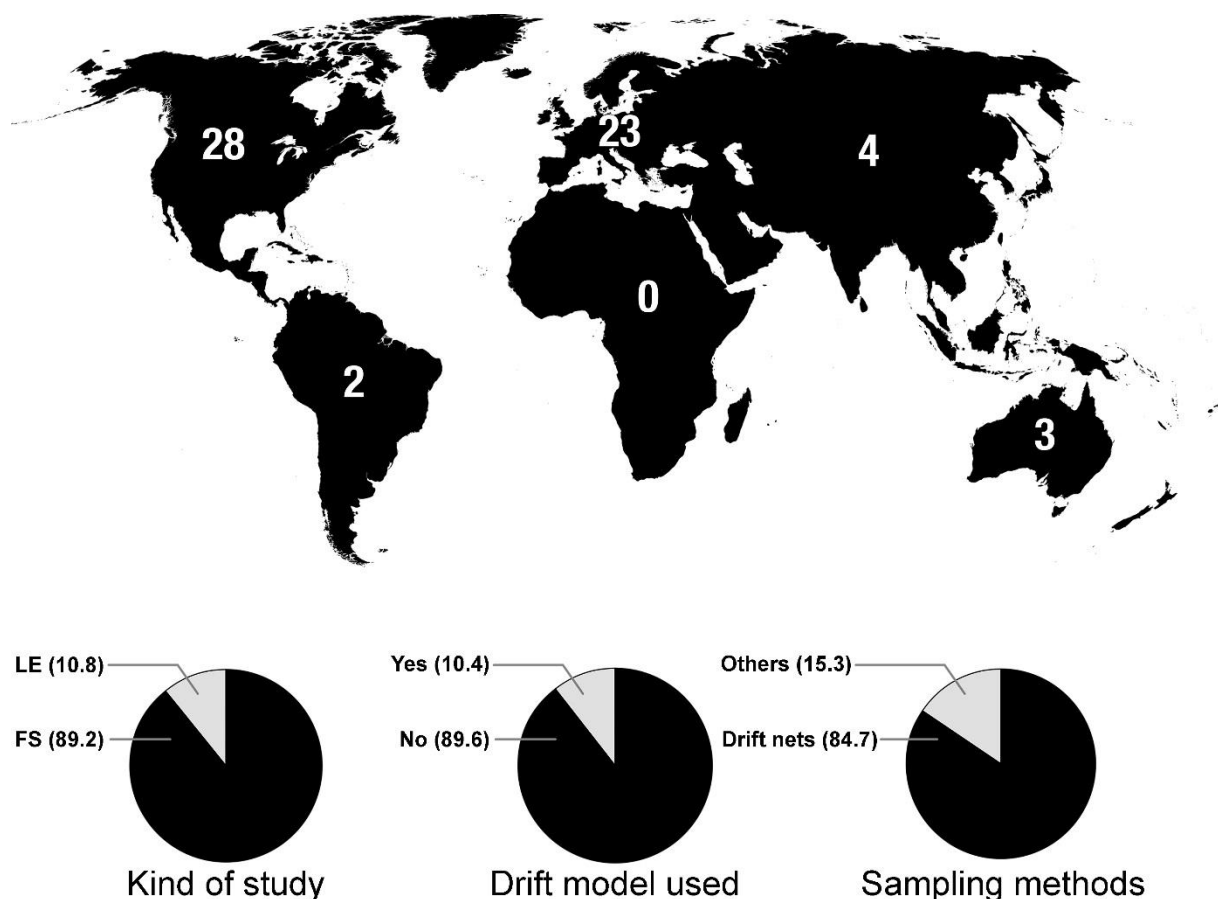


Figure 2. Overview of the geographical distribution of the 60 analyzed drift studies. The percentage of field studies (FS) and laboratory experiments (LE) as well as the frequency of drift model- and driftnet-usage is given in the pie charts below.

The research was conducted in 54 rivers on 4 continents, but mostly in temperate floodplain- and upland rivers in North America and Europe (Fig. 2, Online Resource). Only 10 % of these studies used hydrodynamic or mathematical models to explain or predict drift patterns. We

analyzed all publications using a conceptual framework of organismal movement advocated by Nathan et al. (2008) (Fig. 3). According to Nathan et al. (2008), the movement path of a focal individual results from the dynamic interplay of four basic components:

- i. *internal state* - the different motivations to move or “why do the early life stages of riverine fishes drift?”;
- ii. *navigation capacity* - the orientation ability of moving organisms or “where and when do the early life stages of riverine fishes drift?”;
- iii. *motion capacity* - the different modes (active, passive) of movement or “how do the early life stages of riverine fishes drift?”;
- iv. *external factors* - biotic and abiotic parameters that affect why, how, where and when to drift.

But because of the field of research, we introduced a fifth component:

- v. *internal factors* - a set of intrinsic characteristics (e.g. physiology and morphology) that influence different components of drift movement.

Each publication was scrutinized for specific information associated with the above–outlined model. Information was categorized, where applicable, and displayed in framed white boxes within the five components (Fig. 3). The “not-specified” boxes refer to studies that provide no answers on why, how or where fish drift. Lines between boxes indicate co-occurrence or cause-and-effect relationships, as obtained from the literature. The thickness of frames and lines represent the relative frequency of references to a particular aspect. Both speculative and empirical conclusions – drawn by the authors themselves - on drift characteristics were included in this meta–analysis. A synopsis shows the most common categories (except “not specified”) and linkages (Fig. 4). This will serve as a roadmap to discuss the current state of knowledge in drift research, and identify requirements for future studies. Note, the data content was adapted to accord with Nathan’s framework. Therefore, drift entrance modes and temporal patterns of drift were excluded, and have already been considered in the above.

Internal State: “why do the early life stages of riverine fishes drift?”

The internal state of drifting larvae is not specified in most studies reviewed (Fig. 3). Determining the motivation for a single drift event is a challenging task. It requires the assessment of the psychological (do larva have a psyche?) and physiological state of a small fish, at any given time, driving it to fulfil a particular goal by changing its position. This is compounded by complex phenotypic and genotypic behavior-environment interactions. Perhaps, except for amphidromous species, where the objective is to reach the sea, it is always going to be uncertain whether drift is the result of a desire to reach a destination, or to avoid a

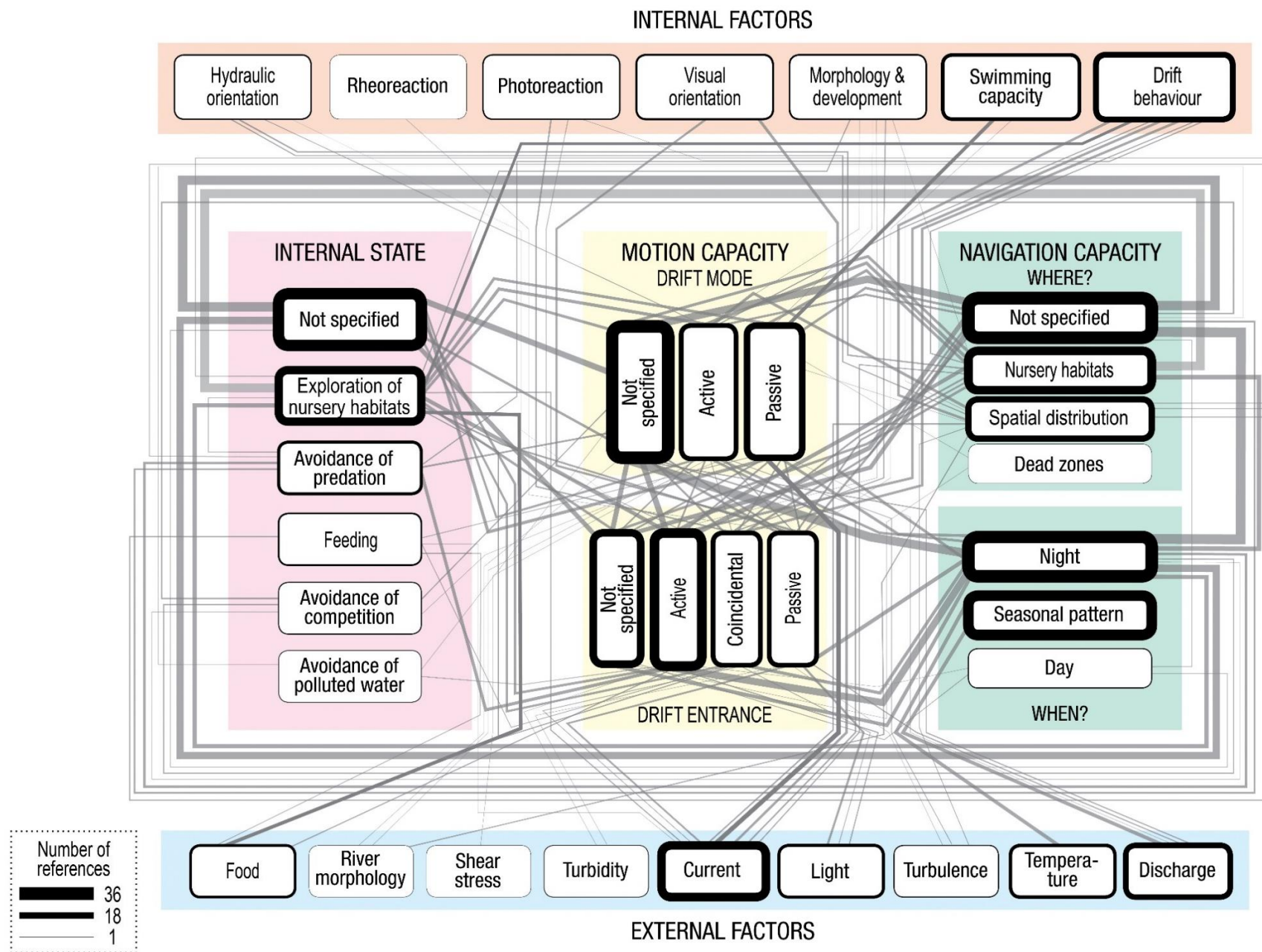


Figure 3. Characteristics of larval fish drift, as derived from the relevant literature, are displayed on the base of a general framework for movement ecology (colored blocks; Nathan et al., 2008). Frame- and line thickness refer to the frequency of described cases and connections. For reasons of clarity, existing links between internal and external factors are not drawn.

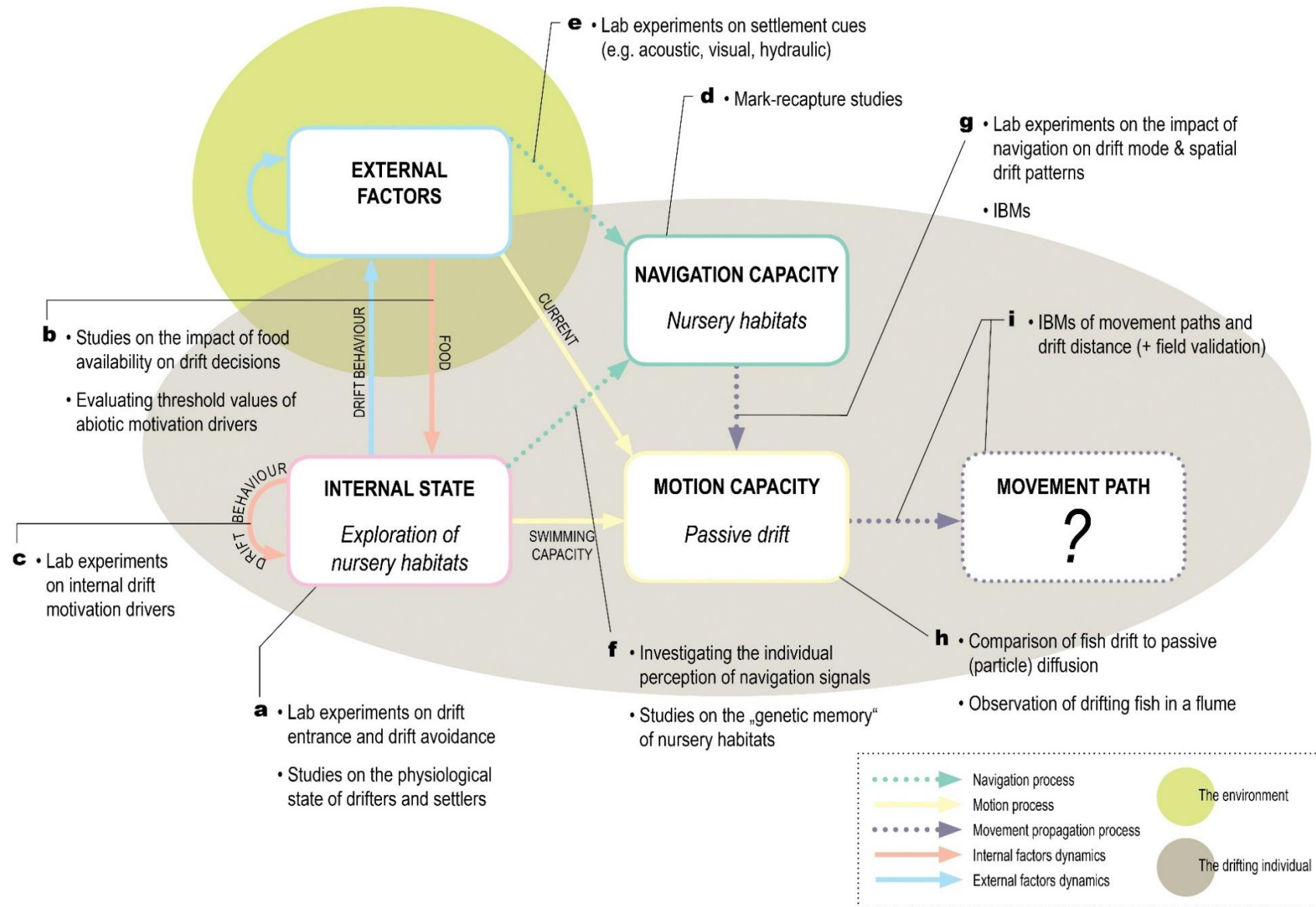


Figure 4. Conceptual model of fish drift inspired by *Nathan et al. (2008)*, showing the processes and relationships (indicated by arrows) between the five basic components (boxes) of dispersal. Dotted lines show knowledge gaps in the reviewed literature (< 5 references). Black lines (a-i) indicate suggested research needs for particular aspects of fish drift. Detailed information of the glossary is given in *Nathan et al. (2008)*. Briefly: the **navigation process** refers to the realized navigation capacity given the impact of the current location, internal state, and external factors on the fundamental navigation capacity of the focal individual; the **motion process** refers to the realized motion capacity given the impact of the current location, internal state, and external factors on the fundamental motion capacity of the focal individual; the **movement propagation process** refers to the realized movement produced by the motion process (optionally affected by the navigation process).

threat, such as competition, predation or poor water quality, at its current location (Nathan et al. 2008).

The perception – perhaps anthropocentric - of larvae looking for the most advantageous feeding grounds underlies many drift studies (Fig. 4). Recently hatched fish are unlikely to be aware of suitable downstream areas (but see *Navigation capacity*). Rather than a ‘motivation’ per se, the ‘exploration of nursery habitats’ may be a by-product of an active drift entrance that potentially refers to ultimate evolutionary payoffs from moving (e.g. gaining energy, dampening population fluctuations by spreading larvae over heterogeneous environments etc.). Whilst this last is hard to prove, the motivation to leave disadvantageous areas can be tested in laboratory experiments on drift entrance by controlling conditions of water quality, predation or competition (Fig. 4a). In this respect, the impact of predator kairomones on young fishes’ drift entrance dynamics, as shown for invertebrates (Winkelman et al. 2008), could be of particular interest. Investigations of the physiological state of drifting (and settling) fish may clarify whether hunger is an important driver of drift.

Specific attention should be given to external factors that stimulate or discourage young fish to move. Food availability, for example, is mentioned a common reason to leave, or look for a specific habitat (Fig. 4). To the best of our knowledge, there is no study that actually investigated food quality or quantity at the starting- or end-point of a drift event. Evaluating the threshold values of other abiotic factors (e.g. current, light), which affect the fish’s internal state, will provide deeper insights into why, when and where young fish enter the flow (Fig. 4b). Furthermore, a profound understanding of an individual’s motivation to drift (i.e. drift behavior) allows more informed conclusions to be drawn on the significance of environmental conditions encountered on the way (Fig. 4): larvae of potamodromous species, for example, that search the river shorelines for suitable habitats, potentially prefer lower currents than those of anadromous species that aim for the distant ocean.

The motivation for drifting is most likely self-regulated by internal factors (Fig. 4). However, detailed knowledge on how (ontogenetic) changes in morphology, swimming capacity, orientation ability or behavior affect the readiness to move, or assist a specific drift strategy, is required. Again, laboratory experiments appear to be the appropriate method (Fig. 4c).

Navigation capacity: “where and when do the early life stages of riverine fishes drift?”

The drift destination is not specified in most work on dispersing fish larvae in rivers (Fig. 3). Indeed, nursery areas are frequently assumed by authors to be where larvae stop drifting (Fig. 4) but there is no sure indication for this conclusion, as most studies do not observe settlement activities (Kennedy and Vinyard 1997; Schludermann et al. 2012; Lechner et al. 2014a). Hence, an increased application of mark-recapture experiments, focusing on drift exit and

habitat choice along the shoreline, will provide valuable information (Fig. 4d). Using genetic and geochemical markers (see reviews by Hedgecock et al. 2007 and Thorrold et al. 2007) or trans-generational tagging approaches, offers the possibility to mark large numbers of fish larvae (Thorrold et al. 2006; Zitek et al. 2014), and should be more commonly incorporated into riverine drift studies.

Almost nothing is known of the navigation ability of drifting fish and the influencing external and internal factors (Fig. 4). This kind of knowledge, however, is indispensable to understand how larvae detect and reach suitable inshore habitats and to predict spatial patterns of drift. Studies on marine species have shown that fish larvae navigate toward settlement areas by reacting to a variety of environmental stimuli (Dixon et al. 2011; Leis et al. 2011; Huijbers et al. 2012). Consequently, we encourage studies on the settlement cues for drifting fish in running waters (Fig 4e). Those cues potentially encompass acoustic (e.g. the sound of the wave-wash) or visual (e.g. shading by vegetation) signals and hydraulic gradients (e.g. current speed, current direction, water depth) that indicate shore proximity. Given the limited observability of small fish in large rivers, the feasibility of such studies is mainly restricted to laboratory experiments.

The internal state of the individual (e.g. neurological and physiological) potentially influences the process of navigation. Studies are needed that examine the species- and stage-specific ability to sense and respond to navigation signals (Fig. 4f). Furthermore, the question arises whether fish larvae, as some birds do (Nathan et al. 2008), possess a genetically coded 'memory' guiding them towards suitable nursery areas. The long-time observation of downstream habitat use (i.e. 'nursery fidelity') by marked larvae from a known spawning ground could throw light on the matter (Fig. 4f).

In future research, the focus must shift to how individuals implement navigation decisions in the process of drifting (i.e. *Motion capacity*). Many studies ascribe the observed spatial distribution patterns (i.e. lateral and horizontal; Online Resource) of drifting fish to active navigation (i.e. active drift), but remain vague about the underlying mechanisms (Brown and Armstrong, 1985; Gadoski and Barfoot 1998; Robinson et al. 1998; Schludermann et al. 2012). Certainly, the observation of individuals in an artificial stream-channel is a potent method to correlate a variety of navigation-related cues to the drift mode under controlled conditions, thereby elucidating spatial patterns of transport (Fig. 4g). The ultimate significance of the suggestions above is debatable, as transferring laboratory results to the field has its drawbacks. A promising approach, in this respect, is the field validation of predicted spatial drift outcomes by biophysical models that incorporate larval navigation abilities recorded in the laboratory (Fig. 4g). These individual based models (IBM) are an emerging tool in oceanic research (Cowen et al. 2006; Christensen et al. 2007; Staaterman and Paris 2014), supporting

the identification of potential nurseries and spawning grounds. In freshwater systems, this technique is in its infancy.

Motion capacity: “how do the early life stages of riverine fishes drift?”

Generally, the mode of transport is not specified in drift studies (Fig. 3). This is at first attributable to the common sampling method, i.e. exposing stationary nets into the current to capture autochthonous fish fry. Missing information on where larvae had started drifting, and the environmental conditions along their route, make reliable statements on the drift mode impossible. The frequent reports of passive drift caused by strong currents (Fig. 4), thus often derive from a simple comparison between values of current speed (measured at the net opening) and larval swimming performance (Corbett and Powles 1986; Gadomski and Barfoot 1998; Wolter and Sukhodolov 2008).

The eulerian observation of larval movement (using drift nets) in relation to passive particles is a promising approach for a rough identification of the drift mode (Fig. 4h). The spatio-temporal drift patterns of marked and recaptured individuals can be either compared to those of physical floats, ideally featuring some larval attributes (e.g. shape and density), or to those of virtual particles, simulated using specific tracking software on the base of hydrodynamic models (Schludermann et al. 2012; Lechner et al. 2014a).

Flume experiments have a great potential to reveal specific peculiarities of the drift mode, however, they are rarely applied (Persat and Olivier 1995; Kynard et al. 2007a; Kaminskas 2011; Pavlov et al. 2011; Zens 2015). We suggest that future work should focus on the transport mode of different species (e.g. invasive, endemic, riverine, lentic, benthic), developmental stages, ecological guilds (e.g. reproduction and current) etc. in the laboratory, where abiotic factors (i.e. current, temperature, turbidity and turbulence) are changed while observing drifting fish (Fig. 4h).

Movement path: “which way do drifting larvae take?”

So far, there is no existing knowledge on the exact route of drifting young fish in rivers (Fig. 4). The limiting factor is, again, the traditional method of collecting larva: drift net samples are point measurements, providing no information on the processes *between* two points. However, the instructive in situ tracking of larval movement, as demonstrated in marine studies (Huebert and Sponaugle 2009; Paris et al. 2013), is made problematic by swift currents, turbid water and the nocturnal drift activity in rivers (Kennedy and Vinyard 1997).

In our opinion, the most practicable and sophisticated way is to simulate larval movement paths with IBMs and validate the results in the field (Fig. 4i). This requires a specific understanding of *navigation capacity* and *motion capacity*. Furthermore, high resolution 3D-hydrodynamic

river models are needed to predict a larva's reactions towards hydraulic gradients *en route*. The field validation should preferably be based upon mark-recapture studies at different spatial scales with well-understood model species (see Lechner et al. 2014a).

In order to set the spatial limits of a movement path, it might initially be useful to focus on the distance covered during a drift event. Mathematical models have been used to estimate drift distances of some sturgeon species by integrating flow velocity and empirical data on drift duration, drift mode and swimming height (Kynard et al. 2007a; Braaten et al. 2008; Braaten et al. 2012), but these sorts of studies are rare. There is an urgent need for research regarding the drift distance of other fishes (Fig. 4i).

Data on the spatial characteristics (i.e. route and distance) of fish drift are important to evaluate the connectivity of key habitats (spawning-rearing) and will have implications for river management and restoration projects. Information on the average drift distance, for example, could influence the designation of protected areas downstream of known reproduction sites.

Conclusion

This review clearly shows that we are far from a general understanding of the processes and patterns of fish drift. As stated previously, the most common technique in the investigation of the drift of the young stages of fish is the deployment of stationary drift nets. This technique is unsuitable for finding answers to the pressing questions in the field that we have identified. We believe that laboratory observations and experiments are essential to elucidate the sensorial, physical and behavioral capabilities of fish larvae, which will in turn provide information on the processes involved in *navigation capacity*, *motion capacity* and *internal state*. The information gained will improve riverine drift models. These are a rarely-used, but powerful tool for understanding dispersal, and will shed light on movement path and/or settlement behavior.

Increasing our understanding of the nature of the dispersal ecology of the early life stages of riverine fishes is urgently needed. The increasing human impact on rivers worldwide impinges on all aspects of the ecology of fishes, but young fish are particularly vulnerable. Implications of river channelization and flow regulation: (1) disturb localized settlement and movement in inshore areas (Braaten et al. 2012); (2) disrupt natural dispersal signals and affect drift distance (Elsworth et al. 2010b; Usvyatsov et al. 2013); (3) increase washout-effects and catastrophic drift entrance during high water levels and navigation-induced wave wash (Bischoff and Wolter 2001; Kucera-Hirzinger et al. 2009; Schludermann et al. 2013); and (4) jeopardize drifting fish by entrainment into water abstraction sites (Carter and Reader 2000; Pavlov et al. 2008; Bracken and Lucas 2013). An integrated approach to the ecology of drifting fish in rivers will greatly contribute to effective conservation and management of riverine fish populations.

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Supplementary Material

A tabulated analysis of 60 relevant publications on the dispersal of the early developmental stages of freshwater fish. Glossary: Types of study were field study (FS), laboratory experiment (LE) and review (R); Developmental stages under investigation (DUI) were alevins (ALE), ammocetes (AMO), eggs (EGG), embryos (EMB), fry (FRY), juveniles (JUV), larvae (LAR) and young-of-the-year (YOY). "Not specified" (n.s.) marks a lack of relevant information in the reference. Species names were adopted from the reviewed papers and have not been adjusted to possible taxonomic shifts.

Reference	Type	River	Drift peak	DUI	Most common taxa	Spatial pattern	Drift distance	General results
Clifford 1972	FS	Bigoray	Jul	FRY	<i>Catostomus commersonii</i>	Higher densities in surface samples.	n.s.	White sucker fry displays a distinct nocturnal drift pattern with highest densities near the surface.
Gale and Mohr 1978	FS	Susquehanna	Jun	LAR	<i>Carpionodes cyprinus</i> , <i>Catostomus commersonii</i> , <i>Etheostoma olmstedi</i> , <i>Cyprinus carpio</i>	Higher densities nearshore and in surface samples.	n.s.	High turbidity and concentrations of water pollutants might increase downstream movements of larvae.
Pavlov et al. 1978	R	Volga, Kuban	Jul	JUV	<i>Blicca bjoerkna</i> , <i>Abramis brama</i> , <i>Rutilus rutilus caspicus</i> , <i>Alburnus alburnus</i> , <i>Scardinius erythrophthalmus</i>	Size and species dependent.	n.s.	Horizontal and vertical distribution of migrating young fishes is size and species dependent and includes active and passive mechanisms.
Muth and Schmulbach 1984	FS	James	Jul	LAR	<i>Aplodinotus grunniens</i> , <i>Dorosoma cepedianum</i> , <i>Catostomidae</i> , <i>Cyprinidae</i>	n.s.	n.s.	Taxa display contrary diel patterns with maximum drift densities during day and night.
Brown and Armstrong 1985	FS	Illinois	Jun-Jul	LAR	<i>Ictalurus punctatus</i> , <i>Pylodictis olivaris</i> , <i>Lepomis spp.</i>	Higher densities nearshore and in surface samples.	n.s.	Fish larvae accidentally enter the drift during the initiation of feeding activity.
Carter et al. 1986	FS	Colorado	Jul	LAR	<i>Catostomus latipinnis</i> , <i>Catostomus discobolus</i> , <i>Rhinichthys osculus</i> , <i>Gila robusta</i> , <i>Cottus bairdii</i>	Higher densities nearshore.	n.s.	Drift entrance of native species is coincided with active feeding.
Corbett and Powles 1986	FS	Apsley Creek	May	EGG, LAR	<i>Stizostedion vitreum vitreum</i> , <i>Catostomus commersonii</i>	Highest densities in mid-depth.	n.s.	Passive drift of walleyes and white suckers from spawning sites to nurseries is governed by flow velocity.
Harvey 1987	FS	Brier Creek	n.s.	LAR, JUV	<i>Lepomis cyanellus</i> , <i>Lepomis megalotis</i> , <i>Notropis boops</i>	n.s.	n.s.	Drift densities of small fish (<10mm) of certain species increase during flood events.
Copp and Cellot 1988	FS	Rhone, Jonage Canal	n.s.	EMB, LAR	<i>Lepomis gibbosus</i> , <i>Gobio gobio</i>	Higher densities at the bottom during day and at the surface during night.	n.s.	Drift of gudgeon and pumpkinseed takes place at defined developmental stages.
Iguchi and Mizuno 1990	FS, LE	Mina, Tateishi, Omo-dani	n.s.	EMB	<i>Rhinogobius brunneus</i>	Vertical distribution depends on illumination preference.	n.s.	Diurnal drift patterns of embryo vary along river courses due to light preferences and topographical features.

Reference	Type	River	Drift peak	DUI	Most common taxa	Spatial pattern	Drift distance	General results
Peñáz et al. 1992	FS	Rhone	n.s.	LAR, JUV	<i>Rutilus rutilus</i> , <i>Leuciscus cephalus</i> , <i>Barbus barbus</i>	Higher densities nearshore.	n.s.	Drift and downstream migrations can be intense during later larval and juvenile stages.
Pavlov 1994	R	Volga, Ili, Amanzon, Nanai, Aljvero	n.s.	LAR, JUV	n.s.	Dependent on hydraulic and biological mechanisms.	n.s.	This conceptual work highlights the mechanisms of downstream migrations.
Johnston et al. 1995	FS	Valley	May	LAR	<i>Catostomus commersonii</i> , <i>Carpiodes cyprinus</i> , <i>Stizostedion vitreum</i>	n.s.	n.s.	River discharge in the 35 days preceding the median date of drift is the main predictor of larval abundance.
Persat and Olivier 1995	LE		n.s.	EGG, LAR	<i>Chondrostoma nasus</i>	n.s.	n.s.	First displacements of larval nase are concomitant with the light induced emergence from the substratum.
Johnston 1997	FS	Catamaran Brook, Miramichi	n.s.	YOY	<i>Salmo salar</i> , <i>Catostomus commersonii</i> , <i>Cyprinidae</i>	Highest densities near the surface.	n.s.	Condition of drifting fry varies between two rivers allowing conclusions about habitat quality.
Araujo-Lima and Oliveira 1998	FS	Solimões, Amazonas	n.s.	EGG, LAR	<i>Characiformes</i> , <i>Clupeiformes</i> , <i>Sciaenidae</i>	Taxon specific lateral distribution.	500-1300 km in 15 days.	Larval drift of many species is linked to the hydrological cycle and either occurs at rising or lowering water levels.
Gadomski and Barfoot 1998	FS	Columbia, Deschutes	Jun-Jul	EMB, LAR	<i>Cottus spp.</i>	Highest densities near the surface at night.	n.s.	Diel patterns of drift densities and factors influencing these patterns vary and are species specific.
Jurajda 1998	FS	Morava	Jun	LAR, JUV	<i>Rhodeus sericeus</i> , <i>Rutilus rutilus</i>	n.s.	n.s.	The limnophilic bitterling may have evolved active drifting behaviour as adaption to the fluvial environment.
Robinson et al. 1998	FS	Little Colorado	May-Jul	EGG, LAR	<i>Gila cypha</i> , <i>Rhinichthys osculus</i> , <i>Catostomus discobolus</i> , <i>Catostomus latipinnis</i>	Highest densities nearshore.	At least 8.6 km.	Spatial dispersal patterns are controlled by habitat selection of actively drifting fish.
deGraaf et al. 1999	FS	Lohajang	Jun	LAR	<i>Catla catla</i> , <i>Labeo rohita</i> , <i>Cirrhinus mrigala</i>	Highest densities near the surface.	n.s.	Lateral connection between river and floodplains drives reproduction success and larval densities of the Indian carps.

Reference	Type	River	Drift peak	DUI	Most common taxa	Spatial pattern	Drift distance	General results
Carter and Reader 2000	FS	Trent	Jun-Jul	YOY	<i>Alburnus alburnus</i> , <i>Rutilus rutilus</i> , <i>Abramis brama</i>	Larger 0+ fishes were concentrated instream.	n.s.	Drifting fish are vulnerable to entrainment into water abstraction sites.
D ´Amours et al. 2001	FS	Des Prairies	May-Jun	LAR	<i>Stizostedion vitreum</i> , <i>Stizostedion sauger</i> , <i>Catostomus commersonii</i> , <i>Carpiodes cyprinus</i> , <i>Acipenser fulvescens</i>	Tendency for higher densities near the surface at night and near the bottom during day.	n.s.	Nocturnal drift densities are higher near the surface and in the right half of the river.
Reichard et al. 2001	FS	Morava, Kyjovka	Jun	EMB, LAR, JUV	<i>Rutilus rutilus</i> , <i>Rhodeus sericeus</i> , <i>Alburnus alburnus</i> , <i>Pseudorasbora parva</i>	n.s.	n.s.	Drift patterns of single species differ between two adjacent lowland rivers.
Auer and Baker 2002	FS	Sturgeon	Jun	LAR	<i>Acipenser fulvescens</i>	n.s.	n.s.	Most lake sturgeon larvae drift in lower currents over sandy substrate.
Copp and Faulkner 2002	FS	Lee	n.s.	EGG, LAR	<i>Alburnus alburnus</i> , <i>Rutilus rutilus</i> , <i>Barbus barbus</i>	n.s.	n.s.	Highest densities of drifting fish larvae occur in high velocities.
Reichard et al. 2002a	FS	Morava	n.s.	n.s.	<i>Rhodeus sericeus</i> , <i>Alburnus alburnus</i>	n.s.	n.s.	Drift entry in cyprinid fishes is rather a behavioural decision than a passive displacement.
Reichard et al. 2002b	FS	Morava, Kyjovka	Jun-Jul	LAR	<i>Rutilus rutilus</i> , <i>Rhodeus sericeus</i> , <i>Alburnus alburnus</i> , <i>Pseudorasbora parva</i> , <i>Carassius auratus gibelio</i>	n.s.	n.s.	Interannual variability in seasonal dynamics of drift abundance and species composition is correlated with water temperature and spawning success.
Oesmann 2003	FS	Elbe	n.s.	LAR	<i>Sander lucioperca</i> , <i>Perca fluviatilis</i> , <i>Abramis brama</i> , <i>Gobio sp.</i> , <i>Gymnocephalus cernuus</i>	Higher densities nearshore.	n.s.	Compared to stream cyprinids, smelt use swift currents in the mid-channel as means of transport.
White and Harvey 2003	FS	Smith, Van Duzen	Mar-Apr/ May-Jun	EMB, LAR, AMO	<i>Cottus aleuticus</i> , <i>Cottus asper</i> , <i>Lampetra tridentata</i>	No cross-channel differences of drift density.	n.s.	Different fish taxa in coastal streams display different drift patterns in order to facilitate or avoid transport into estuaries.
Bujold et al. 2004	FS	Western Brook, Stag Brook	Jun-Jul	YOY	<i>Salmo salar</i>	n.s.	n.s.	Drifting Atlantic salmon fry is significantly shorter and weighs less than resident fry.

Reference	Type	River	Drift peak	DUI	Most common taxa	Spatial pattern	Drift distance	General results
Humphries and King 2004	FS	Campaspe River, Broken River	Oct-Dec	LAR	<i>Maccullochella peelii peelii</i> , <i>Cyprinus carpio</i> , <i>Retropinna semoni</i> , <i>Philypnodon grandiceps</i>	n.s.	1.8 km in 3 hours.	Fish larvae can be categorized obligate-, facultative-, or non-drifters regarding the importance of the process in their early life history.
Reichard and Jurajda 2004	FS	Jihlava	Jun-Jul	LAR, JUV	<i>Rutilus rutilus</i> , <i>Leuciscus cephalus</i> , <i>Leuciscus leuciscus</i>	Higher densities nearshore.	n.s.	Higher flow velocity during elevated discharge does not increase drift abundance.
Reichard et al. 2004	FS	Dyje	n.s.	LAR, JUV	<i>Abramis brama</i> , <i>Abramis bjoerkna</i> , <i>Rutilus rutilus</i>	Higher densities nearshore.	n.s.	Body size and developmental stage of drifting fish is positively correlated with distance from bank.
Zitek et al. 2004a	FS	Danube/Marchfeldkanal	n.s.	LAR, JUV	<i>Proterorhinus marmoratus</i> , <i>Alburnus alburnus</i>	n.s.	n.s.	The occurrence of different species in the drift is related to defined steps of larval development.
Zitek et al. 2004b	FS	Danube/Marchfeldkanal	Jun	LAR, JUV	<i>Proterorhinus marmoratus</i> , <i>Alburnus alburnus</i>	n.s.	n.s.	Water temperature is the driving factor of drift seasonality.
Humphries 2005	FS	Broken	n.s.	EMB	<i>Maccullochella peelii peelii</i>	n.s.	n.s.	Murray cod embryos begin drifting when they reach a specific developmental stage.
Daufresne et al. 2005	LE		n.s.	ALE	<i>Salmo trutta</i>	n.s.	n.s.	Velocity changes during emergence advance the attainment of a constant final proportion of displaced fish.
Sonny et al. 2006	FS	Mehaigne	Jun	LAR	<i>Rutilus rutilus</i> , <i>Leuciscus cephalus</i>	n.s.	n.s.	Total lengths of drifting fish vary between dusk, night and dawn suggesting behavioural decisions as matter of drift entrance.
Johnson and McKenna 2007	FS	Sandy Creek, Orwell Brook, Trout Brook	n.s.	LAR	<i>Etheostoma flabellare</i> , <i>Rhinichthys atratulus</i> , <i>Hypentelium nigricans</i>	n.s.	n.s.	Downstream drift of fantail darter, northern hogsucker and blacknose dace is a nocturnal event.
Kynard et al. 2007a	LE		n.s.	EMB, LAR	<i>Scaphirhynchus albus</i>	n.s.	304 km in 11 days.	Swimming height and holding ability in eddies of drifting pallid sturgeon embryos change with ontogeny and stream velocity.

Reference	Type	River	Drift peak	DUI	Most common taxa	Spatial pattern	Drift distance	General results
Kynard et al. 2007b	LE		n.s.	EMB, LAR, JUV	<i>Acipenser transmontanus</i>	n.s.	350 km in 50 days.	Free embryos do not have a behavioural dispersal. There might be a velocity trigger for drift entrance in early larvae.
Reichard and Jurajda 2007	FS	Morava, Kyjovka	Jun-Jul	EMB, LAR, JUV	<i>Abramis brama</i> , <i>Abramis bjoerkna</i> , <i>Alburnus alburnus</i> , <i>Leuciscus cephalus</i> , <i>Gobio sp.</i> , <i>Rutilus rutilus</i>	n.s.	n.s.	Species- and stage dependency of drift either reflects adaptations to riverine conditions or susceptibility to enter the flow.
Braaten et al. 2008	FS	Missouri	n.s.	LAR	<i>Scaphirhynchus albus</i> , <i>Scaphirhynchus platyrhynchus</i>	Highest densities near the bottom.	39-250 km in 6 days and 134-530 km in 11 days.	Insufficient length of free-flowing river stretch might explain the lack of larval pallid sturgeon survival.
Durham and Wilde 2008	FS	Canadian	Jun	LAR	<i>Notropis girardi</i> , <i>Cyprinella lutrensis</i> , <i>Macrhybopsis tetranema</i> , <i>Hybognathus placitus</i> , <i>Platygobio gracilis</i>	n.s.	n.s.	Reproductive success and seasonal variation in drift density is positively associated with annual discharge.
Hay et al. 2008	FS	Missouri	Jun	LAR	<i>Aplodinotus grunniens</i> , <i>Carpionodes carpio</i> , <i>Ictiobus bubalus</i> , <i>Ictiobus cyprinellus</i>	n.s.	n.s.	Temperature, variation in temperature and variation in discharge predict the presence of drifting larvae.
Pavlov et al. 2008	R	Volga	n.s.	LAR, JUV	<i>Rutilus rutilus</i> , <i>Perca fluviatilis</i> , <i>Sander lucioperca</i> , <i>Gymnocephalus cernua</i> , <i>Salmo salar</i> , <i>Salvelinus alpinus</i> , <i>Cichlasoma octofasciatum</i>	High densities at outer banks of the river.	n.s.	Behavioural and ecological drivers of downstream movements are discussed.
Wolter and Sukhodolov 2008	FS	Spree	n.s.	LAR	<i>Blicca bjoerkna</i> , <i>Rutilus rutilus</i> , <i>Alburnus alburnus</i> , <i>Perca fluviatilis</i>	n.s.	n.s.	Modelling results and field observations indicate a passive displacement of emerging fish larvae to non-transit zones in a river.
Braaten et al. 2010	FS	Missouri	n.s.	LAR	<i>Scaphirhynchus albus</i>	Highest densities near the bottom and on the outside bend and mid-channel.	n.s.	Larvae of pallid sturgeon predominantly drift in high-velocity areas in the thalweg.
Ellsworth et al. 2010a	FS	Williamson	n.s.	LAR	<i>Delitistes luxatus</i> , <i>Chasmistes brevirostris</i>	Highest densities in mid-channel and near the surface.	n.s.	Information about spatial and diel drift patterns can minimize larval entrainment in a water withdrawal structure.
Ellsworth et al. 2010b	FS	Provo	n.s.	LAR	<i>Chasmistes liorus</i>	n.s.	n.s.	Sufficient discharge rates are crucial for transporting larvae into suitable nursery habitats.

Reference	Type	River	Drift peak	DUI	Most common taxa	Spatial pattern	Drift distance	General results
Jiang et al. 2010	FS	Yangtze	May	Egg, LAR	<i>Pseudolaubuca sinensis</i> , <i>Hemiculter leucisculus</i> , <i>Saurogobio dabryi</i> , <i>Sinibotia supercilialis</i> , <i>Cyprinus carpio</i>	n.s.	n.s.	The drift distance of pelagic eggs of the four major Chinese carps, necessary to develop, is reduced by the the Three Gorges Dam.
Maeda and Tachihara 2010	FS	Teima Stream	Oct	LAR	<i>Rhinogobius giurinus</i> , <i>Rhinogobius spp.</i> , <i>Microphis brachyurus</i> , <i>Microphis leiaspis</i> , <i>Redigobius bikolanus</i>	n.s.	n.s.	Drift entrance of investigated gobiid species and pipefishes may be provoked by male parents.
Braaten et al. 2012	FS	Missouri	n.s.	EMB	<i>Scaphirhynchus albus</i>	Highest densities in the mid-channel.	Several hundred km during the drift period (~10 days).	Long distance drift of pelagic pallid sturgeon larvae to suitable rearing habitats is disrupted by dams and reservoirs.
Schludermann et al. 2012	FS	Danube	n.s.	LAR	<i>Chondrostoma nasus</i>	n.s.	n.s.	Larval dispersal has a strong active component with drifting fish moving towards the shore.
Bracken and Lucas 2013	FS	Derwent	n.s.	AMO	<i>Lampetra sp.</i>	Transformers drifted in the main channel.	n.s.	<i>Lampetra</i> sp. transformers and larvae are susceptible to entrainment by run-of-river hydropower.
Janáč et al. 2013	FS	Dyje	May-Jul	n.s.	<i>Rutilus rutilus</i> , <i>Proterorhinus semilunaris</i> , <i>Neogobius melanostomus</i>	n.s.	5.2 to 10.4 km per night.	Passive downstream drift is an important dispersal factor for round goby and tubenose goby in newly colonised rivers.
Johnson et al. 2013	FS	Orwell Brook, Trout Brook, Little Sandy Creek	n.s.	ALE	<i>Oncorhynchus mykiss</i>	n.s.	n.s.	The downstream drifting fry is significantly smaller than the resident fry.
Usvyatsov et al. 2013	FS	Saint John	Jun	LAR	<i>Acipenser brevirostrum</i>	No consistent spatial pattern.	n.s.	Temperature and night-time discharge are important variables in predicting timing and extent of larval Shortnose Sturgeon drift.
Lechner et al. 2014a	FS	Danube	n.s.	LAR	<i>Chondrostoma nasus</i>	n.s.	n.s.	Retention potential, connectivity and accessibility of nurseries along an artificial shoreline affect spatio-temporal dispersal patterns of larval nase.
Lechner et al. 2014b	FS	Danube	May-Jun	LAR, JUV	<i>Cyprinidae</i> , <i>Gobiidae</i> , <i>Percidae</i> , <i>Cottidae</i>	n.s.	n.s.	Drifting fish display family and stage specific responses to certain hydraulic variables.

Chapter 2: The drift mode (active vs. passive) and its controlling factors

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The influence of discharge, current speed and development on the downstream dispersal of larval nase (*Chondrostoma nasus*) in the River Danube

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ABSTRACT

In this study, we investigated the mode (active vs. passive) of larval downstream dispersal (drift) and its influencing factors in the nase carp (*Chondrostoma nasus*), a fluvial specialist. Marked nase larvae (early and later stages) together with equivalent numbers of passive particles were released in the main channel of the River Danube (Austria) at different flow- (low-flow, high-flow) and current- (over-critical and under-critical) conditions. Larvae and particles were recaptured with 12 simultaneously exposed drift nets at varying distances (65m – 510m) from release. We supposed differences in the spatial dispersal patterns between larvae and particles to derive from fish activity. In addition we hypothesized that river discharge, developmental stage, current speed and distance from release influence these differences. We found that drift activity was independent of developmental stage or current speed at release. Though, drift activity was higher during low-flow. Apparently, nase larvae deliberately enter the current during low river discharge because the prevailing hydraulic conditions facilitate active and oriented drifting. Furthermore, drift activity was highest near the points of release. This might be due to an intrinsic higher motor activity of fish getting placed into novel surroundings and/or the ensuing reduction of swimming speed and prevalence of passive drift.

Introduction

Movement is a fundamental process in the lives of virtually all organisms (Nathan et al, 2008). Therefore, understanding the temporal and spatial patterns of movement of individuals, species and populations is central to effective conservation and management (Baguette et al., 2012). The movement – or dispersal - of early life history stages of fishes (i.e. eggs, free embryos, larvae) from spawning sites to appropriate rearing habitats affects the survival and fitness of the individual, and, consequently, year-class-strength, probability of completion of the life-cycle and population health (Daewel et al., 2011; Hinrichsen et al., 2012). The dispersal of eggs can generally be described using passively drifting particles (Dudley et al., 2007) or 3-d hydrodynamic models (Peck et al., 2009; Pacariz et al., 2013). For a long time, the same

was also assumed for larvae, because of their presumed poorly-developed behavioural, physical and sensory capabilities (Brown and Armstrong, 1985; Roberts, 1997). Indeed, the early life stages of fishes are often referred to as 'ichthyoplankton' (Muth and Schmulbach, 1984; Bialecki et al., 1999; Martin and Paller, 2008), with all the implications of passivity that that term brings.

The earlier assumptions of passive dispersal by fish larvae were overturned by marine studies, revealing that larvae are capable of detecting fine-scale hydraulic, chemical and auditory cues, and exhibit sophisticated behaviour (e.g. directional swimming), relevant for effective dispersal (e.g. travel distance or encounter rates with suitable nursery areas) (Staaterman et al., 2012; Mouritsen et al., 2013). Reef fish larvae, for example, orientate towards odours and sounds of their natal reef and use directional currents to get there (Paris & Cowen 2004; Leis et al., 2011; Paris et al., 2013). Observations of larvae moving along hydraulic gradients (Stoll & Beeck., 2012), adapting swimming and drifting speeds to the prevailing flow regime (Hogan and Mora, 2005), or regulating depth distribution according to currents (Kunze et al., 2013), further emphasize an active response to the hydrodynamic environment. The interactive effects of temporally unstable hydrodynamics and ontogenetically variable larval behaviour are increasingly being used in oceanic dispersal models to gain more realistic simulation results (Vikebo et al., 2011; Sponaugle et al., 2012; Nolasco et al., 2013).

Comparable studies in rivers and streams are scarce, but understanding of patterns and processes are improving rapidly. The dispersal of young fish in lotic systems is primarily mediated by the current, and is termed drift (Pavlov, 1994). Most riverine species spawn demersal eggs (Balon, 1975), and initial drift peaks occur when recently-hatched individuals emerge from the substrate and enter the current (Persat & Olivier, 1995). Ideally, these fish reach suitable inshore settlement areas where environmental conditions match rearing requirements (Schiemer et al., 2002). Subsequent drifting events between adjacent nursery habitats serve to optimize growth and minimize predation or competition (Pavlov, 1994; Humphries, 2005). Generally, drift in rivers follows a circadian rhythm, peaking after dusk (Johnston et al., 1995; D'Amours et al., 2001). The nocturnal drift entry of young fishes is supposed to rely on active behavioural decisions (Reichard et al., 2002; Boujold et al., 2004; Sonny et al., 2006). On the other hand, there is still a general perception that the transport of free embryos and larvae per se is a passive process, caused by a negligible swimming performance and overriding environmental forces (see Lechner et al., 2016). The critical swimming speeds that young fishes can maintain increase with body size and developmental stage (Flore and Keckeis, 1998; Flore, 2001; Kopf et al., 2014), but are limited to values $< 0.15 \text{ m s}^{-1}$ during the early ontogeny of many freshwater species (see Wolter and Arlinghaus, 2003). Accordingly, the average flow velocities in rivers are considered over-critical for free embryos and larvae; i.e. the individuals cannot hold position and are washed downstream (Bardonnnet,

2001; Wolter and Sukhodolov, 2008). This process is intensified during elevated discharge, due to the associated increase in current speed, turbulence and turbidity (Harvey, 1987; Bischoff and Wolter, 2001; Reichard and Jurajda, 2004), potentially resulting in high population losses (Mion et al., 1998; Peirson et al., 2008).

In light of recent findings, however, equating riverine larvae being transported downstream to passive particles is not appropriate. Drift surveys in the Austrian Danube showed that travel paths of larvae exhibit family-specific correlations with hydraulic forces, even at over-critical flows (Lechner et al., 2014a), and clearly deviate from those of modelled passive particles (Schludermann et al., 2012). Consequently, passive transport models in rivers overestimate by a long way the covered distance of drifting larvae (Braaten et al., 2012). It seems reasonable to conclude from this recent evidence that active larval drifting behaviour in rivers has evolved to facilitate movement, minimise mortality while drifting and fulfil physiological and other requirements through locating and settling in appropriate rearing habitats (Robinson et al., 1998).

The overarching objective of this experimental study was to expand our understanding of the nature of the mode of drifting - active vs. passive - of young fishes in running waters. Specifically, we aimed to clarify the influence of river discharge, current velocity and developmental stage (and related swimming performance) on the dispersal pathways of drifting larvae. This experiment is the first attempt to directly compare larval dispersal with passive diffusion in their natural environment. The results are expected to influence the design of the first individual-based larval dispersal model (ILAM) in rivers (see Glas et al., this issue), as well as future river management measures.

An in situ comparison between the spatial dispersal patterns of marked fish larvae (*Chondrostoma nasus*, Cyprinidae) and passively drifting particles was performed in the main stem of the Austrian Danube. The study was conducted in two consecutive years (2011, 2012) with different flow regimes (low-flow, high-flow), providing contrasting hydraulic environments. Within each year, early and later larval stages were simultaneously released at two adjacent points, featuring over-critical and under-critical current conditions, together with the same number of particles. The spatial dispersal patterns were surveyed with stationary drift nets at several sampling stations further downstream. We assumed differences in recapture rates of fish and passive particles arose from larval activity, which has been discussed elsewhere (Metaxas, 2001), and hypothesized that:

I.) Differences in recapture rates of fish and passive particles will be smaller during elevated than low discharge, because the harsh hydraulic conditions at high flows limit the ability of larvae to influence their movement and force larvae to drift more passively;

II.) Differences in recapture rates of fish and passive particles will be smaller for earlier than later larval stages, because the limited swimming performance of less developed individuals form the basis of passive dispersal;

III.) Differences in recapture rates of fish and passive particles will be smaller at the over-critical than the under-critical release points, because strong currents, exceeding the larvae's swimming speed, limit the ability of larvae to influence their movement and force larvae to drift more passively;

IV.) Differences in recapture rates of fish and passive particles will increase with increasing distance from the release points, because larval activity patterns will, with time, increasingly differentiate themselves from purely passive transport.

Material and Methods

Study area

The experiment was performed in the main stem of the Austrian Danube, between river kilometres 1890.0 and 1893.8 (Fig. 1). At the study site, the average values for river width, water depth and flow velocity were approx. 300 m, 3 m, and 2.5 m s^{-1} , respectively. Although located in a national park area (www.donauauen.at), this free flowing river stretch is characterized by profound man-made alterations.

The right shoreline is formed by artificial, steep and straightened embankments (rip-rap). Additionally, rock wing-dikes (groynes), perpendicular to the main flow direction, support navigability and prevent bank erosion. The left shoreline, where this study was conducted, has been revitalized in the course of a river restoration project between 2007 and 2009 (Tritthart et al., 2014). The rip-rap was removed and the original groynes were modified (Fig. 1), enabling a bankside flow along a newly formed gravel bar, which serves as a dispersal corridor for young fish (Lechner et al., 2014b). The modified groynes submerge at a discharge around $1200 \text{ m}^3 \text{ s}^{-1}$.

The study area is characterized by a diverse fish fauna, including several endangered species (Schiemer and Spindler, 1989), such as the nase carp. The nase, a common rheophilic cyprinid in the Danube, has become a flagship species for the conservation of large European rivers (Schiemer et al., 2002). This is, inter alia, due to its life cycle: recently hatched larvae drift from swift flowing spawning sites to littoral nursery habitats (Persat and Olivier, 1995; Keckeis et al., 1997; Reichard et al., 2001), meaning that river conditions are critical to the survival of this species early in its life.

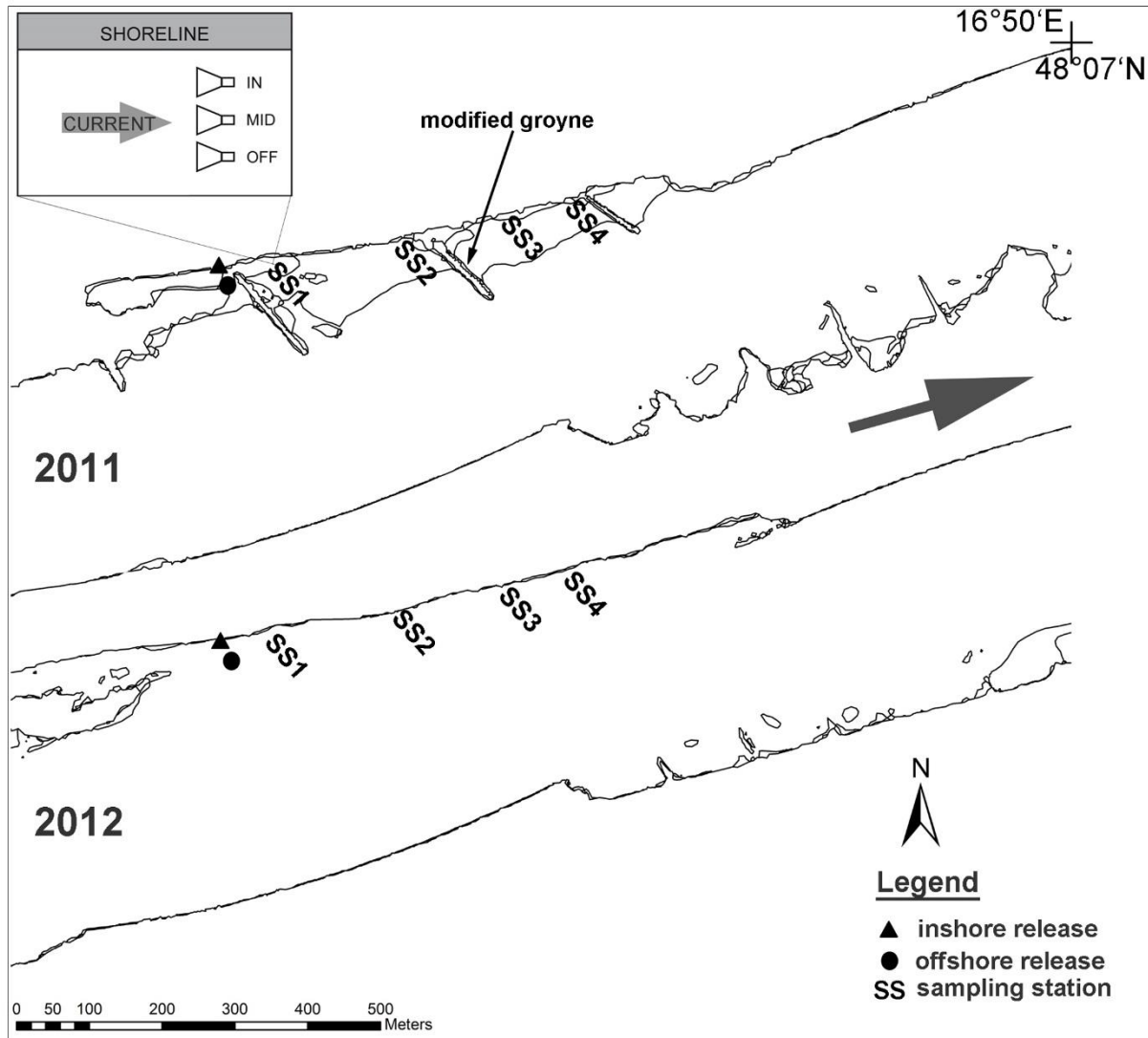


Figure 1. Study area during low flow ($1010 \text{ m}^3 \text{ s}^{-1}$) in 2011 and elevated discharge in 2012 ($2050 \text{ m}^3 \text{ s}^{-1}$) with release points and sampling stations. The drift net set-up (inshore: IN, midshore: MID, offshore: OFF), likewise applied at each sampling station, is outlined in the upper left corner. Current direction is indicated by arrows.

Larval supply and marking

The acquisition of fish larvae and tagging methodology are described in detail elsewhere (Lechner et al., 2014b). Briefly, adult nase carp were obtained from a natural spawning population by electrofishing, and hand-stripped in the laboratory. The eggs of eight (2012) to ten (2011) females were mixed with the sperm of several males, using the dry method. Fertilized eggs were divided into two oxygenated rearing flumes, with different temperature regimes (cold flume: $11.7 \pm 0.7 \text{ }^\circ\text{C}$ in 2011 and $11.4 \pm 0.8 \text{ }^\circ\text{C}$ in 2012; warm flume: $14.8 \pm 3.3 \text{ }^\circ\text{C}$ in 2011 and $16.8 \pm 1.2 \text{ }^\circ\text{C}$ in 2012). As higher water temperatures accelerate tissue differentiation and growth (Seikai et al. 1986; Pepin, 1991), individuals from the warmer flume were more developed (fourth larval stage, L4) and larger (mean standard length: 12.7 ± 1.8

mm in 2011 and 14.3 ± 0.9 in 2012) at the day of release than their conspecifics from the cooler flume (second larval stage, L2; 11.7 ± 1.9 mm in 2011 and 13.4 ± 0.8 in 2012).

L2-individuals were characterized by a large finfold, instead of differentiated ventral, dorsal and anal fins (Fig. 2). Many larvae had a truncated posterior margin of the caudal fin, in which the lepidotrichia started to ossify. According to Penaz (1974), L2-nase already show rheophilia. Although the embryonic finfold was still present at the fourth larval stage, the ventral, dorsal and anal fins began to separate within it (Fig. 2). L4-nase had ossified rays in the incised homocercal caudal fin. According to Penaz (1974), these fish display enhanced nimbleness and rapid movement. Swimming performance linearly increases with body length (Flore et al., 2001) and is boosted by the differentiation of fins and the postcranial skeleton (Ott et al., 2012). Accordingly, the spatial drift patterns of later stages should reflect this improvement. All larvae were tagged with a chemical marker (Alizarin Red S, ARS; Sigma Aldrich®). The application of systematic multiple staining events created unique sequences of fluorescent rings in larval otoliths (Fig. 2).

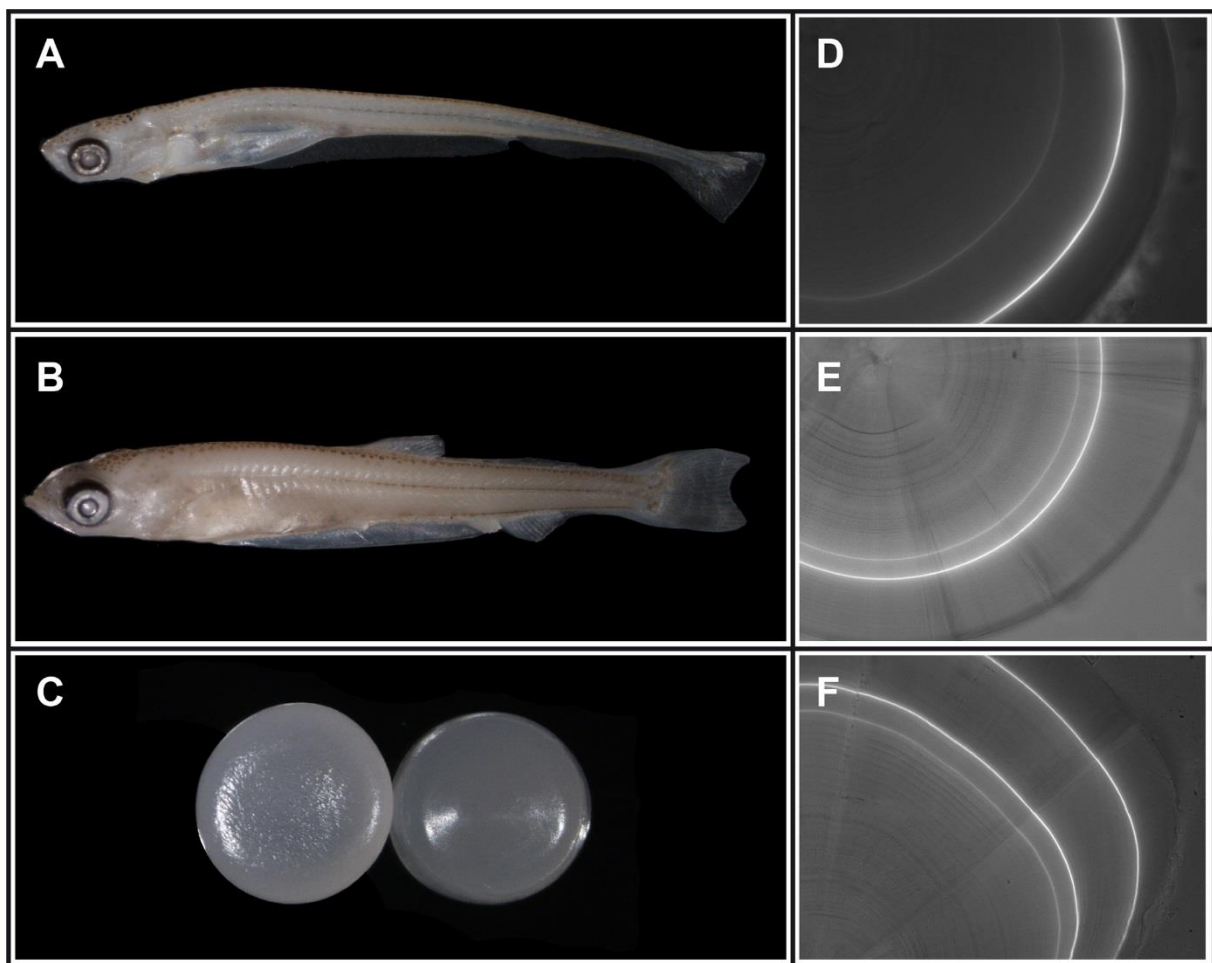


Figure 2. Recaptured nase in the second (A; total length: 11.1 mm, weight: 3.6 mg) and fourth larval stage (B; total length: 13.5 mm, weight: 6.2 mg). White plastic particles (C; diameter: 4.0 mm) as released at the offshore points. Exemplary marking sequences in larval otoliths, indicating release point and developmental stage of tagged individuals e.g. L4+IR (D), L2+OR (E) and L4+OR (F). (©Aaron Lechner)

Using this labelling key, recaptured individual could be allocated to a release point (i.e. inshore release, IR; offshore release, OR) and a developmental stage (L2, L4). The effectiveness of the marking procedure was tested several times on a random basis and found to be 100%. Following each staining event, individuals with identical marks were transferred to separate flumes with two different temperature regimes as mentioned above, yielding a total of 8; 4 warm, 4 cold.

After 34 (2011) to 46 (2012) days in the laboratory, during which larvae were daily fed with nauplii larvae (Great Salt Lake Artemia Cysts, Sanders®) and dry food (Vipagran Baby, Sera®), fish were prepared for release. Two subsamples of 100 individuals were taken from one cold and one warm flume. These larvae were overdosed with tricaine methanesulfonate (MS-222, Sigma-Aldrich®, St. Louis) and then weighed to 0.01 g. The mean weight was used to extrapolate larval counts from the total moist mass within each flume. All remaining larvae were packed into well-oxygenated polyethylene bags and transported to the study site.

Drift experiment

In both years of investigation, experiments were conducted on two consecutive days in May. Four drift sampling stations (SS1-SS4) were installed at increasing distances (65-290-400-510 m) downstream of the predefined release points (Fig. 1). Exact positions of the SS were mapped with a dGPS device (GS 20, Leica®, St.Gallen). Each SS consisted of three parallel nets (IN, MID, OFF), set in a row perpendicular to the shoreline (Fig. 1). The distances between single nets were variable and adjusted to the prevailing hydraulic conditions at the SS, ensuring the security of equipment and people. The conical shaped nets (length 1.5 m, mesh size 500 µm) featured a circular mouth (diameter 0.5 m) and a removable plexiglass jar at the cod end (diameter 7.5 cm). They were fixed to stationary iron rods with a mountaineering cord (length 2 m), making them flexible in the current. A mechanical flowmeter (2030R, General Oceanics®, Miami), attached to the net opening, measured the volume of filtered water.

Larvae were acclimated to the temperature of the Danube by gradually adding river water to the transport bags for 20 min. Afterwards, the bags were positioned at the exact locations of release, which were a low-flow inshore area (IR) and a point further offshore in the mainstream (OR). The release sites of both years are shown in Figure 1. Corresponding values for flow velocity and water depth are given in Table 1. Immediately before release, passive particles (P) (polyethylene pellets, diameter 4 mm, density 0.93-0.95 g cm⁻³, see Fig. 2) were added to the bags equal to the number of contained larvae. Particles were black at the IR and white at the OR. In order to match the natural circadian rhythm of drift (Zitek et al., 2004), larvae (and particles) were released at sunset, 20:15 hrs.

Table 1. Measured values of water depth and current velocity at both release points (IR, OR) for the separate study years.

Year	Release	Depth [m]	Velocity [m s^{-1}]
2011	IR	0.22	0.06
	OR	0.29	0.23
2012	IR	0.30	0.08
	OR	0.54	0.50

Drift sampling (deployment of drift nets) at all SS started synchronously with release, and was carried out for 30 min and thereafter repeated in hourly intervals over 3-5 h periods. All samples were preserved in 96% ethanol and taken to the laboratory for continuative analysis.

Sample processing and statistical analysis

Each sample was suspended in a water bath, to separate larvae and particles from organic flotsam, and then manually sorted. All nase larvae were extracted from the samples and checked for reference marks. Therefore, lapilli (located most anteriorly in the pars superior) were dissected and embedded in epoxy resin (Crystalbond™, Aremco®, New York). Afterwards, these otoliths were ground, polished and screened under wavelengths of 515-565 nm with an epifluorescence-light microscope (Zeiss®, Axio Imager M1 with Axio Vision 4.8.2 software for image analyses). A selection of different mark sequences is shown in Figure 2.

If the number of potential recaptures in the sample was ≤ 5 , all larvae were checked for marks. Otherwise, subsamples were inspected and the overall number of recaptures was extrapolated by:

$$N_{RC} = \frac{N_{MS}}{N_S} \times N_{PR}$$

where N_R is the total number of recaptures, N_{MS} is the number of marked individuals in the subsample, N_S is the number of larvae in the subsample and N_{PR} is the number of potential recaptures in the sample. Subsampling was not performed for particles, which were all counted.

Then, recapture rates (RR in %) of larvae and particles from each subgroup (i.e. L2_IR, L2_OR, L4_IR, L4_OR, P_IR and P_OR) were calculated for the single drift nets:

$$RR = \frac{N_{RC}}{N_{RL}} \times 100$$

where N_{RC} equals the number of recaptures and N_{RL} equals the number of released fish or particles.

We regarded a difference (*DIFF*) in the recapture rate of larvae (RR_L) and particles (RR_P), deriving from the same release points within each net, as a measure of fish activity/behaviour. We used absolute values of *DIFF*, because negative or positive values indicate fish activity/behaviour relative to passive particles (i.e. preference or avoidance). As *DIFF* displayed strong positive correlations with the overall recapture rates ($RR_L + RR_P$) in the nets (which in turn were dependent on the distance between net and release point), and might be influenced by the volume of filtered water (*Vol*) in the nets, a standardisation was necessary to ensure net comparability:

$$DIFF = \left| \frac{RR_L - RR_P}{RR_L + RR_P} \right| \times \frac{1}{Vol}$$

This procedure required a pre-treatment of the data in order to integrate samples when either larvae or particles were absent from the nets. In such cases, *DIFF* was always 1, irrespective of the actual difference in the *RR* of larvae and particles. This information, however, is essential for our study questions. The addition of a constant amount (i.e. 0.001), lower than the smallest value in the data (i.e. 0.007), to all *RR* constituted a feasible solution to keep the original differences and to bring *DIFF* in relation to these values. Afterwards, *DIFF* ranged between 0 (same *RR* of larvae and particles) and 0.05 (large differences in *RR*) and was positively correlated to the numerical difference in larvae and particle counts within the nets (Spearman $Rho = 0.67$, $P < 0.001$).

Generalized linear models (GLM) were developed to test, according to the hypotheses, which factors (*year*, *stage*, *release*, *station*) best explain variation in the dependent *DIFF*. The *glm* procedure with quasipoisson distribution in R was used. All factors were fixed. QQ plots of residuals and residual deviance relative to degrees of freedom were inspected and indicated a good fit to the final model.

The hydro-geomorphological data (i.e. flow velocity and water depth) come from a fully three-dimensional model (RSim-3D) of the sampling site (Tritthart & Gutknecht, 2007). All figures and analysis were done in Arc Gis 10.0®, SigmaPlot 12.0® and R statistical package (R 3.2.3, R Development Core Team; www.r-project.org/).

Methodological considerations

We are aware that some of the observed differences might be because of the different characteristics (e.g. buoyancy, shape etc.) of fish and polyethylene pellets. Downstream drifting larvae, spread over the water column, are exposed to different regimes of turbulence, shear stress and current velocity than floating particles (Tritthart et al., 2009). Nevertheless, the surface-current driven particle transport should accurately reflect the main direction of flow and thereby a spatial (lateral) corridor of passive dispersal. Additionally, differences in the

vertical distribution of particles and larvae should be buffered by drift nets, which covered the upper 65 % of the water column in most cases (92% in 2011, 90% in 2012). It has been demonstrated that larval drift densities are highest near the surface (Johnston, 1997; Gadomski and Barfoot, 1998). Regardless, the potential differences between fish larvae and plastic particles affect all our comparisons among factors (*years, stage, release, station*) equally and so could be considered a systematic error at worst.

Results

Environment

The discharge of the River Danube during the sampling in 2011 ranged from 1010-1155 $\text{m}^3 \text{s}^{-1}$ and was close to RLF (regulated low flow); i.e. the discharge that is exceeded 94% of the time (Fig. 3). All modified groynes were exposed. The re-established bankside flow passed a heterogeneous shoreline, with many shallow bays and debris dams acting as retention zones. Large slack-water areas extended downstream beyond the remaining groyne structures. The median current speeds near-shore (0-15 m), where larval drift densities are presumably highest (Reichard et al., 2004), were below the maximum sustainable water velocity (MSWV) of released nase; i.e. the current velocity at which fish cannot maintain their position in the water column for more than 2 min (Fig. 3; Flore et al., 2001).

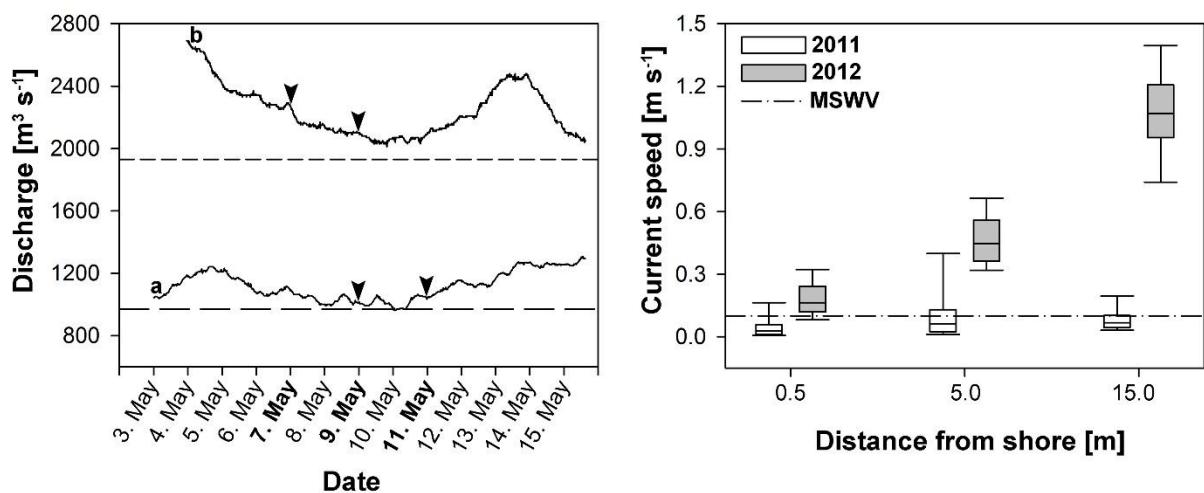


Figure 3. Left: Discharge regimes during sampling periods in 2011 (a) and 2012 (b). Arrows and bold letters indicate sampling dates. Long-dashed line is RLF, short-dashed is MF. Right: Box blots display current speeds at different distances from the shoreline. The dashed line corresponds to the maximum sustainable water velocity of nase larvae (Flore et al., 2001) calculated by $MSWV = 4.39 + 0.456 \cdot TL$, where TL is the mean total length of all recaptured individuals.

The discharge of the River Danube was distinctly elevated in 2012, relative to its level in 2011, ranging from 2050-2250 $\text{m}^3 \text{s}^{-1}$, which is clearly above MF (mean flow) (Fig. 3). All modified groynes were submerged (Fig. 1) and normally lentic areas downstream were then flowing.

The bankside flow passed the remaining gravel-shoreline or a steep erosion bank, which formed the transition to the adjacent floodplain forest. Median values of current velocity were over-critical ($>MSWV$) in 2012, at all measured distances from the shore (Fig. 3).

Flow conditions were under-critical at the IR and over-critical at the OR points, irrespective of the year (Table 2). Between years, though, differences in water depth and current velocity were higher at the OR than at the IR points.

Dispersal

General

In both study years, a total of 97 drift samples were taken, of which 76 contained a sum of 5255 marked nase larvae and 4168 plastic particles, and the remainder were empty. The overall RR of larvae and particles and those of single groups were all higher in 2012 than in 2011 (Table 2). However, this result is mainly attributable to one net (2012, SS1, OFF, exposed simultaneously with release) which captured 1349 marked fish (i.e. 28% of the overall RR for both years) and 1325 particles (i.e. 18% of the overall RR for both years), all deriving from the OR. By contrast, the mean RR per standardized volume (1000 m³) of filtered water (i.e. RR_vol) of most groups and all larvae combined were higher in 2011 than in 2012 (Table 2). This difference was significant for total larvae ($n=76$, Mann-Whitey- $U=1,369$, $P<0.05$). No inter-annual difference in the overall RR_vol of particles was detected ($n=76$, $U=1,230$, $P=0.251$).

Table 2. Numbers of released (Rel) and recaptured (Rec) nase larvae and plastic particles (P) as well as the corresponding recapture rates ($RR = Rec/Rel \cdot 100$) and the means of volume standardized RR ($RR_vol = RR \cdot 1000 \text{ m}^{-3}$) with standard deviations (SD) are given for individual developmental stages (L2, L4), points of release (IR=inshore release, OR=offshore release) and years of investigation (2011, 2012).

Release	Stage	2011				2012			
		Rel [N]	Rec [N]	RR [%]	$RR_vol \pm SD$	Rel [N]	Rec [N]	RR [%]	$RR_vol \pm SD$
IR	L2	11585	187	1.62	0.85 ± 1.36	10190	517	5.08	0.73 ± 1.56
	L4	12558	107	0.86	0.48 ± 0.81	9358	431	4.60	0.73 ± 1.24
	P	24143	381	1.58	0.91 ± 2.10	19549	861	4.40	0.66 ± 1.95
OR	L2	14202	713	5.02	2.59 ± 6.94	8080	919	11.37	1.62 ± 5.42
	L4	10116	1145	11.31	5.96 ± 19.24	8480	1235	14.56	1.95 ± 8.89
	P	24318	1467	6.03	3.01 ± 12.94	16560	1459	8.81	1.34 ± 3.92
Larvae total		48461	2153	4.44	2.33 ± 6.18	36109	3102	8.59	1.22 ± 3.38
Particles total		48461	1848	3.81	1.09 ± 7.41	36109	2320	6.43	0.97 ± 2.22

Testing the hypotheses

Plotting the mean RR_vol of different groups in single nets, displayed a distinct variation in the spatial distribution of recaptured larvae and particles (Fig. 4).

The GLM results indicate that study year and sampling station are significant predictors of $DIFF$, whereas developmental stage and the point of release are not (Table 3). All interactions between factors were tested and were found to be non-significant (Table 3).

Regarding the study year, differences between fish larvae and particles was smaller in 2012 (Fig. 5). With respect to the sampling stations, the median of *DIFF* was highest farthest upstream (SS1, Fig.5).

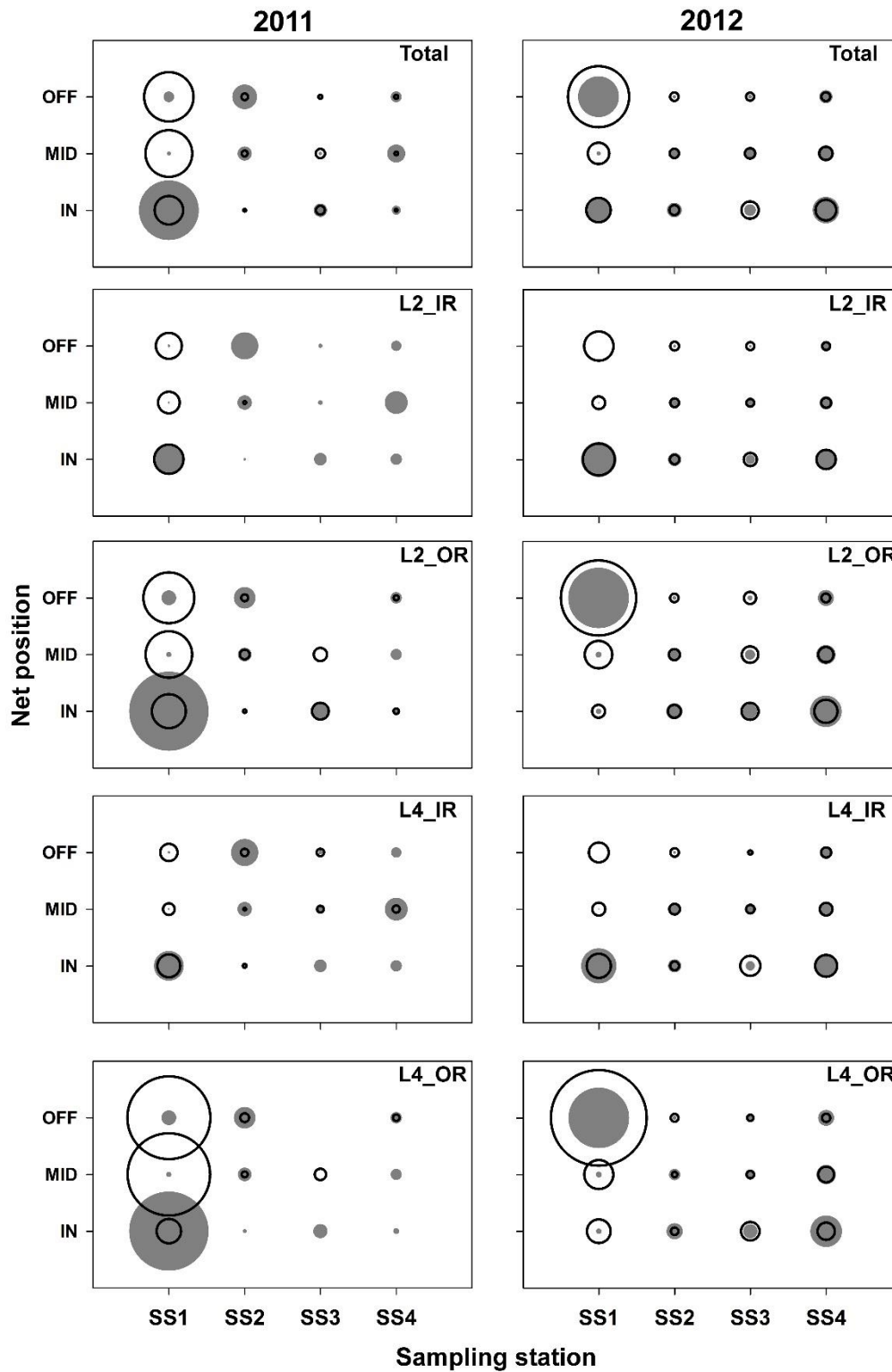


Figure 4. Bubble plots of mean recapture rates per 1000 m³. Bubble sizes refer to the mean *RR_vol* of nase larvae (black edge, no fill) and plastic particles (no edge, grey fill) at single sample points, specified by sampling station (SS1-SS4) and net position (IN, MID, OFF). Results are plotted within separate sampling years (2011, 2012) for all larvae combined (Total) and subgroups defined by developmental stage (L2, L4) and point of release (IR, OR).

Table 3. Results of the GLM, analyzing the impact of four factors (and all possible interactions) on *DIFF*. Note: Significant results are presented in bold

Factor	df	Dev. Res	F	P
Year	1	1.5635	20.927	<0.001
Stage	1	0.0004	0.006	>0.05
Release	1	0.1932	2.580	>0.05
Station	3	2.3902	10.660	<0.001
Stage x Release	1	0.0368	0.483	>0.05
Stage x Station	3	0.1555	0.694	>0.05
Stage x Year	1	0.0158	0.211	>0.05
Release x Station	3	0.0339	0.152	>0.05
Release x Year	1	0.1349	1.806	>0.05
Station x Year	3	0.2829	1.262	>0.05
Stage x Release x Station	3	0.0727	0.325	>0.05
Stage x Release x Year	1	0.2351	3.146	>0.05
Stage x Station x Year	3	0.0747	0.333	>0.05
Release x Station x Year	3	0.3350	1.496	>0.05
Stage x Release x Station x Year	3	0.1526	0.681	>0.05

Discussion

Active and passive mechanisms of fish drift in rivers have been commonly postulated (Robinson et al., 1998; Humphries, 2005; Janáč et al., 2013) but rarely tested and observed in situ (but see Lechner et al., 2016). To date, studies have tracked drift movements by snorkelling (Kennedy and Vinyard, 1997), related larval pathways to numerical particle tracing (Schludermann et al., 2012) and compared temporal dispersal patterns of young fish and passive floats (Lechner et al., 2014b). In summary, all results indicated active drifting behaviour and self-directed dispersal. The present paper highlights the first in-situ observation of the spatial distribution of drifting larvae, opposed to an absolutely passive element of dispersal (i.e. particle transport).

Generally, our results show that larval nase disperse unlike passive particles. Below, our results are discussed in detail following the order of the formulated hypotheses.

Discharge

Our hypothesis has been confirmed as differences in the spatial dispersal patterns of drifting larval nase and plastic particles were smaller during high channel flow in 2012. Theoretically, this observation could be because of passive wash-out in 2012 or deliberate entering and active dispersal in 2011.

The first possibility, that larvae were washed downstream passively during high flow could be because a rise in river discharge often involves a decline of current-reduced inshore habitats (Korman et al., 2004) which are preferably used by young nase (Keckeis et al., 1997), and if such refuges are scarce, strong currents during elevated discharge (Fig. 3) may induce extensive wash-outs of 0+ fish communities (Harvey, 1987; Bischoff and Wolter, 2001). Once entrained, regaining habitat and shelter is limited by the larvae's weak swimming performance (Wolter and Sukhodolov, 2008), and a passive longitudinal displacement is likely. These findings are, however, equivocal, as other studies have detected no influence of elevated river discharge, and the concomitant increase in current speed, on drift abundance (Reichard et al., 2001; Reichard and Jurajda, 2004). In addition, higher wash-out rates in 2012 should be reflected in higher overall mean *RR_vol* of larvae. In fact, the mean number of drifting fish per 1000 m³ was significantly higher during low-flow in 2011, suggesting an alternative possibility.

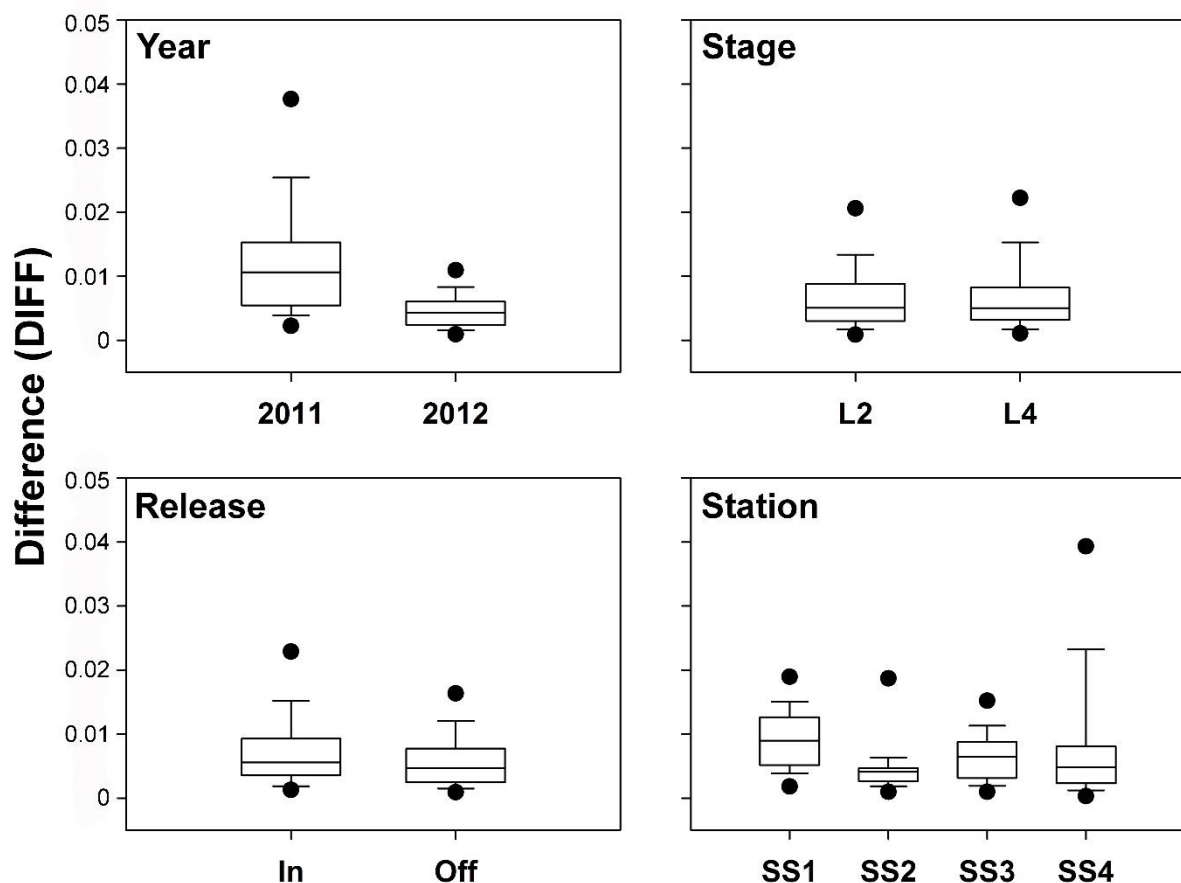


Figure 5. Box plots (median; 25th and 75th percentile; 5% and 95% outlier) of *DIFF* for the four tested factors.

The second possibility, that larvae deliberately entered the drift and dispersed actively under mild hydraulic conditions in 2011 could be because low flows, and the associated low values of turbidity, turbulence and current velocity (Fig.3; Rakowitz et al., 2014), promote orientation and swimming performance of fish larvae (Lupandin, 2005; Liao, 2007; Reeves and Galat,

2010), ultimately resulting in a significant higher deviation from particle transport. The active drifting of nase larvae, along the investigated shoreline in 2011, was also indicated by their temporal dispersal patterns (Lechner et al., 2014b). It could be argued that the higher mean *RR_vol* of larvae in 2011 are a result of dilution effects during elevated discharge in 2012. This is contradicted by the finding that the mean *RR_vol* of plastic particles did not differ between years.

In summary, a significant influence of the river flow on larval fish drift was revealed. Low discharges may motivate young nase to enter the current, perhaps by providing favourable hydraulic conditions for active (and oriented) downstream movements. During high-flows, larvae apparently stay inshore and avoid drifting. If entrained, however, they rather disperse passively. Generally, it has been shown that elevated river discharge at the sampling site is not associated with high wash-out rates of fish larvae. The revitalized gravel bar seems to be quite insensitive to discharge-driven changes in suitable shoreline-habitat availability. This should be beneficial for the young stages of species with similar habitat requirements

Developmental stage

Our hypothesis was not confirmed as the overall differences in the spatial dispersal of drifting larval nase and plastic particles were not affected by stage. Surprisingly, earlier developmental stages (L2), with supposed weak swimming and orientation abilities, displayed clear deviations from passive transport. Our results are consistent with associated laboratory experiments by Zens et al., (this issue): the authors investigated the drift mode of nase larvae in a racetrack flume and detected, even in high currents, a high percentage of active, oriented L2-fish. Apparently, the underlying capacities are likewise executed in the wild surrounding of a large river. In agreement with our study, dispersal simulations in the Colorado River also demonstrated that low swimming performances of young fish can result in high deviations from passive diffusion models (Korman et al., 2004).

Stage-specific peculiarities in (active) spatial dispersal cannot be derived from *DIFF* alone; drift patterns where younger individuals concentrate near the bank and older ones in mid-channel (Reichard et al, 2004), or vice versa (Braaten et al., 2010), could remain concealed. Such characteristics are revealed in the unequal distribution of L2- and L4-nase over the sampling area, i.e. in particular drift nets, potentially originating from differences in behaviour, orientation and swimming. Studies on the upstream and downstream trajectories of young nase in a racetrack flume, for instance, found correlations between developmental stage (L2, L4) and the frequency of occurrence of pre-defined movement patterns (i.e. *active upstream*, *active downstream*, *active-passive*, *passive*) in a velocity gradient (Glas et al., this issue).

In summary, downstream drifting of the nase includes a strong active component, already shown during early ontogeny. Assuming this is representative for many other riverine species, 'ichthyoplankton' is a misleading term, at least for their larval stages.

Current velocity

Our hypothesis was not confirmed as the spatial deviations from passive transport were not smaller for those larvae released in high current velocities. Indeed, the maximum individual values of *DIFF* were recorded for L4 larvae released offshore and collected at the first sampling station.

Our results indicate that drifting nase larvae are active in over-critical flows. Correspondingly, the flume experiments of Zens et al. (this issue) showed that small nase, even if they can't hold position in strong currents, are able to reduce their downstream transport and perform lateral movements. In previous studies on larval nase dispersal in the Danube, individuals from the (over-critical) offshore release points were found in proximity to these points in inshore-nets and -habitats (Schludermann et al., 2012; Lechner et al., 2014b), indicating active movement towards the shore. In addition, Warner sucker larvae (*Catostomus warnerensis*), placed in high currents mid-stream, avoided downstream displacement by actively moving inshore (Kennedy and Vinyard, 1997).

It is quite possible that the activity level of drifting larvae is unexpected high in swift currents: the concomitant increase of swimming- with current-speed has been shown in many studies on specific threshold values in swimming physiology (e.g. critical swimming speed, U_{crit} : Plaut, 2001; Fisher et al., 2005). Potentially, larvae that are abruptly transferred from transport bags into over-critical currents, intuitively try to resist it or to evade it by swimming with high power (in lateral directions).

Distance from release

Our hypothesis was not confirmed as, contrary to our expectations, the highest median value of *DIFF* was recorded at SS1, closest to the point of release.

Behavioural experiments with juvenile fish have found that motor activity increases after being placed into a novel situation (Pavlov et al., 2008). This exploratory behaviour, in combination with the above-mentioned swimming reactions at release, might have caused the observed patterns in our study. Additionally it is possible that nase larvae, after the first 'shock' of release, voluntarily drifted passively. Experiments with reef fish have shown that larvae, as it becomes uneconomical to try to swim against the current, reduce swimming speed and go with the flow (Hogan & Mora, 2005).

Conclusion

The measure *DIFF* has proven to be a suitable first approach to reveal activity patterns of drifting fish larvae and the underlying influencing factors.

The downstream dispersal of nase larvae in the Danube can be classified as *active-passive* process (according to Lechner et al., 2016). There is strong evidence that behavioural and physiological traits impact on the spatial drift characteristics. It is, however, questionable whether these findings are transferable to other species. Active drifting and the associated behaviour may be a peculiarity of fluvial specialists, unincisive in stagnophilous and indifferent species. Comparable experiments with representatives of the particular guilds are desirable.

With respect to the nase, insights gained by this study on the drift mode and the spatial drift patterns constitute convertible knowledge in species conservation and river management. For example, it can be assumed that (unpredictable) events of elevated discharge, common in regulated rivers (Robinson et al., 1998; Humphries et al., 2002), are disruptive as they prevent active (and oriented) dispersal of larvae. The detected activity of drifting individuals in over-critical flows implies a high energy consumption (Wieser, 1995). The availability of suitable settlement sites and a quick arrival of these locations might therefore be crucial for larval survival. But especially such retention sites are scarce in regulated rivers (Schiemer et al., 1991).

Furthermore, our results suggest that upcoming mathematical models of nase drift distance and derived statements on habitat connectivity in rivers must incorporate a “behaviour-activity” term into their equations. A next logical step, the correlation of (positive and negative) *DIFF* values with the abiotic conditions (i.e. current speed, current direction, water depth, turbulence etc.) upstream of drift nets, would allow for a specification of this term and shed a light on the fundamentals of preference and avoidance. Then, more precise predictions on the spatial distribution of drifting larvae in the river cross section could be made. This, in return, would precise drift based population estimates and aid the design of “larval-friendly” anthropogenic river structures. The negative impacts of water abstraction systems, power stations and weirs on drifting fish are manifold (e.g. entrainment, injuries, stranding, stress, death) but might be reduced when built at sites where drift densities are minimal (Koehn & Harrington, 2005; Pavlov et al., 2008; Ellsworth et al., 2010; Bracken & Lucas, 2013).

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Shoreline configurations affect dispersal patterns of fish larvae in a large river

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The dispersal patterns of marked larvae of the nase carp (*Chondrostoma nasus* L.) were observed alongside dissimilar shoreline configurations in the main channel of the free-flowing Austrian Danube and compared with those of floating particles to investigate the mode of dispersal (active–passive). Individuals of different larval stages and floats at similar densities were released at an artificial rip-rap with groynes and a rehabilitated gravel bar. In both habitats, marked individuals were recaptured during the sampling period of 4 d after release. Relevant shoreline attributes for larval dispersal, such as the accessibility of nursery habitats, connectivity between adjacent habitats, and retention potential, were more pronounced at the gravel bar than at the rip-rap. At the gravel bar, larvae moved upstream and downstream within the connected bankside nurseries and displayed longer residence times. Larvae settled in groyne fields along the rip-rap as well; however, longitudinal dispersal was disrupted by groynes, forcing larvae to enter the main channel. Rather than settling in subsequent groyne fields, we assume that these larvae are displaced downstream and potentially lost from the local population.

Keywords: Danube, gravel bar, groyne fields, hydraulic conditions, larval drift, settlement.

Introduction

Dispersal is a key component of species' life history strategies (Stevens et al., 2012) and a valuable adaptation in spatially and temporally fluctuating environments (Tauber et al., 1986). Dispersal is an active or passive transport process between two sites and includes distinct phases (departure-transport-settlement) (Bennetts et al., 2001). Investigations of fish dispersal in both marine and freshwater habitats have traditionally focused on the dispersal of young developmental stages (i.e. eggs, larvae, juveniles) between spawning sites and nurseries (Hjort, 1926; Pavlov, 1994). Spawning areas often do not match larval requirements (Humphries, 2005). Accordingly, a rapid transport to, and settlement in, food-rich, safe nurseries is crucial (Pavlov et al., 1978; Urho, 1999) and impacts future year class strength via survival (Dickey-Collas et al., 2009; Hinrichsen et al., 2001; Houde, 2002). Furthermore the spatial scale and degree of connectivity between these habitats is essential for genetic diversification, the design of marine protected areas as well as river- and fisheries management (Basterretxea et al., 2012; Huret et al., 2007; Savina et al., 2010). Identifying the triggers and mechanisms of dispersal is a prerequisite to draw well-founded conclusions about

the rate of larval exchange between spawning sites and nurseries. In both, marine and freshwater habitats, the transport of larvae and eggs combines passive elements related to abiotic factors as currents (Hogan and Mora, 2005; Rochette et al., 2012), discharge (Harvey 1987), wind forcing (Dalley et al., 2002) or temperature (Peck et al., 2009), and a suite of active behavioral reactions (i.e. olfaction, vision, vertical and horizontal movements : reviewed in Leis, 2007; phototaxis: Reichard et al., 2002a; habitat choice: Robinson et al., 1998; orientation: Staaterman et al., 2012).

Whilst numerous studies in marine habitats incorporated these information to individual based models and particle tracing approaches in order to model the dispersal of young fish (see review in Peck and Hufnagl, 2012), the corresponding efforts in the world's large rivers are rare (Korman et al., 2004; Schludermann et al., 2012; Wolter and Sukhodolov, 2008).

By observing movement patterns of introduced nase carp (*Chondrostoma nasus*, L.) larvae in the Austrian Danube, the present study is designed to improve our understanding of dispersal and retention processes of early stages in fluvial ecosystems. The nase is a characteristic rheophilic cyprinid species inhabiting the hyporithral and epipotamal zones of large European rivers. It is a good model organism in applied river restoration, inter alia as physiological and morphological features of larval nase are well analyzed (Kamler et al., 1998; Keckeis et al., 2001; Schludermann et al., 2009) and their habitat requirements are representative for the early stages of many fluvial fish species (Schiemer et al., 2002). The larvae hatch at fast flowing spawning sites (aeration of demersal eggs) necessitating subsequent movements in suitable nurseries, characterized as highly productive, shallow (≤ 0.4 m), low-current (< 0.1 m. s⁻¹) areas along the shoreline which provide a variety of microhabitats (Keckeis et al., 1997). Due to the comparatively weak swimming performance of embryos and larvae as well as the highly dynamic environment of the spawning sites, dispersal of ichthyoplankton in large rivers is noted as passive drift: individuals are transported from site to site by the flow (Pavlov, 1994). Recent studies have revealed that larval fish use hydraulic gradients for orientation (Lechner et al., 2013; Stoll and Beeck, 2012), even while drifting and are capable of actively piloting towards the shoreline (Schludermann et al., 2012). Nonetheless, nurseries should be easily available (accessibility), connected with spawning sites and adjacent nurseries (connectivity) and offer long residence times (retention). High accessibility and longitudinal connectivity will reduce drift duration and thereby mortality (Brown and Armstrong, 1985; Harvey, 1987; Keckeis et al., 1997). A high inshore retention will enhance community persistence and minimize wash-out effects once young fish are settled (Schiemer et al., 2001).

The littoral zones of large rivers have undergone major alterations in the course of channelization and development (Dynesius and Nilsson, 1994). Few natural riverbanks remain intact, and the artificial shorelines have long been considered inappropriate and un-colonizable

for young fish (Schiemer et al., 1991). At the same time, several studies have revealed that frequently-used structural components of river engineering, such as rip-raps and groynes, enhance physical diversity and habitat complexity on small scales and may be valuable habitats for young fish (White et al., 2010). Nevertheless, alterations to the shoreline clearly change the hydrological and hydraulic characteristics of bankside zones (Shields et al., 1995; Tritthart et al., 2009), what may affect dispersal relevant attributes and thereby drift and settlement patterns of young fish. Accordingly, a disruption of the natural dispersal process during early development due to improper river-management and the increased fragmentation of key habitats could lead to a decrease or loss of characteristic fluvial species (Keckeis et al., 1996).

Accommodating the objectives of this study to actual anthropogenic river alterations (i.e. regulation, shoreline-embankment), dispersal of nase larvae was investigated alongside a revitalized, near natural (gravel bar) and an artificial (rip-rap) shoreline. We hypothesized that the gravel bar performs better regarding accessibility, connectivity and retention potential. This should be manifested in (a) higher entry rates of drifting larvae into suitable inshore habitats, (b) larval exchange processes between adjacent nurseries and (c) longer residence times of young fish in these areas compared to the rip-rap. The simultaneous observation of early and later larval stages and passive particles addresses the character of dispersal (active-passive) at both shores.

Material and Methods

Study area

The study was conducted in the main channel of the Austrian Danube, within the “Danube Alluvial Zone National Park”, east of Vienna (Fig. 1). The stretch between river km 1890-1893.8 provides shoreline situations with distinctly different hydro- geomorphological characteristics. On the right shore, straightened artificial embankments with basaltic blocks (rip-rap) and groynes arranged perpendicularly to the main channel axis deflect flow to improve the navigability at low water and simultaneously stabilize and protect banks against erosion. Alternating groynes and groyne fields, create characteristic embayments along the regulated riverbank. Groyne fields are temporally stochastic habitats and their availability for the riverine fauna depends on the discharge. At low flows (discharges smaller than mean flow in the study area), groyne fields are deposition zones with typical hydraulic patterns and prolonged water retentivity (Sukhodolov et al., 2002). They may serve as important nurseries and refuges for young fish (Bischoff & Wolter, 2001) as well as incubator areas for planktonic algae (Engelhardt et al., 2004). On the left shore, the riparian zone was adjusted to a near-natural state (gravel bar) in the course of an ecologically oriented river engineering project in the years 2007-2009. The rip-rap was removed and the groyne shapes structurally altered (cutting at the groyne

roots to re-establish bankside flow) to improve habitat quality by enhancing longitudinal and lateral connectivity and self-dynamic processes.

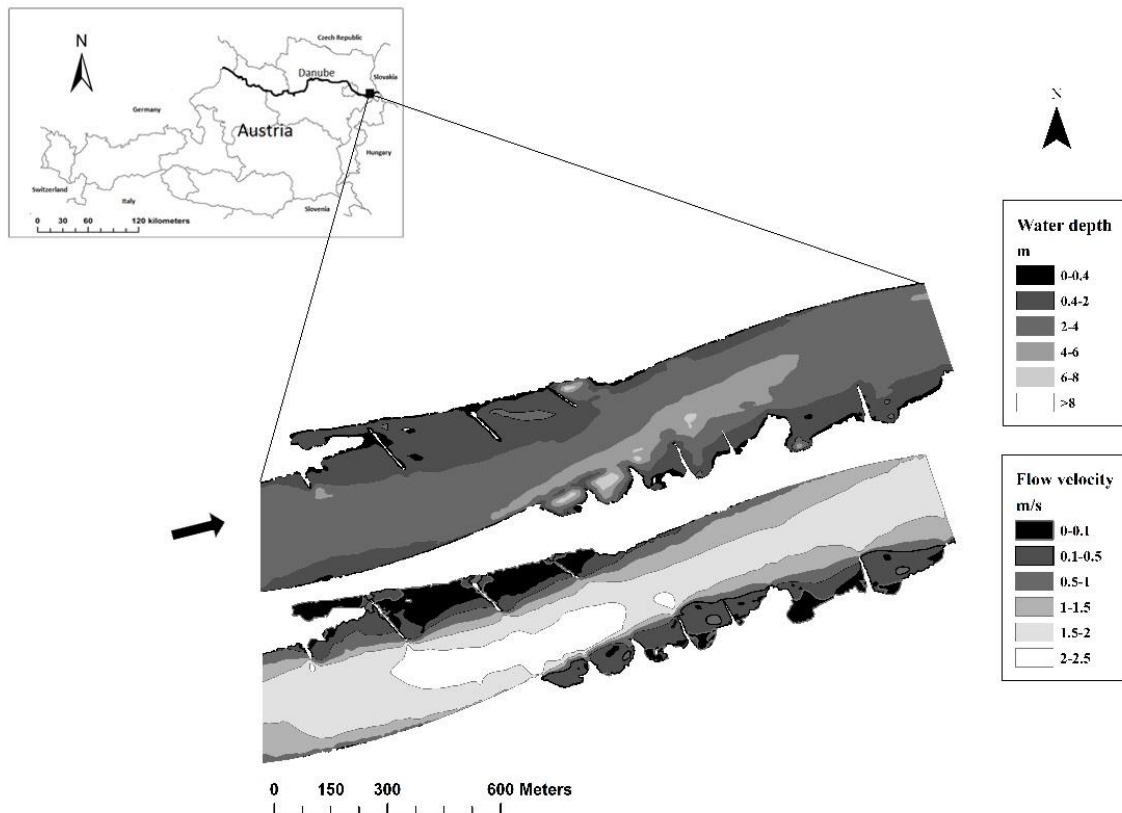


Figure 1. Overview of the study area with flow velocity and depth profiles for a discharge of $1143 \text{ m}^3 \text{ s}^{-1}$. Flow direction is indicated by the arrow.

Study design

Acquisition and rearing of larvae

Ripe adults of *C. nasus* from a natural spawning population were caught in a tributary of the Danube (Schwechat River) by electrofishing. A total of 10 females (2093 g eggs in total) and 14 male (201 g milt in total) were hand-stripped. Promiscuous fertilization of the spawn was applied (one clutch was mixed up with sperm of several males) using the dry method. Afterwards, fish were returned to the river.

The fertilized eggs were divided into two identical, well-oxygenated through-flow rearing flumes with attached temperature control units. The duration of incubation, growth rate and differentiation of tissue are positively correlated to water temperature (Keckeis et al., 2001). Therefore, running different temperature regimes in both flumes provided an opportunity to accelerate and decelerate fish development. Embryos in the cooler flume (mean water temperature $\pm \text{S.D.} = 11.7^\circ\text{C} \pm 0.7^\circ\text{C}$) hatched on day 22 post fertilization and were in the

second larval stage (mean standard length $\pm$ S.D= 11.7 mm $\pm$ 1.9 mm) at release (12 days post hatching). Embryos in the warmer flume (14.8°C $\pm$ 3.3°C) hatched 8 days earlier and were already in the fourth larval stage at release (12.7 mm $\pm$ 1.8 mm).

According to Peñáz (2001), the second larval stage (L2) constitutes the transition to an exclusively exogenous feeding (yolk sac fully depleted). Individuals are characterized by a finfold instead of ventral and anal fins and a diphyercal caudal fin. At this stage, *C. nasus* larvae show a positive phototaxis and fill the posterior chamber of their swim bladder. In the fourth larval stage (L4), fish already possess a two-chambered swim bladder, rays in the slightly incised caudal fin, anlagen of ventral fins, and shaped mesenchymal lobes at the position of the dorsal and anal fins. Swimming ability is known to increase with body length (Flore and Keckeis, 1998) and differentiation of fins (Leavy and Bonner, 2009).

Marking larvae

The otoliths of larvae were labelled with a fluorochrome dye (Alizarin Red S, ARS; Sigma Aldrich®) to help identify recaptured individuals and determine their origin and initial developmental stage at release. Short-term mass-marking was applied according to Beckman and Schulz (1996). In brief, larvae were immersed for 3 min in a buffered ($ph=8$) ARS-solution (1%). NaCl (5%) was added to facilitate the incorporation of the chemical (osmotic shock). A dichotomous labelling key was developed for the release attributes Shore (Left, Right), Developmental Stage (L2, L4) and Point (Inshore, Offshore), whereas a mark encodes one of both features (Table 1). Accordingly, multiple staining events were carried out, with individuals receiving up to four rings in their otoliths. First staining was applied 14 (warm flume) and 6 days (cold flume) after hatching, respectively. The last staining took place on the day before release (on days 23 and 15 post hatching). Two-day intervals between successive markings were maintained to minimize mortality rates. The total numbers of marked individuals and the conversion of the ring sequence are shown in Table 1.

Table 1. Total numbers of released nase larvae differentiated for shorelines, developmental stages (L2, L4), and release points (inshore, IR; offshore, OR). Mark sequences in the otoliths are shown as binary code, where numbers indicate days with staining (1) and no-staining (0) and (-) indicate two day intervals.

Shore	Stage	Release	Code	Number
Gravel bar	L2	IR	1-0-0	11585
		OR	1-1-0	14202
	L4	IR	1-0-0-1	12558
		OR	1-1-0-1	10116
Rip-rap	L2	IR	1-0-1	14428
		OR	1-1-1	12428
	L4	IR	1-0-1-1	7062
		OR	1-1-1-1	14812
Σ				97191

Release and field sampling

All marked larvae were acclimatized to the prevailing water temperatures in the Danube and subsequently released in the river. At both shorelines, fish larvae were introduced in habitats with distinctly different hydraulic conditions. At the rip-rap, these were the shallow deposition zone of a groyne field (inshore release=IR) and the head of the adjacent groyne (offshore release=OR). At the gravel bar, the riparian zone of the gravel shore (IR) and a point 10 m away in the fast flow (OR) served as release points. To match the natural circadian rhythm of drift activity (Reichard et al., 2002b), larvae were released at dusk (1930-2030 h). Both shorelines were sampled alternately.

At each release point, larvae were introduced together with equal numbers of floats (spherical resin pellets, 4 mm diameter, density: 0.93-0.95 g cm⁻³, white-colored for OR and black for IR) representing passive elements of dispersal. Diverging drift and settlement patterns between these floats and released larvae may therefore indicate active mechanisms and reveal shore-specific differences of dispersal mechanisms.

Field sampling started on both shorelines contemporaneously with release (day 1) and was repeated one (day 2) and four (day 5) days post release on each shore. A combination of stationary drift nets and point abundance sampling (PAS) was applied to survey larval drift and settlement patterns (Fig. 2). Drift sampling intended to capture larvae that were washed downstream or entered the current. Triplets of conically shaped drift nets (0.5 m diameter, 1.5 m long, 500 µm mesh) were exposed in the flow at three (rip-rap) to four (gravel bar) sampling sites encompassing a stretch of 2-870 m (rip-rap) respectively 20-520 m (gravel bar) downstream of the release points. Simultaneous exposure of the net triplets at all sampling sites started at dusk and was carried out for 30 min in hourly intervals for a total of 5 h. A flow meter (2030R, General Oceanics®, Miami) was attached to the lower third of each net entrance to measure the volume of filtered water.

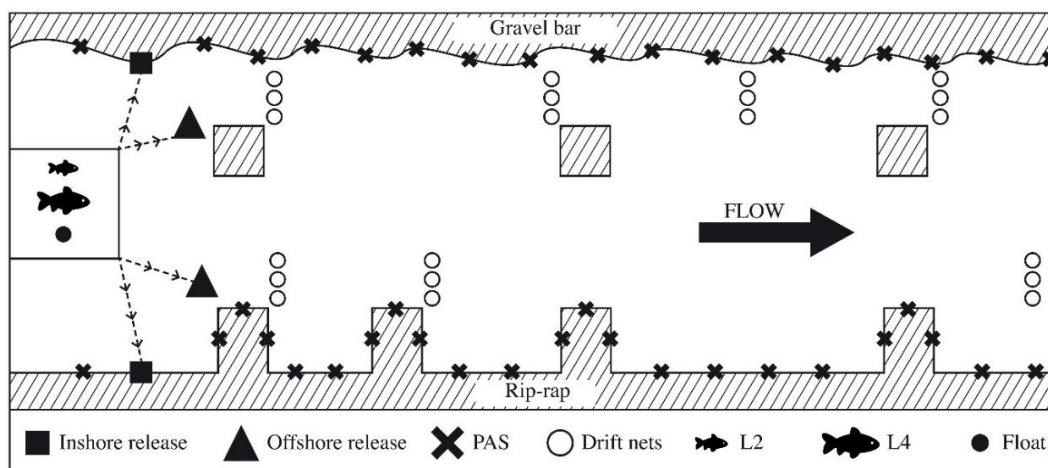


Figure 2. Sampling design. Shaded squares along the gravel bar represent remains of former groynes.

The PAS intended to collect individuals that left the current and settled in inshore areas or maintained their position therein. This approach addresses the microhabitats and is quite robust against temporal and spatial heterogeneity of distribution (Persat & Copp, 1990). Using a dip net (0.4 m diameter, 400 µm mesh size) a figure-8 sweep pattern was carried out, covering an area of approximately 0.75 m² (Schludermann et al., 2012) every 10-30 m along the shoreline. The PAS sampling stretch was adjusted to the shoreline accessibility and ranged from 220 m (gravel bar) and 50 m (rip-rap) upstream of the release points to 540 m (gravel bar) respectively 880 m (rip-rap) downstream of these points.

Exact positions of PAS and drift sampling points were mapped with a dGPS device (GS 20, Leica®, St. Gallen). All captured fish were overdosed with Tricaine (MS-222, Sigma-Aldrich®, St. Louis), preserved in 96% ethanol and taken to the laboratory for further analyses.

Sample processing

In a first step, fish were separated from other (mostly organic) material and separated into different families (i.e. Cottidae, Cyprinidae, Gobiidae, Percidae and others). As no reliable key is available for species determination of early larval stages, potential recaptures were separated from autochthonous cyprinids based on criteria of developmental stage and body length (mean body length at release $\pm$ 5 mm; growth rates in Keckeis et al., 2001). From the potentially recaptured individuals, subsamples were taken (50% of the sample or 30 individuals if sample size was > 60 individuals) and checked for ARS-marks. For this purpose, otoliths (lapilli) were dissected, embedded in synthetic resin (Crystalbond™, Aremco®, New York) polished with abrasive paper and screened under wavelengths of 515 to 565 nm with an epifluorescence-light microscope (Zeiss® Axio Imager M1 with Axio Vision 4.8.2 software for image analysis).

Data analysis

Recapture rates (*RR*) were calculated (N_{rec}/N_{rel} ; *N* = number of individuals, *rec*= recaptured, *rel* = released) for the particular groups (gravel bar and rip-rap; IR; OR, L2 and L4 and floats). The numbers of released larvae and floats were corrected for the number of removed individuals over time. To make single drift samples comparable, *RR* were standardized by the volume of filtered water. The measured *RR_Vol* refers to the number of individuals per 1000 m³. For PAS, *RR_Vol* is given in individuals per 0.75 m². In the following, the terms “drift rate” (*DR*) and “settlement rate” (*SR*) are used instead of *RR_Vol*-drift/settlement. Shore specific differences in accessibility, retention potential and connectivity were analyzed performing systematic pairwise comparisons of drift- and settlement rates (Bonferroni adjusted Mann-Whitney-U-Tests and Wilcoxon-Tests in SPSS 20.0®) and illustrations of spatio-temporal dispersal patterns (in Arc Gis 10.0® and SigmaPlot 12.0®).

The hydraulic conditions alongside both shores were analyzed using the fully three-dimensional (3D) model RSim-3D (Tritthart, 2005). This model approximates fluid motion (as governed by the Reynolds-averaged Navier-Stokes equations), numerically based on a polyhedral computation mesh. Flow and pressure fields were linked iteratively to each other using the SIMPLE Method (Patankar and Spalding, 1972). A standard k- ϵ model (Lauder & Spalding, 1974) was applied to achieve turbulence closure. Water surface elevations were derived from computed pressure fields. The model RSim-3D has been validated on several flume experiments and river engineering applications, as detailed in Tritthart (2005) and Tritthart and Gutknecht (2007). Within the study area, bathymetric measurements (single- and multibeam measurements) in combination with airborne laser-scannings were conducted by the Austrian waterways authority (via donau) between February 2010 and October 2011. These served as a basis for a digital terrain model. Readings of a water level gauge at the downstream boundary of the study area (May 2011) were taken at several discharges. Afterwards, a rating curve was created based on these data and the catalogue of officially published characteristic water levels of the Danube River (which correspond to characteristic runoff values). This rating curve served as a boundary condition for the hydrodynamic model. Water surface elevations were measured within the study area at various discharges between May 2011 and December 2012. Additionally several flow velocity measurements were conducted in two cross-sections (river km 1892.3 and 1893.4) using Acoustic Doppler Current Profiler (ADCP) and Acoustic Doppler Velocimetry (ADV) devices. The hydrodynamic model for the study reach was successfully calibrated and validated for five characteristic discharges where measured and officially published water levels as well as flow velocity measurements were available. The equivalent bed roughness had a value of 0.03 m; the equivalent bank roughness was estimated at 0.30 m, and groynes and rip raps were characterized by an equivalent roughness of 0.80 m.

Results

Shoreline characteristics

The gravel bar was characterized by large low-flow areas between adjacent groynes, ranging from the immediate bank line up to 150 m offshore (Fig. 3). Smaller areas with stronger currents close to the bank were situated at the former groyne roots. Shallow reaches (water depth ≤ 0.4 m) preferred by young fish were evenly distributed along the whole sampling site. No pronounced lateral gradient of current velocity was observed, and the median value was below $0.1 \text{ m} \cdot \text{s}^{-1}$ even 15 m offshore (Fig. 4).

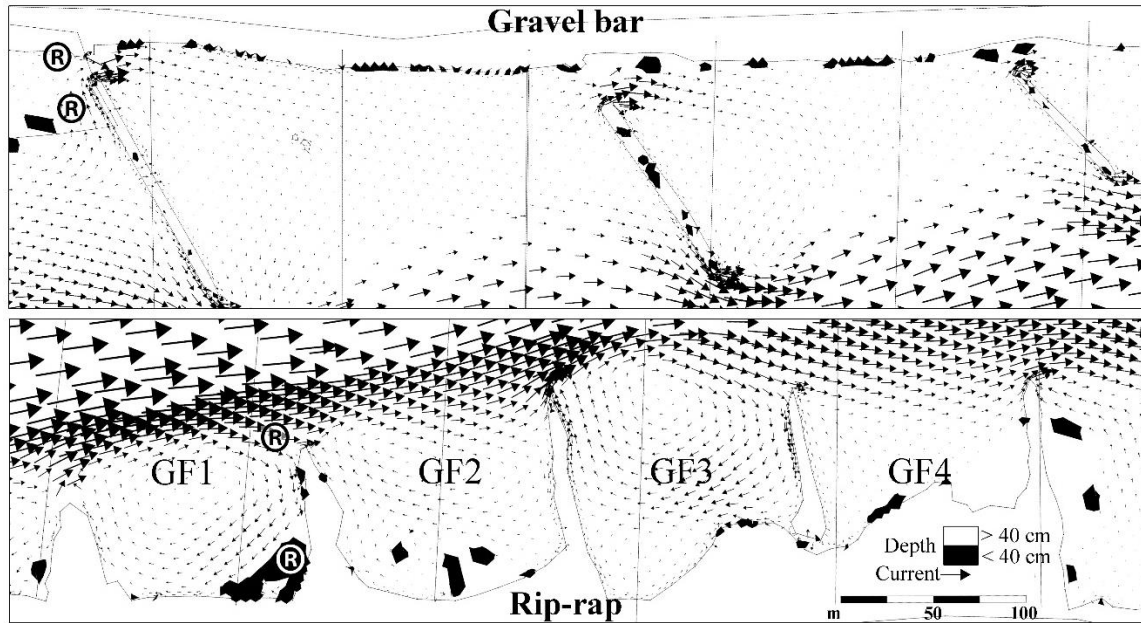


Figure 3. Flow patterns on both shores are illustrated by arrows. Arrow size is proportional to current speed and directly comparable between shores. Shallow habitats, preferred by fish larvae, are shown as black areas. Consecutive groyne fields along the rip-rap are labelled (GF1-GF4). Release points are indicated (®).

The riverbed morphology comprised a shallow slope with median values of water depth increasing from 0.14 m (0.5 m offshore) to 1.05 m (15 m offshore). The turbulent kinetic energy 5 m offshore was higher than both closer and farther away from the bank. At a prevailing discharge of $1143 \text{ m}^3 \text{ s}^{-1}$, the investigated gravel bar provided about 671 m^2 of suitable larval habitats (according to Keckeis et al., 1997) per 100 m shoreline-length (and a total of 3627 m^2 at the whole sampling site, Table 2). The rip-rap was characterized by a steep velocity gradient between the groyne fields and the main channel (Fig. 3).

Table 2. Total length of investigated shoreline, total area of suitable nurseries, and nursery area per 100 m shoreline are given for both shores. Additionally, mean numbers of settling individuals in nurseries along 100 m shoreline-stretches on each sampling day are given.

	Gravel bar	Rip-rap
Shoreline length [m]	540	1816
Total nursery area [m^2]	3627	2785
Nursery area /100 m shore	671	153
Settlers /100 m shoreline [mean]		
Day 1	16.4	7.0
Day 2	5.1	1.8
Day 5	2.1	0.1

The recirculating flow patterns varied between adjacent groyne fields (GF1-GF4) relative to current strength, current direction and vortices profile (Fig. 3). Shallow areas were scattered at inshore deposition zones. The current velocity and water depth increased with distance from shore and were at the threshold of suitability even in proximate inshore areas (Fig. 4). The

turbulent flows along the rip-rap were stronger than at the gravel bar and apparently independent of the distance to the shoreline. The rip-rap offered about 153 m² of suitable nursery areas per 100 m shoreline-length (and a total of 2785 m², Table 2).

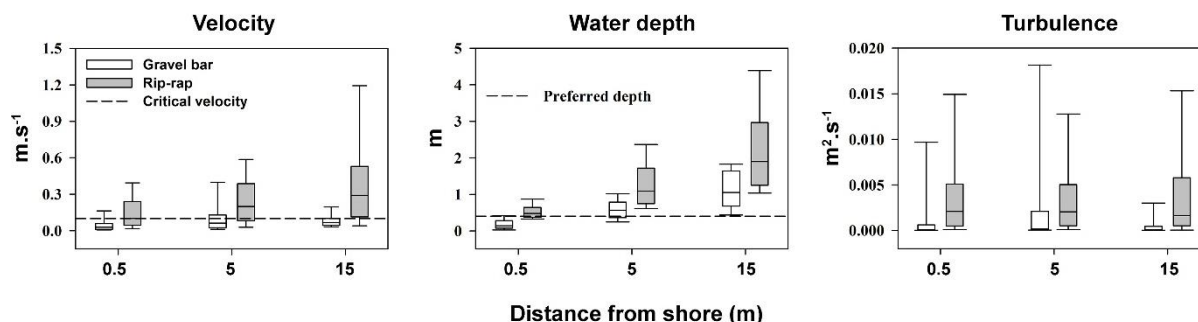


Figure 4. Lateral gradients of flow velocity, water depth and turbulence at both shorelines. Values were derived from the hydrodynamic model (RSim-3D) by calculating the variables every 2 m on modelled lines (0.5, 5 and 15 m offshore) extending from the release points to the downstream end of the sampling site. Horizontal lines represent observed thresholds of suitability in 0+ nase habitats (Keckeis et al., 1997).

Larval dispersal

A total of 97.191 marked nase larvae were released and 3054 individuals were recaptured during the first week of observation, yielding an overall recapture rate of 3.14%. Most larvae were caught in the stationary drift nets (2462) and fewer individuals (592) were counted in the PAS samples (Table 3). Altogether, 93% of recaptured drifting larvae (2293) were caught along the gravel bar whereas 74.1 % of all settling individuals (439) were derived from the rip-rap.

Mean drift rates (*DRs*) of all groups (L2, L4, F; IR, OR) tended to be greater at the gravel bar (Fig. 5). Here, *DRs* of all larvae combined were significantly higher than at the rip-rap (Fig. 6)

Furthermore, overall larval *DRs* at the gravel bar explicitly outran those of floats at the same shore (Fig. 6). No distinct differences between overall *DRs* of larvae and floats were observed within the rip-rap (Fig. 6). Pronounced differences in *DRs* of larvae and floats between both release points were found only at the gravel bar, where *DRs* of OR-fish and floats were increased (Fig. 5). No clear distinctions between *DRs* of all groups, originating from the same release points, were detected within each shore (Fig.5). No inter-shore differences in overall larval settlement rates (*SRs*) could be detected (Fig. 6), and merely *SRs* of IR-L2-nase proved to be higher at the gravel bar (Table 4).

Table 3. Total numbers or recaptured larvae and mean RRs (*RR Vol*) at both shorelines (GB, gravel bar; RR, Rip-rip) for both developmental stages (L2, L4) in driftnets and PASs.

					Numbers				Mean RR Vol ± S.D							
Shore	Day	Method	Samples	Individuals	IR		OR		IR				OR			Total larvae
					L2	L4	L2	L4	L2		L4		L2		L4	
Gravel bar	1	D	33	2152	187	107	713	1145	0.6400 ± 1.2346		0.3615 ± 0.7320		1.9618 ± 6.1172		4.5177 ± 16.8591	1.7668 ± 5.4495
		PAS	8	72	28	9	10	25	0.0297 ± 0.0703		0.0089 ± 0.0122		0.0087 ± 0.0166		0.0305 ± 0.0572	0.0183 ± 0.0336
	2	D	59	89	20	43	8	18	0.0233 ± 0.0785		0.0464 ± 0.1267		0.0067 ± 0.0239		0.0279 ± 0.0699	0.0256 ± 0.0477
		PAS	25	65	21	24	11	9	0.0072 ± 0.0123		0.0077 ± 0.0193		0.0031 ± 0.0076		0.0037 ± 0.0095	0.0056 ± 0.0089
	5	D	57	52	22	8	14	8	0.0469 ± 0.1543		0.0148 ± 0.0544		0.0254 ± 0.0687		0.0223 ± 0.0829	0.0273 ± 0.0604
		PAS	14	16	2	10	2	2	0.0011 ± 0.0042		0.0057 ± 0.0213		0.0009 ± 0.0034		0.0013 ± 0.0048	0.0024 ± 0.0064
Rip-rap	1	D	54	152	35	5	58	54	0.1460 ± 0.5345		0.1038 ± 0.6884		0.3670 ± 1.4228		0.1377 ± 0.4134	0.1937 ± 0.6039
		PAS	19	317	6	13	164	134	0.0022 ± 0.0051		0.0097 ± 0.0327		0.0696 ± 0.2622		0.0477 ± 0.1560	0.0344 ± 0.1136
	2	D	58	15	2	5	3	5	0.0027 ± 0.0150		0.0301 ± 0.1427		0.0089 ± 0.0491		0.0089 ± 0.0359	0.0101 ± 0.0286
		PAS	27	117	8	5	55	49	0.0021 ± 0.0094		0.0027 ± 0.0117		0.0163 ± 0.0845		0.0123 ± 0.0599	0.0089 ± 0.0415
	5	D	49	2	2	0	0	0	0.0031 ± 0.0163		0.0000 ± 0.0000		0.0000 ± 0.0000		0.0000 ± 0.0000	0.0009 ± 0.0048
		PAS	23	5	0	0	3	2	0.0000 ± 0.0000		0.0000 ± 0.0000		0.0010 ± 0.0037		0.0006 ± 0.0030	0.0005 ± 0.0013
Total	GB	D	149	2293	229	158	735	1171	0.1690 ± 0.6362		0.1041 ± 0.3774		0.4469 ± 2.9581		1.0201 ± 8.0599	0.4119 ± 2.6361
		PAS	47	153	51	43	23	36	0.0092 ± 0.0305		0.0073 ± 0.0186		0.0034 ± 0.0091		0.0076 ± 0.0258	0.0068 ± 0.0160
	RR	D	161	169	77	56	80	80	0.0509 ± 0.3153		0.0457 ± 0.4075		0.1263 ± 0.8372		0.0494 ± 0.2471	0.0689 ± 0.3592
		PAS	69	439	29	47	177	145	0.0014 ± 0.0064		0.0037 ± 0.0187		0.0259 ± 0.1473		0.0182 ± 0.0904	0.0131 ± 0.0653

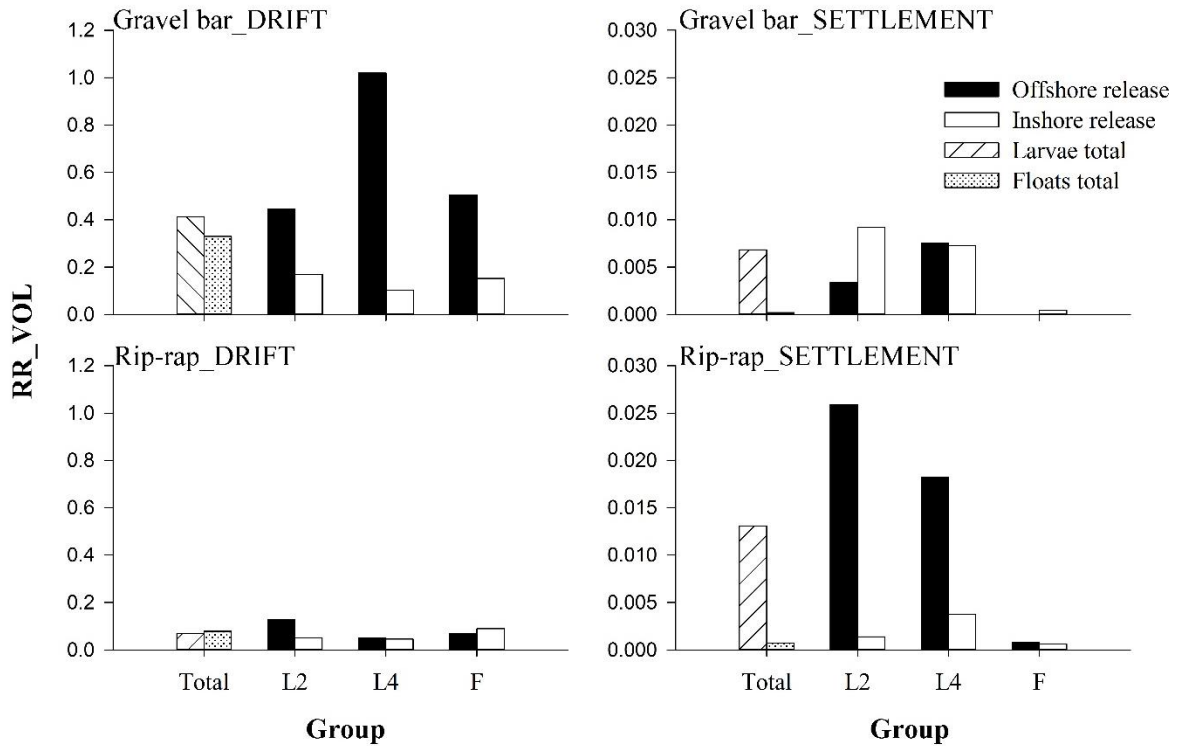


Figure 5. Mean recapture rates (*RR-Vol*) of drifting and settling larvae or both shorelines relating to the total amount of recaptured larvae and floats (F) and single groups (L2, L4) and release points (inshore, offshore).

However, overall larval *SRs* significantly exceeded float retention at both shores (Fig. 6). A detailed analysis of these dissimilarities with regard to shore, point of release and larval stage is given in Table 5: the mean *SRs* of IR- and OR-larvae (L2 and L4) at both shores revealed higher values than float retention but not all combinations proved to be statistically significant. Considerable differences of *SRs* concerning the point of release were observed at the rip-rap for both larval stages, where OR larvae dominated the catch and clearly exceeded *SRs* of IR-larvae (L2 and L4) at both shores (Fig. 5). At the gravel bar, no differences of larval *SRs* with respect to the point of release were observed. However, a generally higher portion of IR-larvae was found compared to the rip-rap (Fig. 5). Overall more floats ($p=0.019$) were retained at the rip-rap (Fig. 6).

Table 4. Pairwise comparisons (Mann-Whitney U-Test) of larval *SRs* (L2 and L4) and floats (F) retention between shorelines and for each release point separately.

IR				OR			
Gravel bar				Gravel bar			
	L2	L4	F	F	L4	L2	
Rip-rap	n=116				n=116		Rip-rap
L2	U=1.27				U=1.61		L2
	$p=0.002$				$p=0.967$		
L4		n=116			n=116		L4
		U=1.39			U=1.55		
		$p=0.031$			$p=0.568$		
F			n=116	n=116			F
			U=1.748	U=1.78			
			$p=0.105$	$p=0.025$			

Table 5. Pairwise comparisons (Wilcoxon signed-rank test) of larval (L2 and L4) *SRs* and floats (F) retention for each release point and each shoreline separately.

	IR		OR	
	Gravel bar Floats	Rip-rap Floats	Gravel bar Floats	Rip-rap Floats
L2	n= 47 W=3.19 <i>p</i>=0.001	n=69 W=0.71 <i>p</i> =0.474	n= 47 W=2.36 <i>p</i> =0.018	n=69 W=2.84 <i>p</i>=0.004
L4	n=47 W=2.81 <i>p</i>=0.005	n=69 W=1.07 <i>p</i> =0.283	n=47 W=2.52 <i>p</i> =0.012	n=138 W=2.47 <i>p</i>=0.01

Analysing the temporal dispersal patterns of larvae at both shorelines revealed peaks in *DRs* on the first day of sampling at which 94% of all drifters at the gravel bar and 90 % at the rip-rap respectively were caught within 5h after release (Fig. 7). Subsequently, the mean *DR* at the rip-rap was characterized by a steep, continuous decrease over time whereas the mean *DR* stabilized at a low level from day 2 onwards at the gravel bar. Overall trends for drifting floats were similar to larvae, although at lower orders of magnitude at the gravel bar.

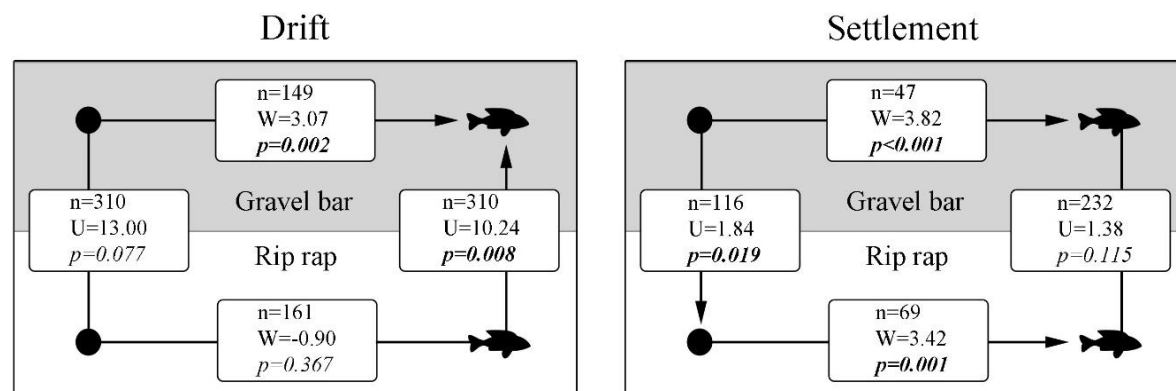


Figure 6. Differences between *DRs* and *SRs* of larvae (fish symbols) and floats (filled circles) within (Wilcoxon test) and between (U-Test) the shorelines. The arrows point towards superior values. Significance level was (Bonferroni) adjusted to 0.025.

Temporal characteristics of larval settlement also revealed a decreasing trend, with higher *SRs* on day 1 and day 2 at the rip-rap, and conversely on day 5 with higher *SRs* at the gravel bar (Fig. 7). At the gravel bar, floats were recaptured only on day 1, though they were found in PAS samples taken at the rip-rap during the first two days of observation.

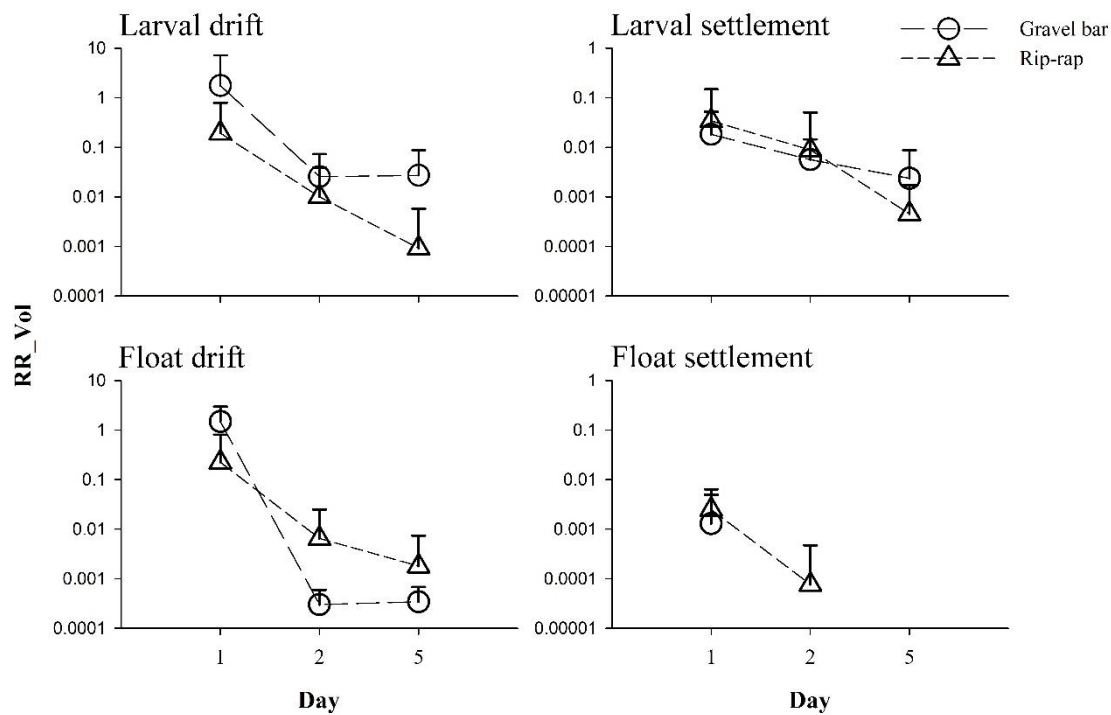


Figure 7. Temporal characteristics of drift and settlement at both shorelines. Values are plotted on a logarithmic scale.

Spatio-Temporal dynamics

Gravel bar. Day 1: The combined spatial and temporal aspects of larval drift and settlement displayed a pronounced drift peak at sampling station 1 (SS1), comprising both stages, but mainly including OR-individuals (Fig. 8a, 9a). The *DRs* drastically decreased at successive sampling stations downstream (SS2-SS4) where primarily OR-L2-nase and L4-nase from both release points entered the nets. Settled larvae were detected up to 300 m downstream of the release points (IR-L2).

Day 2: Predominately IR-L2-nase drifted along the whole gravel bar (Fig 8b), lower *DRs* of L4-nase (IR and OR) were detected at all four sampling stations (Fig. 9b). Settling individuals from both stages and release points were regularly distributed between 35 m upstream to 425 m downstream of the release points.

Day 5: The *DRs* of both larval stages at the gravel bar were slightly higher than on day 2 (Fig 8c, 9c), and IR-L2-nase dominated the drift. Settlement of nase larvae ranged from 150 m upstream to 85 m downstream of the release points. The catch comprised IR- and OR-L2-nase (only downstream) as well as IR-L4-nase (only upstream).

Rip-rap. Day 1: The *DRs* of both stages on day 1 were distinctly lower at the rip-rap compared to the gravel bar. Instead of peaking at SS1, closest to the points of release, *DRs* of both

stages were highest at SS2. The SRs at the rip-rap were remarkably high but restricted to the first (GF1) and second (GF2) groyne field (max. 170 m downstream of release). Settled IR-larvae were primarily recaptured in GF1, OR-larvae were dominant in GF2 (Fig 8a, 9a).

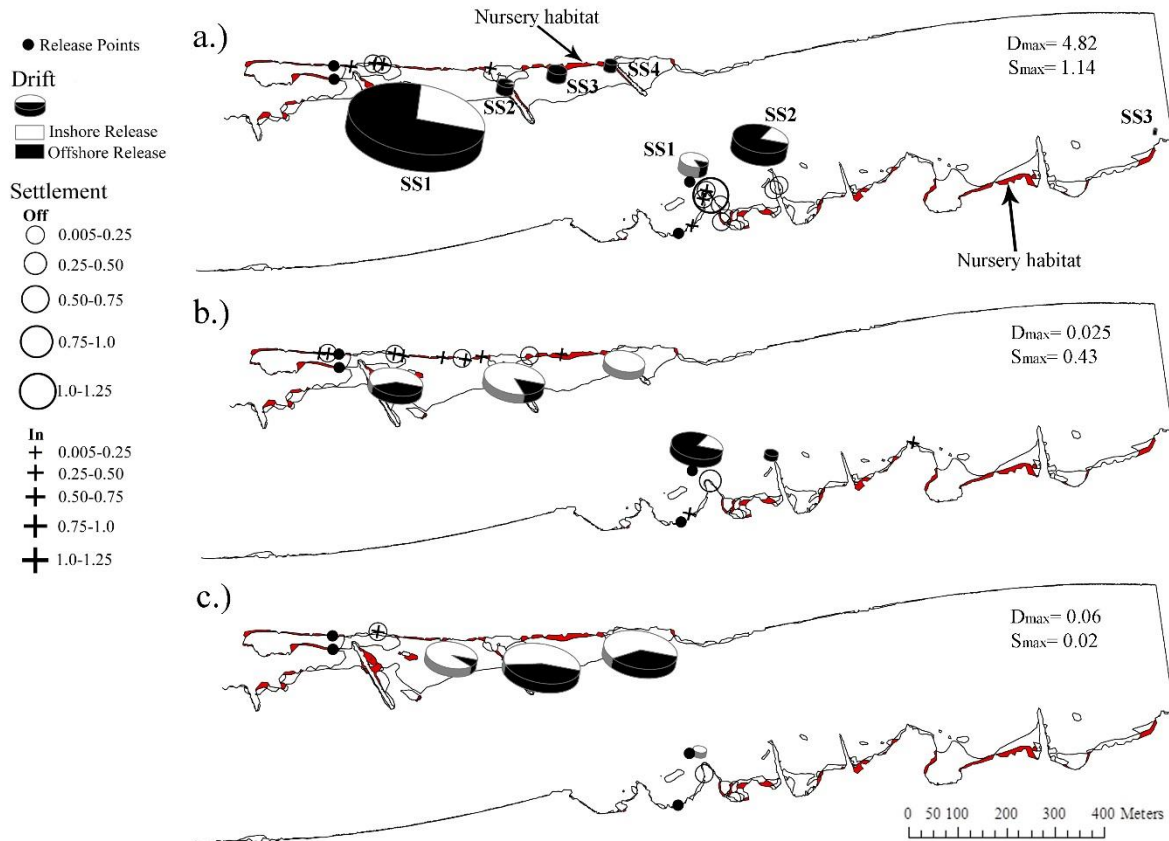


Figure 8. *DRs* (pies) and *SRs* (symbols) of L2-nase at all sampling stations (SS1-SS4) are shown for the day of release (a) and subsequent samplings on day 2 (b) and day (5). Pie sizes refer to the maximum mean *DR* on a given day. For comparisons between days, maximum values of mean *DRs* (D_{max}) are given. Maximum *SRs* (S_{max}) are given too. Red areas along the shorelines show suitable nurseries according to Keckeis et al. (1997).

Day 2: Overall, highest *DRs* on day 2 were recorded for L4-nase at the rip-rap whereas IR-larvae dominated at SS1 and SS3 and OR-larvae at SS2 (Fig. 9b). Drift activity of L2-nase was restricted to SS1 and SS2 (with high numbers of OR-individuals) (Fig. 8b). With the exception of one individual (IR-L2) captured along the shoreline 450 m downstream of release, all other observations of larval settlement were made in GF1 and GF2 (Fig. 8b, 9b).

Day 5: Low *DRs* of IR-L2-nase were observed only at SS1 (Fig. 8c, 9c). Apart from that, no further recaptures in drift were detected. Settling larvae were still found in GF1 (L2-OR) and one single individual was recaptured 700 m further downstream (L4-OR).

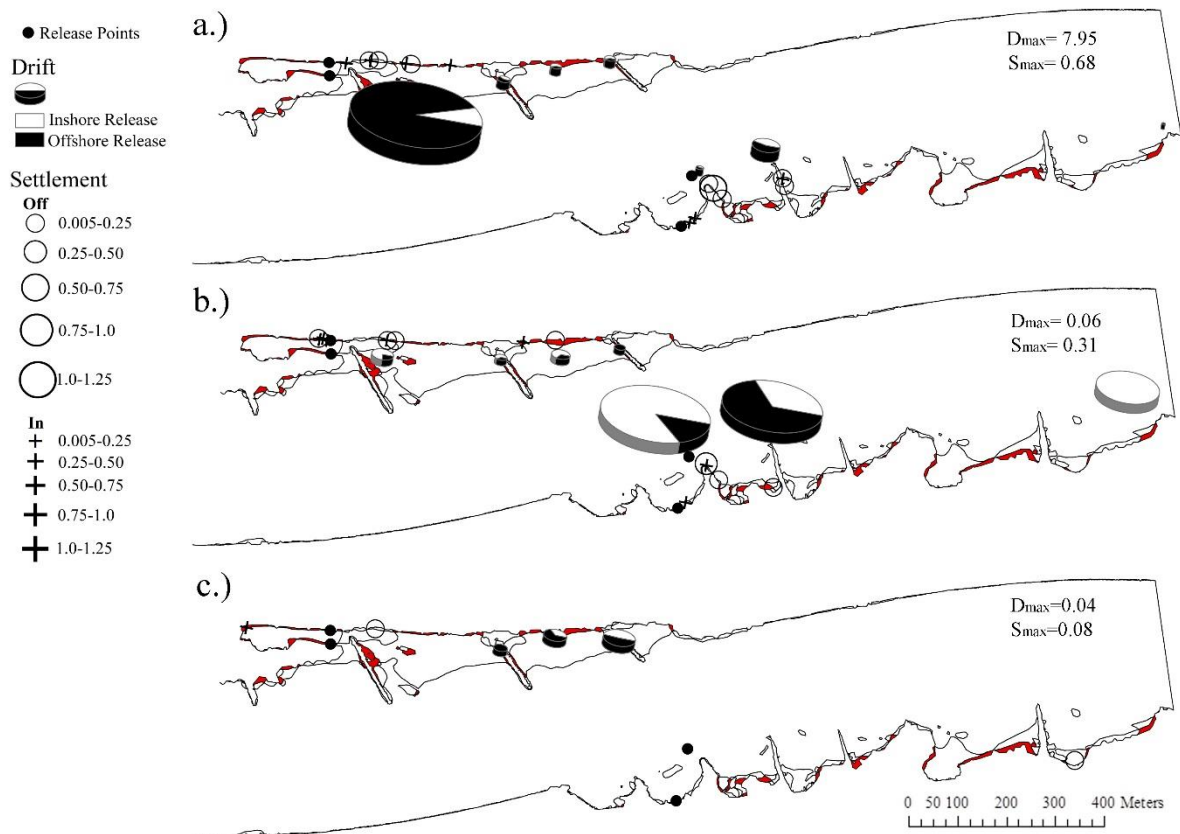


Figure 9. *DRs* (pies) and *SRs* (symbols) of L4-nase at all sampling stations (SS1-SS4) are shown for the day of release (a) and subsequent samplings on day 2 (b) and day (5). Pie sizes refer to the maximum mean *DR* on a given day. For comparisons between days, maximum values of mean *DRs* (D_{max}) are given. Maximum *SRs* (S_{max}) are given too. Red areas along the shorelines show suitable nurseries according to Keckeis et al. (1997)

Discussion

This study compares two typical shoreline configurations of a free-flowing stretch of a large river with regard to their suitability for, and influence on, larval fish dispersal. Drift and settlement patterns of two introduced larval stages (L2, L4) of the nase carp and passive floats were recorded alongside a revitalized gravel bar and a modified rip-rap with groynes.

Shoreline accessibility

Shoreline accessibility refers to the hydro-geomorphological shore characteristics that enhance the arrival of larvae from offshore spawning habitats in littoral areas by ending the drifting phase and facilitating settlement in suitable nurseries. In this study, *SRs* of OR-larvae and floats served as a basis to discuss accessibility of inshore nursery habitats. Higher *SRs* of OR-larvae at both investigated shorelines compared to passive float retention reflected larval swimming ability and behavior. Mean *SRs* of OR-larvae were even higher at the artificial rip-rap. In contrast to the gravel bar, settlement at the artificial rip-rap shoreline was restricted to nurseries located short distances from the release points. We ascribe the high accessibility of

these particular areas partly to passive introduction facilitated by small scale flow patterns. This was denoted by simultaneous recaptures of OR-floats exclusively in GF1 and GF2 and a general higher passive retention rate of passive floats at the rip-rap compared to the gravel bar. Groyne fields along rip-raps are characterized by a large-scale vortex with a clockwise current, interfaced to the main channel by a mixing layer (Sukhodolov et al., 2002). Large turbulent structures in this narrow strip of the mixing field play an important role for the exchange of momentum and matter – and presumably fish larvae – between the river and its groyne fields (Schwartz and Kozerski, 2003; Uijttewaalt et al., 2001) and could therefore have enhanced passive larval introduction. The exchange rates between single groyne fields vary, depending on the flow patterns within the fields (Fig. 3), the groyne shape, the position of a groyne field in a sequence, the aspect ratio (between groyne length and length of the groyne field), as well as the discharge and flow velocity of the main channel (Tritthart et al., 2009; Uijttewaalt et al., 2001). According to the marginal larval *SRs* downstream of GF2 (of both, OR-larvae and IR-larvae that entered the flow) we propose the average accessibility of the artificial shoreline to be comparatively low. In general, the active or passive entrance of drifting larvae into conventional groyne fields along the rip-rap seems to be selective, and losses to the main channel may outnumber larval input into these artificial structures by far.

Distinct initial drift peaks caused by OR-larvae were recorded at the gravel bar at SS1 (Fig 8a, 9a). Trajectories of those larvae were short and led from the swift flowing areas at the offshore release points into drift nets placed in a short distance (45 m) downstream. Larval transport over such a short distance in high, overcritical currents may predominantly be a passive process (Pavlov, 1994). However, there is evidence that these wash-outs do not account for higher population losses: *DRs* displayed a strong longitudinal decrease (SS1-SS4) on day 1 and OR-larvae were still drifting and settling along the gravel bar until day 5. The prolonged drift pattern suggests that OR-larvae were able to delay or prohibit dislodgement or they settled before and re-entered the drift. We propose the large areas between adjacent modified groynes at the gravel bar to act as catch basins for drifting larvae, as they feature low current and turbulence regimes (see Fig.1, Fig.4) and are “decoupled” from the main channel. These conditions should foster orientated and energy-saving swimming towards the shallow littoral nursery habitats (Flore and Keckeis, 1998, Webb and Cotel, 2011).

Connectivity

Shoreline connectivity refers to the longitudinal and lateral connection of adjacent larval habitats in the sense that young fish can move between these areas. The analysis of connectivity based on spatial-temporal distribution patterns of larvae and floats in drift nets set and in point abundance samples. Longitudinal connectivity at the gravel bar was indicated by the even distribution of settling larvae along the shoreline and the observed upstream

migrations of larvae on day 2 and day 5. The longitudinal connectivity at the rip-rap, within the investigated shore-length, was distinctly lower than at the gravel bar. In order to explore and colonize new nursery habitats, retained larvae in GF1 and GF2 must pass groyne heads and enter high currents. Once in the drift, fish rather got lost to the main channel and rarely reached adjacent littoral zones by re-entering subsequent groyne fields due to poor accessibility.

Retention

The retention potential refers to the shoreline's capability of accommodating high larval population densities. The settlement rates of IR- and OR-larvae served as a base to analyze retention at the two shore configurations. The inshore "population" at the gravel bar was potentially composed of IR-larvae that successfully stayed and moved along the shore as well as OR-larvae that successfully reached these areas due to their high accessibility and connectivity. Here, larvae of both stages and release points were still detected drifting and settling until day 5. Although, the investigated shoreline at the rip-rap was more than three times longer, the gravel bar provided a larger total area of suitable larval habitats. Consequential, mean numbers of retained larvae per 100 m shoreline-length were higher at the gravel bar each day (Table 2).

At the rip-rap, suitable larval habitats were patchy distributed at inshore gravel-areas and within smaller bankside gyres which are known to have high retention capacities for passive particles (Tritthart et al., 2009). This was indicated by larval settlement until day 5 in GF1 and longer/higher passive retention of floats. Nevertheless, the decrease of larval abundance over time at the rip-rap was steeper. The dominant hydraulic conditions for larvae in the groyne fields were harsh. High levels of turbulence can affect fish behavior and physiology by challenging swimming speeds and increasing costs of locomotion (Utne-Palm and Stiansen, 2002; Liao, 2007). In combination with over-critical current speeds these flows may have transported larvae from the center of the large vortex towards the interface with the mixing layer and enhanced advection into the main channel. Additionally, the proximity to the shipping channel presumably enhances negative effects of navigation induced wave wash on young fish at the rip-rap. By altering the direction and speed of currents and dislocating microhabitats (Guhr, 2002; Kucera-Hirzinger et al., 2009; Wolter et al., 2004) wave wash may have increased larval displacement from the observed groyne fields. As drifting fish rarely re-entered and settled in adjacent nurseries the probability of retention downstream of GF2 was very low.

Conclusion

The large, shallow low-flow areas and the modified, newly created groyne structures along the left shore of the River Danube in the Danube Alluvial Zone National Park enabled dynamic dispersal processes of nase larvae. Cutting the groyne roots improved habitat diversity and

quality by increasing connectivity of inshore nursery areas and directing a substantial part of the flow to the shore. Large lentic areas behind the remaining groynes became connected by this bankside flow, adjacent to suitable inshore nursery habitats, presumably providing a safe route for larval dispersal. Larval drift rates in the re-established bankside flow were high but these population losses were probably lowered by the hydraulic conditions and bank geomorphology which matched larval requirements and boosted shoreline accessibility, connectivity and retention.

The conventional groyne fields along the right bank were found to be suboptimal nursery habitats for young fish due to stronger currents, higher turbulence and greater water depths. Fish larvae may drift into groyne fields, but this seems to be more likely a stochastic event depending on several factors such as structural properties of the groynes, distinct flow patterns at the interface of river and groyne field, size and intensity of the mixing layer, as well as discharge- and navigation-induced currents. Active or passive movements of larvae out of these groyne fields are attended by strong currents at the groyne heads and a concomitant passive dislodgement of fish larvae downstream. Overall this may lead to high mortalities and population losses, especially because the hydraulic and morphological features of the right shore seemed to inhibit re-entering subsequent groyne fields and nurseries. This study shows that these structures are disadvantageous by potentially interrupting dispersal pathways and settlement of riverine fish larvae.

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Chapter 4: Microplastics in rivers: a potential threat for drifting fish



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Short communication

The Danube so colourful: A potpourri of plastic litter outnumbers fish larvae in Europe's second largest river



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ABSTRACT

Previous studies on plastic pollution of aquatic ecosystems focused on the world's oceans. Large rivers as major pathways for land-based plastic litter, has received less attention so far. Here we report on plastic quantities in the Austrian Danube. A two year survey (2010, 2012) using stationary driftnets detected mean plastic abundance ($n = 17,349$; mean $\pm$ S.D: 316.8 ± 4664.6 items per 1000 m^{-3}) and mass ($4.8 \pm 24.2 \text{ g}$ per 1000 m^{-3}) in the river to be higher than those of drifting larval fish ($n = 24,049$; 275.3 ± 745.0 individuals. 1000 m^{-3} and $3.2 \pm 8.6 \text{ g}$ 1000 m^{-3}). Industrial raw material (pellets, flakes and spherules) accounted for substantial parts (79.4%) of the plastic debris. The plastic input via the Danube into the Black Sea was estimated to 4.2 t per day.

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Introduction

Plastic, the lightweight and long-lived material, has become a serious environmental hazard (Thompson et al., 2009). The annual global production of the organic polymer has rapidly increased from 1.7 to 280 million tonnes within the last 60 years (Plastic Europe, 2012) resulting in the accumulation of plastic litter in virtually all habitats (Browne et al., 2011). Marine systems are sinks for pre- and post-consumer plastic and the multifaceted negative impacts of plastic pollution on wildlife (reviewed in Cole et al., 2011; Derraik, 2002; Oehlmann et al., 2009) as well as several aspects of debris composition, distribution and abundance have been described here (reviewed in Ryan et al., 2009). Although accumulation of plastic in the ocean is prevalent, there is scarce data on plastic inputs in the oceans (Law et al., 2010). Marine plastics originate from ship or land-based sources (Coe & Rogers, 1997) with the latter to be of greater relevance (Andrady, 2011). A significant portion of the terrestrial plastic is transported to the seas by rivers. Nevertheless, quantifications of plastic loads in rivers found in primary literature are minimal (Moore et al., 2011; Williams and Simmons 1997). Realistic estimations of the plastic flow from rivers to oceans are very important in helping to raise the awareness of the sources of plastic debris and ultimately to drive measures to reduce it.

In this article, we present results from a two-year (2010, 2012) survey on plastic litter transport in Europe's second largest river, the Danube. The main aim of the study was to categorize and to quantify drifting plastic items. In a second step we compare plastic abundance and plastic mass in the river with those of ichthyoplankton (drifting fish larvae and juveniles). Adverse health effects may arise when small fish confuse plastic particles with food items (zooplankton, fish eggs) and ingest them (Carpenter et al., 1972). Finally we give a rough estimate of the input of plastic litter via the River Danube into the Black Sea. To our knowledge, this is the first report on plastic transport in a large river.

The whole study was embedded in a scientific project that highlights larval dispersal and the conservation of riverine fish populations. All sacrificed individuals were handled according to applicable regulations and used for comprehensive analysis (Lechner et al., 2013b)

Methods

Study site

The study was conducted in a free flowing stretch of the Austrian Danube between Vienna and Bratislava. All sampling sites were situated within the "Danube Alluvial Zone National Park" which preserves the last remaining major wetlands environment in central Europe (<http://www.donauauen.at>). Here, the average river width is 350 m and the discharge at mean flow is $1930 \text{ m}^3 \text{ s}^{-1}$. Featuring the world's most international river basin (19 countries, 800.000 km², 81 million people), the Danube is a special case study regarding conservation and management issues (Sommerwerk et al., 2009). As the main tributary (input of $6444 \text{ m}^3 \text{ s}^{-1}$ at mean flow) and major nutrient pathway, the Danube directly affects the Black Sea (BSC, 2009). Beside eutrophication, the vulnerable ecosystems of this continental water face an increasing threat of plastic litter pollution (Topçu et al., 2013). Inputs from land-based sources have gained less attention but are supposed to be high, especially via the Danube River System (Lebreton et al., 2012).

Sampling

The sampling procedure has been accurately described elsewhere (Lechner et al., 2013b). Briefly, we utilized stationary conical driftnets (0.5 m diameter, 1.5 m long, 500 μm mesh) that were fixed to iron rods driven into the riverbed and sampled the top 0.5 m of the water column. Nets covered 60% of the water column in more than 75 % of all cases. The mesh size we used is in the range of other studies that quantified suspended plastics (reviewed in Hidalgo-Ruz et al., 2013). A flowmeter (2030R, General Oceanics®, Miami) was attached to the lower third of each net entrance to measure the volume of filtered water. In this volume-reducing approach,

the filtered sample (containing plastics, fish larvae, organic debris and other items) is collected in a jar attached to the net-end and can be taken to laboratory for further processing.

Duplicates (2010) and triplicates (2012) of driftnets were simultaneously exposed at three (2010) to four (2012) sampling stations along both river margins with maximum distances of 1 km between the single stations and 25 m between the shoreline and driftnets. In 2010, we sampled circadian (24 h) periods with hourly intervals between single sample events. In 2012, sampling started 2 h before sunset (according to ephemeris) and was continued in hourly intervals until midnight. Collecting day and night samples was essential in consideration of realistic comparisons between ichthyoplankton and plastics abundance: larval fish drift is known to exhibit a distinct diurnal rhythm with nocturnal peaks in individual numbers (Pavlov et al., 2008). Therefore, exclusive daytime sampling would have underestimated fish densities by far. The sampling period (Apr-Jul) was chosen to comprise the entire drift season (Lechner et al., 2013a).

Sampling Processing

In the laboratory, plastic items and fish larvae were separated from the samples in a two-step process. Each sample was suspended in a water bath and a density separation (buoyant plastic particles and larvae with intact swim bladders were removed), was followed by a careful visual sorting of the remaining material by the naked eye.

Characterization and quantification of plastics

All plastic pieces and larvae were counted. A subsample (n=500) of fish larvae was taken and all individuals were weighed to the closest 0.01 g (moist mass). Each plastic particle was allocated to one of the categories shown in Figure 1.

Pellets, spherules and flakes characterize different types of industrial raw material that serve as precursors for plastics production. The category “others” encapsulates all other pieces and fragments of plastic consumer products. A subsample (n=500) of each category was taken and all containing items were weighed to the closest 0.01 g and measured to the closest 0.01 mm (Zeiss® Axio Imager M1 with Axio Vision 4.8.2 software for image analysis). Referring to the size-ranges of the defined groups, the collected plastic may be termed mesodebris (2-20 mm; pellets, flakes, big spherules, others,) or microdebris (< 2 mm, small spherules) (Ryan et al., 2009) though different nomenclatures have been used in the literature (Cole et al., 2011; Hidalgo-Ruz et al., 2013).

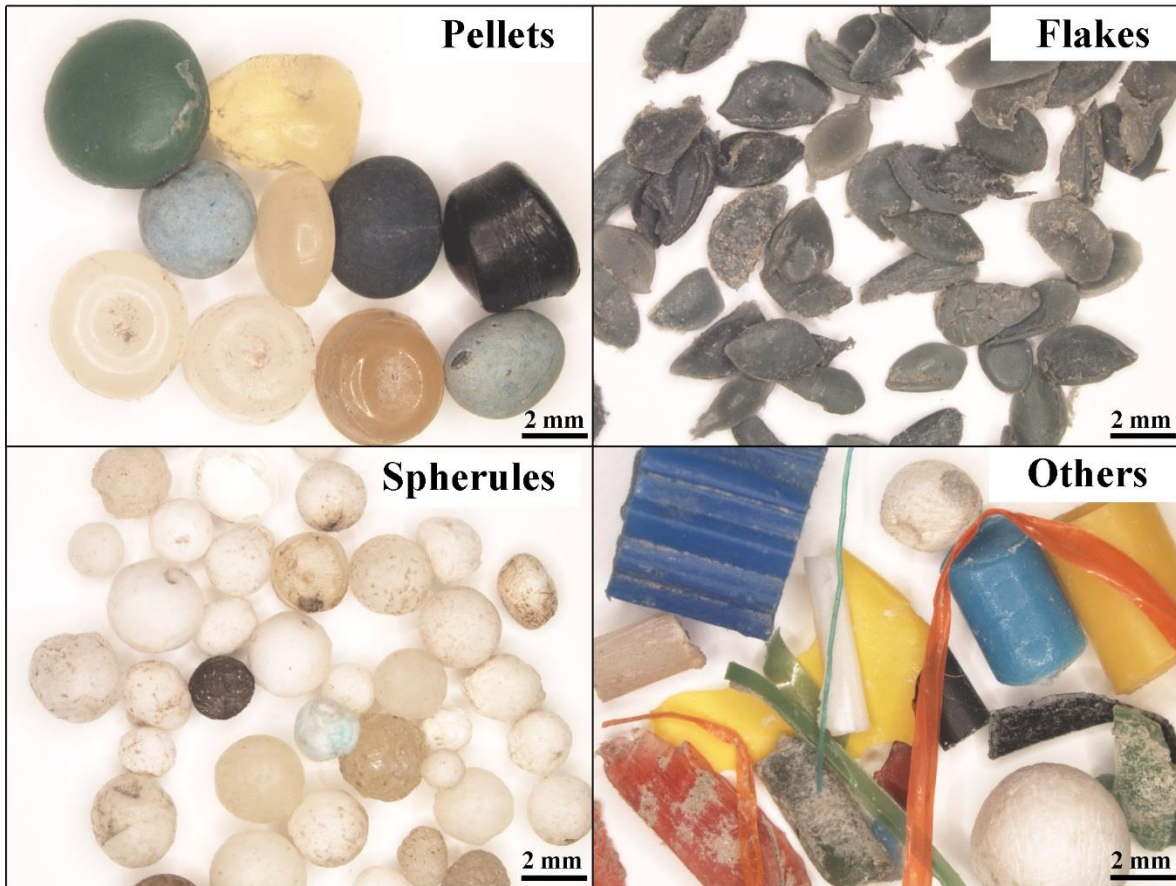


Figure 1. Categories of drifting plastic items in the River Danube: pellets (mean weight $\pm$ S.D: 26.14 ± 4.5 mg; mean diameter $\pm$ S.D: 4.13 ± 0.48 mm), flakes (w: 2.23 ± 1.51 mg; d: 2.81 ± 0.51 mm), spherules (w: 4.45 ± 3.26 mg; d: 2.91 ± 0.65 mm), others (w: 51.6 ± 139.83 mg; d: 15.01 ± 12.58 mm).

The abundance of fish larvae and plastics, below named drift density, is given as individuals and items per volume of filtered water (1000 m^3). Additionally mass values of plastic and larvae are given in grams per volume (1000 m^3). Means of larval and plastic drift densities were compared using Mann-Whitney U-tests (SPSS 20.0®, IBM Corp., Armonk, NY, USA). The plastic input (grams per 1000 m^3) into the Black Sea (BS) was estimated using the simple formula,

$$\text{Input}_{BS} = \text{Load}_{NP} \times F_P$$

where the average plastic load (all categories combined) in the National Park (Load_{NP}) at mean flow (data derived from both sampling years) is multiplied by a factor reflecting the downstream increase in population in the Danube basin (F_P) (ICDPR, 2009; <http://www.icpdr.org>). Refining the result of this approximation by exploring the potential of applying an appropriately adapted sediment transport model coupled with hydrodynamic simulations (e.g. Tritthart et al., 2011) is envisaged for a future detailed study.

Results and Discussion

In both years 951 drift samples were taken (day: 293, night: 658) containing a total of 24,049 larval fish and 17,349 plastic items. Both plastic densities and composition displayed distinct differences between sampling years (Table 1): not only the overall plastic density but also the mean and maximum drift densities of all categories were clearly higher in 2010, with industrial plastics comprising 86 % of the total load. Other plastic litter revealed higher drift densities in 2012 (69 % of the total load) and dominated plastic mass in both years due to the higher mean weight. Combining both years of observation the average plastic load of the river Danube amounts to 316.8 ± 4664.6 items per 1000 m^3 (79.4 % industrial, 20.6 % others) which equates to 4.8 ± 24.2 grams per 1000 m^3 (29.7 % industrial, 70.3 % others).

Table 1. **A:** Mean drift densities (items. 1000 m^3) with standard deviations (S.D), as well as minimum (Min) and maximum drift densities (Max) are shown for different types of plastic and total plastics. Percentages show the contribution of single categories to the overall drift density. **B:** same information is given for plastic mass (grams. 1000 m^3).

Category	2010				2012			
	Mean $\pm$ S.D	Min	Max	%	Mean $\pm$ S.D	Min	Max	%
A								
Pellets	34.9 ± 146.1	0.0	2135.2	3.7	9.3 ± 27.3	0.0	232.6	17.0
Flakes	80.1 ± 317.6	0.0	3568.9	8.5	5.7 ± 9.1	0.0	55.0	10.4
Spherules	693.1 ± 8299.9	0.0	138219.3	73.9	2.0 ± 8.7	0.0	136.3	3.6
Others	129.4 ± 235.5	0.0	2922.0	13.8	38.0 ± 47.2	0.0	465.3	69.0
Total	937.6 ± 8543.8	0.0	141647.7		55.1 ± 75.4	0.0	744.5	
B								
Pellets	0.9 ± 3.8	0.0	55.8	8.4	0.2 ± 0.7	0.0	6.1	11.0
Flakes	0.2 ± 0.7	0.0	8.0	1.6	0.0 ± 0.0	0.0	0.1	0.6
Spherules	3.1 ± 36.9	0.0	615.1	28.4	0.0 ± 0.0	0.0	0.6	0.4
Others	6.7 ± 12.2	0.0	150.8	61.5	2.0 ± 2.4	0.0	24.0	88.1
Total	10.9 ± 43.6	0.0	697.5		2.2 ± 3.0	0.0	30.2	

Pre-production plastics have been found to increasingly contribute to the plastic debris problem in marine habitats (Barnes et al., 2009). Our results identify the Danube as a transport route for plastic raw material and suggest that environmental pollution by this category is a crucial factor in river systems as well. Considerable inter and intra-annual differences in drift densities may be attributed to the pulsed, accidental release of the material during processing, packaging and transport (Moore, 2008). There are dozens of plastic production sites and an unknown number of processing companies in Germany and Austria. Some of them are situated adjacent to the Danube ([http:// www.plasticseurope.org](http://www.plasticseurope.org)). Furthermore, inland navigation is a popular transport mode and cargo ships frequently cruise the Danube (on average 1000 per month at the sampling sites; Kucera-Hirzinger et al., 2008).

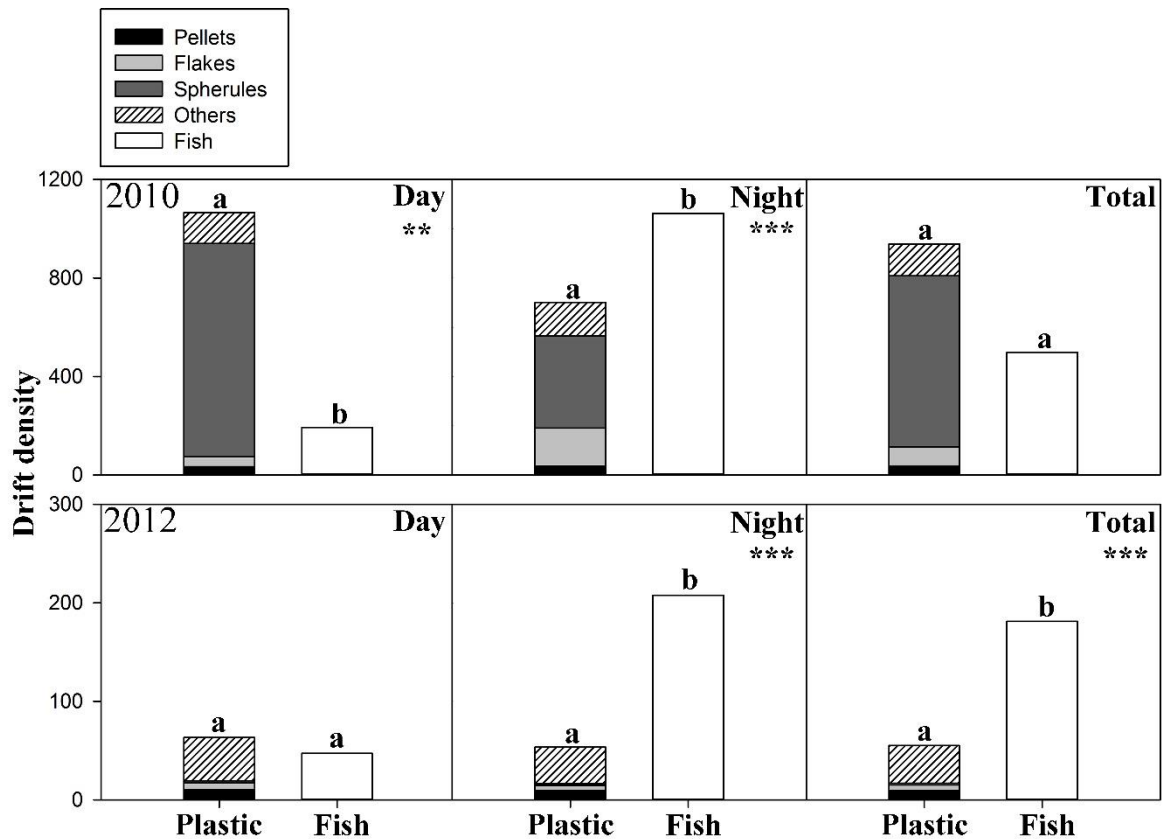


Figure 2. Mean drift densities of plastic and larval fish at daytime (left), during night (mid) and in total (right) are shown for 2010 (upper series) and 2012 (lower series). Asterisks indicate high significant (**; $p < 0.01$) and highly significant (***, $p < 0.001$) differences.

In both years of observation, more plastic items than fish larvae were drifting in the Danube at daytime (Fig. 2). However, differences in plastic versus ichthyoplankton were statistically significant only in 2010 ($n=182$, $Z=-3.22$). Increasing larval densities after dusk exceeded those of plastic in 2010 ($n=99$, $Z=4.59$) and 2012 ($n=559$, $Z=13.94$). Overall, the Danube transported more plastic in 2010 and more ichthyoplankton in 2012 ($n=669$, $Z=13.19$). Pooling all samples, mean larval densities in the Danube were 275.3 ± 745.0 individuals per 1000 m^3 and hence lower than mean plastic densities. In addition, average biomass of drifting larval fish was lower than plastic mass in both years (Table 2). The fish to plastic ratios indicate a high availability of harmful, unsuitable food items to potential consumers.

Table 2. Mean plastic mass and mean biomass of larval fish are given in grams per 1000 m^3 of filtered water.

	2010	2012	Total
Fish	5.8 ± 14.8	2.1 ± 3.2	3.2 ± 8.6
Plastic	10.9 ± 43.6	2.2 ± 3.0	4.8 ± 24.2

The input of plastic litter in the Black Sea via the Danube is estimated to average about 7.5 grams per 1000 m³ s⁻¹ at mean flow (6444 m³ s⁻¹). This yields a total entry at the mouth of 48.2 g per second (Fig. 3), 173.6 kg per hour, 4.2 t per day and 1533 t per year. This is more than the estimated total amount of plastic in the North Atlantic Gyre (1100 t; Law et al., 2010). For several reasons, our values must be regarded as an underestimation of the total plastic load into the Black Sea:

- 1) The amount of filtered microplastics is negatively correlated with the mesh size. Norén et al. (2007) found the abundance of small plastic fibres in a 80 µm net to be five orders of magnitude higher than in a 450 µm net. Therefore we suppose microscopic fragments (<500 µm) to be underrepresented in our samples.
- 2) The same holds true for large floating items (> 5 cm), which did not enter driftnets through the small gap between net-frame and water surface. But especially large material contributes to the plastic mass in oceans (Lattin et al., 2004).
- 3) Compared to Germany and Austria, all other neighbouring countries of the Danube feature lower standards in their wastewater and sewerage treatment ([http:// www.icpdr.org](http://www.icpdr.org)). Their potentially higher contributions to the Danube's plastic load should considerably cumulate and increase the average input at the mouth.

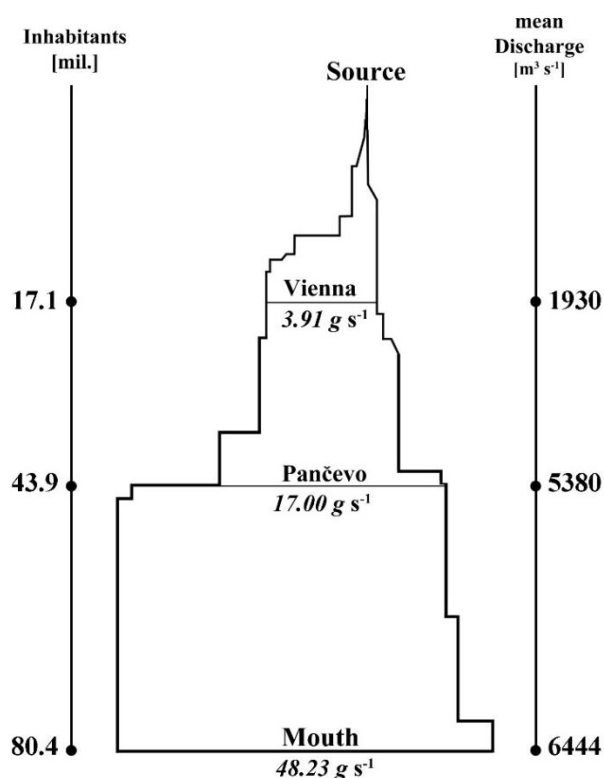


Figure 3. Average plastic load (g s⁻¹) of the River Danube at mean flow. Redrawn after Liepolt (1967).

Plastic is the dominant debris in the Black Sea with a high percentage of items (47%) sourcing in neighbouring countries (among them several of the Danube basin), potentially introduced by river currents (Topçu et al. 2013). There is rare information about land based litter sources and the “Development and improvement of the existing monitoring system to provide comparable data sets for pollutant loads (from direct discharges and river inputs)” is a high priority task of the “Black Sea Strategic Action Plan” (BSC, 2009).

Giving first answers on abundance and composition of plastic litter in the river Danube we hope to serve the cause and help to strengthen the enforcement of national and international regulations on land-based pollution sources (i.e. Operation Clean Sweep®, <http://www.opcleansweep.org>) Furthermore, our results shall give impetus to continuative studies on freshwater plastic pollution. All harmful consequences of plastic contamination described in marine systems (ranging from ingestion of plastic particles by a wide range of organisms to introduction of alien species which raft plastic litter) may operate in rivers and lakes and deserve closer attention.

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4. Concluding Discussion

This doctoral thesis covers previously under-investigated aspects of fish drift in rivers. The presented series of publications includes a critical analysis of the existing work in the field, features drift experiments with a model species (*Chondrostoma nasus*) in a large European River (Austrian Danube) and sheds light on a potential source of danger for (drifting) fish larvae. In the following, the main findings of the thesis are discussed chapter by chapter (except Chapter 1, which is a detailed introduction).

The drift mode (active vs. passive) and its controlling factors

The following quotations are taken from scientific publications on larval fish drift: “*many become swept up by the current and are transported **passively** downstream*” (Armstrong & Brown, 1983); “*the **passive** migrations, when fishes drift by a current without orientation to it, are most common*” (Pavlov, 1994); “*it is likely they were **passively** drifting downriver*” (Gadomski & Barfoot, 1998); “*drift was **passive** and depended on stream velocity*” (Corbett & Powles, 1986); “*many of the larval fishes are **actively** capable of entering and escaping the surface drift currents*” (Carter et al., 1986); “*the intensive downstream migration may be **active** rather than passive*” (Penaz et al., 1992); “*larval dispersal has a strong **active** component*” (Schludermann et al., 2012); “*larvae **actively** drift, probably to minimize mortality and maximize successful dispersal*” (Lechner et al., 2014c).

In drift research, the mode of transport is a controversial and a highly speculative issue. Definitive statements on the drift mode (active or passive) are usually made, although study design and sampling methodology do not allow for such conclusions in most cases (but see Lechner et al., 2016a).

Lechner et al., 2016b is the first study to directly compare (in-situ) larval fish drift with passive diffusion. The differing spatial dispersal patterns of small nase and floating plastic particles, simultaneously introduced into the Danube main-channel, revealed fish activity. Even if they had been released during high channel flow, at an early developmental stage or in over-critical currents, nase larvae were anything but passive drifters. The transferability of these results to other species remains open. Drift activity may be an adaptation to variable flow conditions and therefore most pronounced in typical riverine/rheophilic species. Nonetheless, knowledge about the drift mode of a particular species is a first important step towards successful conservation and river management. For example, in combination with a detailed analysis of the abiotic predictors of larval drift activity/behavior (Lechner et al., 2014c), well-founded predictions of drift densities in the river cross-section are possible. On the one hand, this would refine drift-based population estimates. On the other hand, it would support the strategic planning (e.g. location) of anthropogenic river structures (e.g. water abstraction systems,

hydropower plants) in order to minimize the impact on drifting fish (Koehn & Harrington, 2005; Pavlov et al., 2008; Ellsworth et al., 2010a).

Anthropogenic impacts on the dispersal of riverine fish larvae

The survival of the early life-history stages is crucial for recruitment success and population persistence in riverine fish species (Chambers & Trippel, 1997). The specific needs of embryos, larvae and juveniles (i.e. habitat and food requirements) and their (size-dependent) vulnerability cause naturally high mortality rates during this period (Miller et al., 1988; Houde, 1989; Schiemer et al., 1991; Schiemer et al., 2001). Above all, these stages are sensitive to any changes in flow regime (Mion et al., 1998; Humphries, 2002). Accordingly, the extensive man-made hydraulic alterations of river systems (Rosenberg et al., 2000) may impact young fish the hardest. Especially during drift events, which are per se dangerous, deviations from the natural flow conditions can prove disastrous for dispersing pre-recruits.

A short review on the negative effects of anthropogenic impacts on young fish drift is provided below, including a tabulated analysis of the literature (Tables 1, 2). This will, inter alia, highlight the unique contribution of our work to the topic.

A complex problem for drifting fish is the construction of weirs, dams and impoundments. The associated length-reduction of free-flowing river stretches is a serious hazard for species with propagules, which require a specific drift duration to develop before settling in suitable nurseries (Dudley & Platania, 2007). A premature drift stop of under-developed individuals in unsuitable reservoir areas may cause high mortality rates and serve as a bottleneck for recruitment (Kynard et al., 2007; Braaten et al., 2008; Jiang et al., 2010). Furthermore, fluctuating flow regimes and reduced water temperatures (hypolimnetic releases) downstream of dams can disturb natural dispersal signals (Ellsworth et al., 2010b) and cause adverse variations in drift distance/duration (March et al., 2003; Braaten et al., 2012; Usvyatsov et al., 2013). Passing dams and weirs, especially those with integrated turbines for hydropower generation, can also harm (stress, physically damage, kill) drifting fish (Baumgartner et al., 2006; Bracken & Lucas, 2013). Another threat to downstream-moving embryos and larvae is the abstraction of river water: entrainment into cooling systems and irrigation channels is a potential source of high mortality (Koehn & Nicol, 1998; Carter & Reader, 2000; Koehn & Harrington, 2005; Ellsworth et al., 2010a). Finally, river channelization and the disconnection of floodplains impede localized settlement and dispersal into food-rich habitats (de Graaf et al., 1999; Peirson et al., 2008; Braaten et al., 2012).

Table 1. Impacts of different man-made structures on the downstream dispersal of early fish developmental stages in rivers. Glossary: Species under investigation (SUI); Developmental stages under investigation (DUI) were adults (AD), ammocetes (AM), eggs (EG), free embryos (FE), juveniles (JU), larvae (LA), transformers (TR) and young of the year (YOY). “Not specified” (n.s.) marks a lack of relevant information in the reference. Species names were adopted from the reviewed papers and have not been adjusted to possible taxonomic shifts.

Nr.	Reference	River	SUI	DUI	Anthropogenic impact	Ecological consequences	Bottlenecks for drifting fish	Consequences for drifting fish	Suggested measures
1	Koehn & Nicol, 1998	Murray, Ovens	<i>Maccullochella peelii peelii</i> , <i>Macquaria ambigua</i> , <i>Maccullochella macquariensis</i>	LA	Water abstraction system	Abstraction of river water	Entrainment by irrigation channel	Stranding. Death. Population losses	n.s.
2	Robinson et al., 1998	Little Colorado	<i>Gila cypha</i> , <i>Rhinichthys osculus</i> , <i>Catostomus discobolus</i> , <i>Catostomus latipinnis</i>	LA	Dam construction	Flow alteration. Reduction of warm ponded areas at tributary mouths	Unstable nursery habitats. Cold (hypolimnetic) water releases. Transport in cold main stream	Wash-outs. Thermal shock. Aggravated drift exit	Warming of dam discharge. Diminishing daily flow fluctuations
3	de Graaf et al., 1999	Lohajang	<i>Catla catla</i> , <i>Labeo rohita</i> , <i>Cirrhinus mrigala</i> , <i>Hilsa</i> spp. et al.	LA	Flood control. Levee construction	Disconnection of river and floodplains	Inaccessibility of nursery habitats	Recruitment failure	Maximizing larval influx in floodplains by overshot-type water control structures
4	Carter & Reader, 2000	Trent	<i>Abramis brama</i> , <i>Alburnus alburnus</i> , <i>Rutilus rutilus</i> et al.	YOY	Power station	Abstraction of river water	Entrainment by power station intake	Death	n.s.
5	Humphries et al., 2002	Broken, Campaspe	<i>Maccullochella peelii peelii</i> , <i>Philypnodon grandiceps</i> et al.	LA	Impoundments. Weir construction	Flow alteration (irrigation releases)	High flow velocities	Wash-outs	Reducing irrigation flow levels
6	March et al., 2003	n.s.	n.s.	LA	Dam construction. Water abstraction system	Flow alteration. Disruption of migratory routes	Increased drift duration	Starvation	Halting water abstraction during drift peaks. Alternative withdrawal systems
7	Koehn & Harrington, 2005	Murray, Ovens	<i>Maccullochella peelii peelii</i> et al.	LA, YOY	Impoundments. Water abstraction system. Hydropower plant	Flow alteration. Abstraction of river water	High flow velocities. Turbine and pump entrainment	Aggravated drift exit and settlement. Stranding. Population losses	Increasing the knowledge on spatial and temporal drift patterns. Screens
8	Baumgartner et al., 2006	Artificial channel	<i>Maccullochella peelii peelii</i> , <i>Macquaria ambigua</i>	LA	Weir construction	Alteration of hydraulic conditions	Increased flow velocities, shear stress and turbulence. Pressure changes	Stress. Death	Restrict the operation of undershot gated weirs
9	Dudley & Platania, 2007	Rio Grande, Pecos	Pelagophils	n.s.	Dam construction	River fragmentation and narrowing. Flow alteration	Increased transport (drift) velocities	Drift exit in unsuitable habitats. Recruitment failure	Physical habitat restoration. Restoring connectivity. Dam modification or removal
10	Kynard et al., 2007	Missouri	<i>Scaphirhynchus albus</i>	FE	Dam construction	River fragmentation	Reduction of free-flowing habitats	Drift exit in unsuitable (reservoir) habitats. Recruitment failure	n.s.

Tabelle 2. Impacts of different man-made structures on the downstream dispersal of early fish developmental stages in rivers. Glossary: Species under investigation (SUI); Developmental stages under investigation (DUI) were adults (AD), ammocetes (AM), eggs (EG), free embryos (FE), juveniles (JU), larvae (LA), transformers (TR) and young of the year (YOY). "Not specified" (n.s.) marks a lack of relevant information in the reference. Species names were adopted from the reviewed papers and have not been adjusted to possible taxonomic shifts.

Nr.	Reference	River	SUI	DUI	Anthropogenic impact	Ecological consequences	Bottlenecks for drifting fish	Consequences for drifting fish	Suggested measures
11	Braaten et al., 2008	Missouri	<i>Scaphirhynchus platyrhynchus</i> , <i>Scaphirhynchus albus</i>	LA	Dam construction	River fragmentation. Flow and temperature alteration	Reduction of free-flowing habitats	Drift exit in unsuitable (reservoir) habitats. Recruitment failure	Habitat enhancements. Length extension of free flowing reaches
12	Pavlov et al., 2008	Volga	<i>Perca fluviatilis</i> , <i>Sander lucioperca</i> , <i>Gymnocephalus cernua</i> et al.	LA, JU	Water abstraction system	n.s.	n.s.	n.s.	Increasing the knowledge on spatial and temporal drift patterns
13	Peirson et al., 2008	Yorkshire Ouse, Severn, Trent	<i>Leuciscus leuciscus</i> , <i>Rutilus rutilus</i> , <i>Leuciscus cephalus</i> et al.	AD, YOY	Channelisation. Weir and levee construction	Missing of a dynamic connectivity/exchange between river and floodplains	Impassable man-made structures that prevent fish from entering (rising flood) or leaving floodplains (subsiding flood)	Downstream displacement (rising flood) or stranding in isolated floodplain areas (subsiding flood)	Floodplain rehabilitation
14	Ellsworth et al., 2010a	Sprague, Williamson	<i>Deltistes luxatus</i> , <i>Chamistes brevirostris</i>	LA	Water abstraction system	Abstraction of river water	Entrainment by pump station	n.s.	Spatial and temporal separation of water withdrawal and high drift activity
15	Ellsworth et al., 2010b	Provo	<i>Chasmistes liorus</i>	LA	Channelisation. Dam construction	Loss of habitat complexity. Flow alteration	Insufficient transport flows to reach adequate nursery habitats	Stranding and starvation in cold, unproductive river segments	Habitat restoration. Flow control
16	Jiang et al., 2010	Yangtze	<i>Ctenopharyngodon idella</i> , <i>Mylopharyngodon piceus</i> , <i>Hypophthalmichthys molitrix</i> , <i>Aristichthys nobilis</i>	EG	Dam construction	Dislocation of spawning grounds	Insufficient drifting distance between new spanning grounds and dam reservoir	Drift exit in unsuitable habitats. Recruitment failure	n.s.
17	Braaten et al., 2012	Missouri	<i>Scaphirhynchus albus</i>	FE	Dam construction	Suppression of high flows and water temperature. Channel degradation and fragmentation	Insufficient length of free flowing river stretches between hatch and settling sites	Drift exit in unsuitable habitats. Recruitment failure	n. s.
18	Bracken & Lucas, 2013	Derwent	<i>Lampetra fluviatilis</i> , <i>Lampetra planeri</i>	AM, TR	Hydropower plant	Creation of potential risky passages along natural migration routes	Turbine entrainment	Injuries. Swimming impairment	Synchronization of turbine activity with low drift activity (day)
19	Usvyatsov et al., 2013	Saint John	<i>Acipenser brevirostrum</i>	LA	Dam construction	Flow alteration	Delayed drift entrance. Prolonged drift duration or reduced drift distance	Starvation. Increased predation risk. Drift exit in unsuitable habitats	Flow control according to larval requirements
20	Lechner et al., 2014	Danube	<i>Chondrostoma nasus</i>	LA	Shoreline stabilization (rip-rap, groynes)	Increased current velocities, water depths and turbulent flows	Reduced shoreline accessibility, habitat-connectivity and retention potential	Aggravated drift exit. Wash-outs	Bank renaturation. Groyne modification

Lechner et al., 2014a is the first publication to address the impact of shore embankments on the spatio-temporal drift and settlement patterns of young fish. Groynes and rip-raps improve the conditions for navigation and serve in flood control and bank protection (Reckendorfer et al., 2005; Alauddin & Tsujimoto, 2012). But, according to our findings, they also impinge on the dispersal dynamics of larval fish. By altering the hydraulic conditions along drift routes and reducing the area of suitable inshore habitats, traditional groynes in the Danube River have aggravated the drift exit and sustained settlement of nase larvae. The ultimate effects of the resulting higher wash-out rates remain unclear. It is, however, very probable that the dislocation from nurseries and an increased exposure to main channel conditions (e.g. over-critical currents, high risk of predation) are detrimental to the individual's and the population's health. Downstream dispersal via drift is a common feature in the early life of many riverine fishes (Lechner et al., 2016), and rip-raps and groynes are ubiquitous in large navigated rivers (Shields, 1995; Nienhuis & Leuven, 2001; Ten Brinke et al., 2004). We therefore assume a wide and general validity of our findings. Importantly, our study also demonstrates solutions: bank restoration and specific groyne modifications favor natural dispersal processes. These results must be considered in future regulation/renaturation actions.

Beside altered river morphology, a hitherto ignored human impact on river systems endangers the dispersing ichthyofauna.

Microplastics in rivers: a potential threat for drifting fish

Microplastic particles (i.e. *flakes, fibers, filaments, fragments, pellets and spherules* smaller than 5 mm; Arthur et al., 2009) in aquatic environments pose a many-faceted risk for wildlife, including fish (Cole et al., 2011; Gall and Thompson, 2015). Several studies on plastic ingestion by fish found that a variable percentage of the sampled individuals had microplastics in their digestive system (0.3 %: Cannon et al., 2016; 9.2%: Davison and Asch, 2011; 11%: Lusher et al., 2015; 17-33%: Possatto et al., 2011; 35%: Boerger et al., 2010; 36.5 %: Lusher et al., 2013; 57.8%: Nadal et al., 2016). High ingestion rates are documented especially for larval and juvenile stages (see review by Hoss and Settle, 1990). The assumption is that fish mistake small plastic particles for prey, placing those individuals whose (spatial and temporal) distributions overlap with the distribution of microplastics at a high risk of ingestion (Lusher et al., 2015). The impacts of plastic consumption remain largely speculative but probably comprise the blockage of the digestive tract, reduction of the feeding drive, transport of chemical toxicants to the organism, internal injuries and death (Wright et al., 2013).

So far, studies on plastic pollution and the associated threats to fish almost exclusively stem from marine habitats (Eerkes-Medrano et al., 2015).

Lechner et al., 2014b is the first publication to highlight plastic contamination in a large river. We found that the mass and abundance of drifting plastic items in the Austrian Danube are higher than those of drifting larval fish. Most of the detected plastic (*spherules*) was smaller than 3 mm, therefore consumable for larvae (Mark et al., 1987). Moreover, they showed a visual similarity to fish eggs (a high-quality source of protein, Cahu and Infante, 2000; Fig.2, A). The coexistence of larvae and high densities of their alleged prey in the drift suggests plastic ingestion, which has been confirmed (Fig. 2, B).

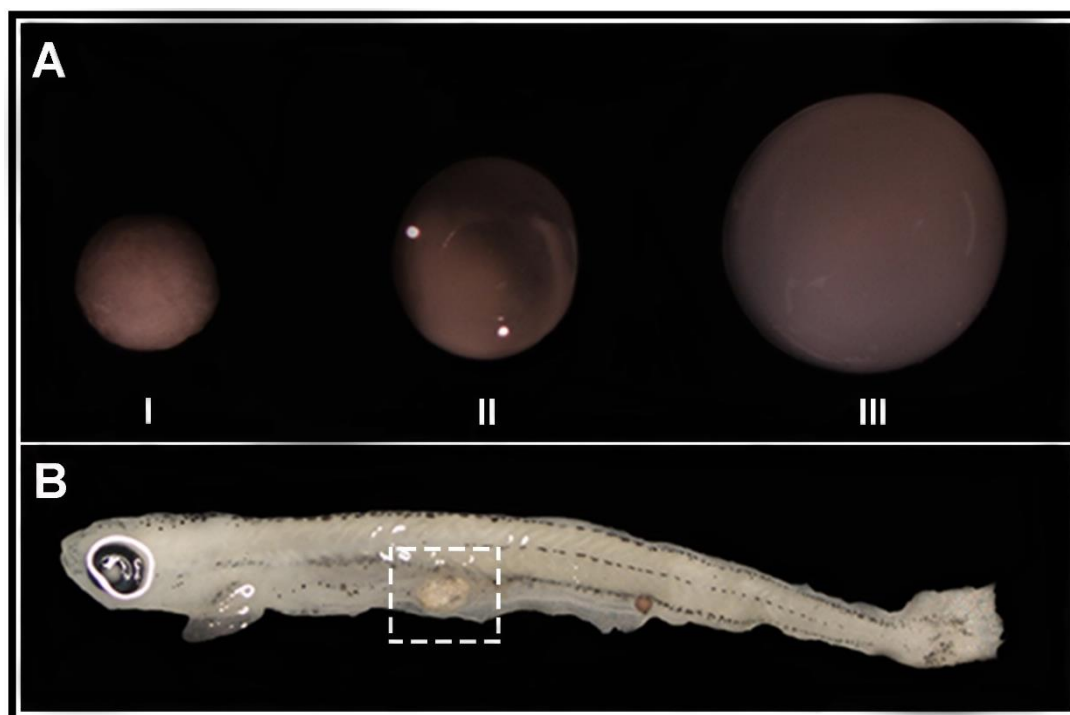


Figure 2. Where is the egg? The upper picture (A) shows a non-fertilized egg (diameter: 1.9 mm) of *Chondrostoma nasus* (II) between two microplastic particles (I, III), captured with drift nets in the Danube River. The lower photograph (B) shows a small nase (total length: 12.7 mm), in the second larval stage, with an ingested plastic item.

Our results were broadly incorporated in subsequent studies on plastic pollution (see Rech et al., 2014; Aytan et al., 2016). They, inter alia, made an important contribution in assessing the global contamination of freshwater habitats (Wagner et al., 2014; Dris et al., 2015) and estimating river-based plastic inputs into the oceans (Jambeck et al., 2015). Above all, our findings have placed a focus on the sources of riverine plastic litter. Industrial precursors, the raw material of plastic production, were the most common plastic-litter-category in the Austrian Danube. Borealis, a global player in the plastic industry, turned out to release considerable amounts of microplastics into the river. This introduction is permitted by the legislation because “the Austrian Ordinance on Waste-Water Emission classifies plastic as a filterable substance. Correspondingly, the upper limit of plastic discharge into running waters is specified as 30 mg/l.” (Lechner & Ramler, 2015).

5. References (of *General Introduction* and *Concluding Discussion*)

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6. Zusammenfassung

Die Ausbreitung früher Fisch-Entwicklungsstadien (Embryos, Larven, Juvenile) via Drift ist ein wesentlicher Prozess, der unter anderem die Basis einer gesunden Populationsentwicklung bildet und als Anpassung an die (räumlich und zeitlich) fluktuierende Ressourcenverfügbarkeit in Fließgewässern interpretiert werden kann. Die vorliegende Doktorarbeit bietet einen generellen Überblick über die Driftforschung der letzten 40 Jahre und widmet sich speziellen noch weitgehend unerforschten Teilaspekten. Im Zuge einer zweijährigen (2011, 2012) Freilandstudie an der österreichischen Donau (östlich von Wien, Stromkilometer 1899.0-1893.8) wurden am Beispiel einer typischen Fließgewässerart (*Chondrostoma nasus*) der Driftmodus und die Auswirkungen anthropogener Uferverbauungen auf die räumlich-zeitliche Driftdynamik untersucht. Im Fokus dieser Studie stand die Beobachtung der Ausbreitung markierter Nasenlarven (ca. 100.000 Individuen, frühe und späte Entwicklungsstadien) von potentiellen Laichplätzen bei unterschiedlichen Durchflüssen (niedrig, hoch), Strömungsverhältnissen (langsam, schnell) und Ufersituationen (verbaut, unverbaut). Unsere Ergebnisse zeigen, dass, entgegen der üblichen Annahme einer primär passiven Ausbreitung, die Drift junger Nasen ein viel komplexerer Prozess ist, der Interaktionen zwischen Individuum und Umwelt auf unterschiedlichen Ebenen integriert. Die Aktivität der driftenden Larven konnte durch einen direkten Vergleich ihrer räumlichen Ausbreitungsmuster mit jenen von passiven Partikeln (Polyethylen Pellets) demonstriert werden. Dieses aktive Driftverhalten war auch bei sehr frühen Entwicklungsstadien (zweites Larvenstadium) und bei Individuen, die sich in überkritischen Strömungsbereichen aufhielten, deutlich ausgeprägt. Der vorherrschende Durchfluss wirkte sich signifikant auf den Driftmodus der Larven aus: eine geringere Wasserführung der Donau, und die damit korrespondierenden „mildereren“ hydraulischen Bedingungen, gingen mit einem vermehrten Drifteintritt und einer höheren Driftaktivität einher. Eine natürliche Ausbreitung der Fischlarven im Untersuchungsgebiet wurde durch künstliche Strukturen zur Uferbefestigung (Blockwurf) und Verbesserung der Schiffbarkeit (Buhnen) gestört. Im Vergleich zum revitalisierten linken Schotterufer wies der verbaute rechte Uferbereich drift-relevante morphologische Defizite auf. Ein geringeres Retentionspotential, eine geringere Konnektivität zwischen Habitaten und eine schlechtere Zugänglichkeit für driftende Fischlarven können sich negativ auf unterschiedliche Phasen der Ausbreitung (Drifteintritt-Drift-Driftaustritt) auswirken. Weitere negative Effekte für die Ichthyofauna können sich durch winzige Plastikpartikel ergeben, welche in großer Menge in der Donau-Drift nachgewiesen wurden. Wie unsere Ergebnisse zeigen konnten, erhöht die optische Ähnlichkeit dieses Mikroplastiks mit Fischeiern, einer bevorzugten Nahrungsquelle, die Gefahr einer versehentlichen Aufnahme, auch durch frühe Entwicklungsstadien.

7. Abstract

This cumulative dissertation deals with what is known as the first migration in a (riverine) fish's life: the current-mediated downstream movements (drift) from spawning sites to potential nursery habitats. We performed a two-year (2011, 2012) mark-recapture experiment with the larvae of a fluvial specialist (*Chondrostoma nasus*) in the Austrian Danube east of Vienna. The goal was to investigate (1) the mode of downstream drift (active vs. passive) and (2) the impact of man-made river alterations on the spatio-temporal drift dynamics.

To examine the drift mode, we observed the simultaneous spatial dispersal of different developmental stages (early and later larvae) and floating passive particles (polyethylene pellets) at different flows (low-flow, high-flow) and current conditions (under-critical, over-critical). We determined that nase drift includes a strong active component which is based on the physical (swimming capacity) and behavioral (orientation) capabilities of fish. Even early larvae, with weak swimming skills, that were released in over-critical currents were not exclusively passive drifters. The river flow caused inter-annual differences in drift activity. During low flow in 2011, nase larvae seemed to deliberately enter the drift and seize the milder hydraulic conditions for active and oriented dispersal. At the higher flow conditions in 2012, fewer larvae drifted and those that did were transported more passively. Knowledge on drift activity and the resulting spatial drift patterns can be crucial for exact estimates of drift distance and population size as well as for species conservation issues.

In order to examine the impacts of river regulation, we observed the dispersal of early and later larvae and passive particles along two dissimilar shoreline configurations: (1) a revitalized, near-natural gravel bank with modified ("green") groynes and (2) a rip-rap with conventional groynes and groyne-fields. We found that the morphological and hydraulic conditions along the rip-rap disrupt natural dispersal processes. A low shoreline accessibility (i.e. bank characteristics that facilitate drift exit and settlement), a bad retention potential (i.e. the bank's capability of accommodating high larval population densities) and insufficient habitat connectivity (i.e. the connection of adjacent larval habitats) at the rip-rap induce wash-outs, extended drifting periods and ultimately high mortality rates and population losses.

In order to examine larval dispersal, we used fine-mesh stationary drift nets. Beside larvae, those nets captured enormous amounts of small plastic particles. Such microplastics pose a threat to aquatic organisms. As shown in marine habitats, small fish may mistake these small particles for prey and ingest them. Among the possible adverse consequences are blockage of the digestive system, internal injuries and death. Our results indicate that (drifting) small fish in the Danube face the same risk.

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