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Dispersal and retention of larval fish in a potential nursery habitat of a large temperate river: an experimental study

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Abstract (199 words)

Little information is available on what governs dispersal of fish larvae in natural river systems. Therefore, we aimed to describe dispersal and retention of marked larval nase carp, released at offshore and inshore stations in a known spawning area, along a shoreline nursery habitat of the River Danube. Based on a 3D-hydrodynamic model, we analysed the influence of the hydraulic conditions of the two releasing stations on larval dispersal. We also related observed larval pathways to numerical particle tracing. Drift densities immediately after release were high but declined rapidly within 48 hours, with a recapture rate of 7.6%. Clear differences in the temporal drift pattern were due to significant differences in the hydrodynamic characteristics of the release stations. Some larvae remained in the study reach; most upstream of the release point. These were significantly larger than drifting larvae. We conclude that larval dispersal has an active component and that dispersal and retention patterns are dependent on the habitat structure and hydrodynamic characteristics of the releasing points. This emphasizes the importance of links between the location of spawning sites within the river and variation in flow during early development, the combination of which may contribute to successful recruitment of fluvial fish species.

Keywords: nase carp; River Danube; hydrodynamic model; passive particle paths / particle tracing; active movements

Introduction

Dispersal during early life history is a process fundamental to the population dynamics of aquatic organisms. In fishes it occurs predominantly during the embryonic and larval periods (Brown and Armstrong 1985, Pavlov 1994), and enables expansion of population ranges and ensures mixing of genes (Fuiman 2002, Fuiman and Cowan 2003, Pavlov 1994). In riverine fishes, the mechanisms that govern dispersal - through downstream transport - and retention are considered critical to survival, growth, and the sustainability of populations (Houde 2002). The link between dispersal and population sustainability occurs at the scale of the individual and operates either directly, because of loss through drift, or indirectly, because of reduced growth and entrainment in suboptimal conditions.

Dispersal of the young stages of riverine fish is triggered by abiotic and biotic factors. Abiotic factors include: floods (Arthington et al. 2003, Pavlov 1994), low flows (Humphries 2005, Humphries et al. 1999, Humphries et al. 2002), small-moderate rises in discharge and related increases in turbidity (Daufresne et al. 2005, Korman et al. 2004, Reichard and Jurajda 2004), within-reach variation in current velocity (Pavlov 1994, Reichard et al. 2004), light intensity and oxygen and temperature conditions (Reichard et al. 2002a, Rosenfeld et al. 2001, Sonny et al. 2006). Biotic factors include: physiology (Pavlov 1994, Reichard and Jurajda 2007, Reichard et al. 2004), developmental stage and the concomitant changes in swimming ability (Pavlov 1994, Reichard et al. 2004, Sonny et al. 2006), individual habitat preference (Heggenes and Dokk 2001, Pavlov 1994, Reichard et al. 2004), ontogenetic and seasonal shifts in resource use (Childs et al. 1998, Freeman and Grossman 1993, Gaudin 2001), and the presence of predators (Gaudin 2001, Harvey 1991, Pepin et al. 2003).

Most published studies on larval fish dispersal have focussed on downstream movement and related environmental variables (Korman et al. 2004, Reichard and Jurajda 2004, Zitek et al. 2004). Despite recent advances in our understanding of longitudinal

dispersal of larvae in rivers, specifically because of the use of 1-D dispersion models (Wolter and Sukhodolov 2008), 2-D hydrodynamic models (Ellien et al. 2004, James et al. 2002, Speirs and Gurney 2001) and sophisticated particle tracing approaches to simulate larval movements (Korman et al. 2004), the detailed patterns of larval dispersal and what drives these are not well understood (Reichard and Jurajda 2007, Reichard et al. 2004, Sonny et al. 2006). This is largely due to the lack of detailed information on the number and location of spawning areas, the poor knowledge of whether dispersal is active by swimming or passive by dislodgement, the position and orientation of larvae in the water column and the relationship among development, swimming ability and swimming behaviour of different species (Reichard and Jurajda 2007, Reichard et al. 2004, Sonny et al. 2006).

The question as to whether riverine fish larvae disperse actively or passively remains largely unresolved. Pavlov (1994) argued that larval drift included an active component, as all fish larvae show rheotaxis (Jurajda 1998, Reichard and Jurajda 2007, Robinson et al. 1998). Once threshold current velocities are reached, however, this rheotaxis is not possible and larvae are transported passively downstream (Pavlov 1994). Robinson et al. (1998) hypothesized that if larvae dispersed entirely passively, they would tend to settle predominantly in inshore, low-velocity, depositional habitats and be clumped in distribution, whereas their study found larvae to be predominantly randomly distributed. Several studies, however, have observed clumped distributions of larval fish in rivers (e.g. Keckeis et al. 1997, Price 2010, Schludermann et al. (unpubl.)), so clearly, several models are possible.

In the present study, we investigated larval dispersal and retention patterns of marked nase carp, *Chondrostoma nasus* L., released from inshore and offshore stations in a spawning area of a large temperate river. Our main aim was to describe the timing of movement of experimentally released larvae and compare the path taken by these larvae with a passive particle model to determine whether larvae drift passively or actively. Specifically, we aimed to: a) describe the temporal patterns in drifting larvae; b) determine the pathway taken by

larvae when drifting; and c) determine where those larvae that did not drift out of the study site were retained and how they were distributed. For each aim, we compared larvae released inshore to those released offshore and related larval pathways to a numerical particle tracing method, using a random-walk approach. We also related hydraulic conditions at the release points and drift collection points to conditions in the study site as a whole, derived from a 3 D-hydrodynamic model. Finally, we relate our results to the management of fish in large regulated rivers.

Materials and methods

Study area

The study was conducted in a free-flowing section of the River Danube, East of Vienna (Fig. 1). The study area was located within the approx. 3 km-long test reach of the ‘Integrated River Engineering Project’ (IREP) in the main channel of the River Danube (River km 1921 to 1872.7), where an earlier monitoring programme was conducted (Habersack et al. 2008) that measured water surface elevations, using differential GPS positioning, current velocities and turbulence intensities, using Acoustic Doppler Velocimeter (ADV) and Acoustic Doppler Current Profiler (ADCP) techniques. Based on these data, a three-dimensional hydrodynamic model, using the numerical code RSim-3D (Tritthart and Gutknecht 2007), was established for the river reach to allow for up-scaling of all flow properties to the entire area (Habersack et al. 2008).

A clearly-defined gravel bar was selected in this study reach, as it represented natural spawning habitat for nase, and ripe adult and larval nase were found there in an earlier study (Keckeis et al. 1996, Keckeis et al. 2010) (Fig. 1). Situated at the downstream end of the gravel bar is the Jöhler side-arm; an anastomosing channel approx. 1500 m long, and 50-60 m wide, which is connected to the River Danube once the discharge reaches $2350 \text{ m}^3 \cdot \text{s}^{-1}$. In the

upstream reach of the study area, two hydraulically distinct stations – one inshore and one offshore - were chosen as release points (Fig. 1 and Fig. 2). The hydraulic conditions at these two stations, derived from the hydrodynamic model (see data analysis section), were compared using Student's t-tests based on all modelled discharges between 1930 and 3000 $\text{m}^3 \cdot \text{s}^{-1}$ (Table 1). The station located inshore was shallow, had low current velocities and shear stress, but had high turbulence. The offshore station was located approx. 15 m from the bank, and was deeper, had relatively high current velocities and shear stress, but low turbulence (Table 2).

Study species

The nase carp represents a typical, but endangered riverine fish species of the Austrian Danube and its tributaries. In the last two decades, it has become the focus of much research on the ecology and functional integrity of European river systems (e.g. Keckeis and Schiemer 2001). Nase carp perform spawning migrations in spring, while young nase inhabit tributaries and shallow inshore areas of large rivers. River engineering works have negatively affected nase reproductive success and recruitment, severely reducing the populations in many European rivers (Keckeis et al. 1996, Kirchhofer 1996, Lusk and Halačaka 1995).

Sampling design

Released nase larvae

The progeny of a natural spawning population of nase from a River Danube tributary were used as model organisms. The same sampling procedure for parental fish and the rearing of larval fish in the laboratory was used as described in detail in Bartl and Keckeis (2004). Briefly, rearing temperatures followed the pattern normally experienced in the fish's spawning environment, with an increase of 1°C ($\pm 0.3^\circ\text{C}$) per week, starting from 12.3°C . The increase was necessary to provide optimal conditions for early development and growth

(Kamler et al. 1998). Shortly before release, the water was cooled again to meet the conditions in the River Danube and to minimize mortality.

Approximately half of the 40,000 nase larvae were marked by a single emersion in Alizarin Red (ARS, Sigma) at day 7 after hatching (ph), and so had one ring evident on their otoliths; and the other half were marked by two emersions in ARS at day 7 and day 10 ph, and therefore had two rings on their otoliths. Larvae were released just above the river substratum at dusk (19:30) at day 10 ph (21 April 2008), at the two stations at the upstream end of the gravel bar, with the single-marked larvae released inshore and the double-marked larvae released offshore (Fig. 2). Nase were at larval stage 1 (after Peñáz (1974)) and the mean \pm 1SD total length was 11.8 ± 0.5 mm. These larvae have mixed endogenous and exogenous feeding, their swim bladders are fully functional, and they swim in the water column using an anguilliform swimming mode. Their maximum sustainable current velocity at this stage is approx. $0.1 \text{ m}\cdot\text{s}^{-1}$ (Flore et al. 2000).

Field sampling

Sampling began immediately on release of larvae: short-term drift netting for dispersing larvae and point abundance sampling (PAS) for larvae that did not disperse from the study site (Fig. 2). We assumed that larvae caught in drift nets were drifting, because the current velocities at the drift net sites were greater than nase larvae are able to swim against (Flore et al. 2000). PAS collected 'retained' nase, since if larvae had remained in the current, they would have drifted out of the study site within about six minutes (See Results section).

To follow drift paths of larvae immediately after release (study 1), drift nets (0.5 m diameter, 1.5 m long, 500 μm mesh) were deployed in pairs (one inshore and one offshore) at a distance of 50, 100 and 200 m from the release stations, covering the entire study reach (Fig. 2). From the time of release, drift nets were set for 30 min periods, retrieved, their contents preserved and nets replaced, for a total of 2 h. To investigate retention of larvae

within the study site (study 2), drift sampling was conducted in a randomised block design (with blocks being 40 m lengths of river) one day after release, three days after release and weekly thereafter for six weeks after release (Table 1). Since no drifting larvae were collected after day 2, no results are given beyond this time. The volume of water filtered was measured with a General Oceanics® flow meter placed in the lower third of each net.

Inshore retention of larvae in both studies 1 and 2 was investigated using PAS (Persat and Copp 1990) with a 40 cm diameter, 0.4 mm mesh dip-net, one day after release, three days after release and weekly thereafter for six weeks after release (Table 1). A figure-8 sweep pattern was carried out, covering an area of approx. 0.75 m² every 10 m, from 60 m upstream to 200 m downstream of the release stations (Fig. 4). All points were located within 2 m of the shore, as young-of-the-year (YOY) fish are generally associated with these microhabitats (Schiemer et al. 1991, Wintersberger 1996). At each sampling point, mean depth (m), mean current velocity (m•s⁻¹), shore slope (m•m⁻¹ classified as steep, medium, low) and water temperature (°C) were recorded. Means were calculated from three measurements within the sampled area. All sampling points (drift as well as PAS) were geo-referenced by Leica GS 20.

Fish were euthanized by an overdose of anaesthetic (MS-222) and then preserved in 90% ethanol immediately after collecting.

Laboratory processing

In the laboratory, total length and weight of nase larvae were measured. For each sample, a subsample of 10 larvae was used for subsequent otolith analysis. Lapilli were used to check for marks, as they are the only otoliths to show a concentric daily increment-formation in cyprinids and are deposited from the very beginning of otolith formation. Marks were checked under the emission wavelength of 510 to 560 nm using an epifluorescence/light microscope Nikon Eclipse® E800 with Optimas® 6.2, software for image analysis.

Data analysis

Hydrodynamic model

The topographic data used consists of combined sets of bathymetric measurements from hydrographic surveys and laser scans (conducted in 2006 and 2003/2005, respectively). The bathymetric measurements were repeated once a year until 2008; data comparison showed the physical structures of the study site (near-shore areas of the gravel bar) to be stable throughout that period. Based on current velocities and turbulence intensities measured using ADV and ADCP techniques (for detailed measuring setup see Habersack et al. 2008), a three-dimensional hydrodynamic model using the numerical code RSim-3D (Tritthart and Gutknecht 2007) was constructed and calibrated. The model solved the three-dimensional Reynolds-averaged Navier-Stokes equations by means of the Finite Volume Method on a computation mesh of arbitrarily-shaped polyhedra (Tritthart 2005). Turbulence was modelled by employing the standard two-equation turbulence closure model (Launder and Spalding 1974). Shear stress was derived on the basis of an empirical equation outlined in Versteeg and Malalasekera (2001). The flow velocity gradient was calculated numerically relative to the flow streamlines, i.e. the curves which are tangential to the velocity vector of the flow in any given point of the flow continuum. This was achieved by calculating velocity in a small perpendicular distance (0.1 m) to the left and right of the vectorial flow path, respectively; the gradient was calculated from the velocity difference divided by the point distance, using the definition that a positive gradient corresponds to an increase in velocity from left to right, in the direction of flow.

The 3D numerical model yielded water depths, current velocities and turbulent kinetic energy at six depth layers of a total of 35,000 calculation nodes within a 4 km long river reach, including the study site. These data are available for ten different discharges, from regulated low flow to highest navigable flow. In order to assess the validity of the computed

flow field in riparian zones, calculated and observed velocity profiles were compared. For the velocities observed, root mean square deviations (RMS) were calculated from the raw ADV data. Of the calculated velocities, 85% lay within the RMS range, which is considered an excellent fit, whilst another 15% showed absolute differences of less than $0.1 \text{ m}\cdot\text{s}^{-1}$ with respect to the mean measurement values, which is still considered a good fit (Tritthart et al. 2009).

Particle-tracing

A random-walk particle-tracing approach outlined by Tritthart et al. (2009) was employed. The approach is based on the assumption that particles without mass or other relevant properties - such as significant flow resistance - are passively advected with the flow, as deterministically described by the time-averaged vector flow field calculated by the hydrodynamic model. However, as turbulent fluctuations in the flow field inevitably disturb the particle path, a random component is present that must be modelled as well. The path of a virtual particle in the flow continuum is therefore governed by:

$$\begin{aligned}
 x(t + \Delta t) &= x(t) + \bar{u}(t)\Delta t + u'(t)\Delta t \\
 y(t + \Delta t) &= y(t) + \bar{v}(t)\Delta t + v'(t)\Delta t \\
 z(t + \Delta t) &= z(t) + \bar{w}(t)\Delta t + w'(t)\Delta t
 \end{aligned} \tag{1}$$

where \bar{u} , \bar{v} and \bar{w} are the mean velocities and u' , v' , w' the respective velocity fluctuations along Cartesian coordinates x , y and z (east, north and zenith in a global coordinate system); the particle's position is known at time level t and is calculated for time $t + \Delta t$, where Δt denotes the time step of the computation. The mean velocity components are provided by the hydrodynamic model, whilst the velocity fluctuations are derived from the square root of the turbulent kinetic energy, as provided by the numerical model (Tritthart et al. 2009),

$$\begin{aligned}
u'(t) &= 2 Z_1 \sqrt{k} \\
v'(t) &= 2 Z_2 \sqrt{k} \\
w'(t) &= 0
\end{aligned}
\tag{2}$$

where Z_1 and Z_2 are independent random components in the range of -1 to +1. In order to achieve consistency with the governing advection-diffusion equation, an additional advection term, denoted ‘noise-induced drift’, is included in the modelling framework, following the procedure outlined in Weitbrecht (2004).

The random-walk approach was used to visualize larval drift patterns in time. Drift data as well as PAS data were related to pathways of particle traits. For each experimental scenario, 50 particle traits released at in- and offshore stations (calculated with a time step of 0.05 s) were analysed. The inverse approach was taken for information about the upstream movement of fish larvae.

Larval drift

Drift data was standardised as numbers of individuals per 100 m³ water filtered and transformed after McCune and Grace (2002), as data were not normally distributed. Drift densities were described in relation to time interval after release and to the origin of released larvae: inshore or offshore.

The time-dependent density pattern of drifting larvae was described by a power function for all nets ($y=ax^b$, $a=8258.43$, $b=-1.290$, $F_{1,29}=88.85$, $r^2=0.75$, $P<0.001$). To remove the effect of time, residuals of this function were related to current velocity, velocity gradient, turbulence, and shear stress, which had been derived from modelled discharges closest to the observed ones (Table 1). Medians and interquartile ranges (IQR) of the hydraulic variables were used, since the above-mentioned abiotic variables showed non-normal distributions. Assuming that the nets did not interact longitudinally, the values of the hydraulic variables within semicircles with radius 5, 10 and 15 m from the opening of each net were calculated by

means of buffer analysis in ESRI ArcGIS[®]. The relationships between these hydraulic variables for the three radii and the residual drift densities were examined using regression analysis, and the radius with the highest relationship (10 m radius) was used in subsequent analyses. General linear models were constructed to determine the relationships between the time-independent drift densities (residuals) and hydraulic variables (velocity gradient, median flow velocity, median and interquartile range of shear stress, median and interquartile range of turbulence). The model that best explained the variation in drift densities, whilst reducing the level of complexity of the model, was determined by Akaike Information Criterion (AIC). Hierarchical partitioning of R^2 -values was used to determine the proportion of variance explained independently by each variable. This method allows identification of variables whose independent correlation with the dependent variable is strong.

The data was characterised for two different model discharges (mean discharge, $Q=1930 \text{ m}^3 \cdot \text{s}^{-1}$ and estival mean discharge, $Q=2230 \text{ m}^3 \cdot \text{s}^{-1}$) because releases and sampling of larvae were conducted within this range of discharge.

Point-abundance-sampling

Larval fish densities in inshore microhabitats were determined from 20 samples along the main channel, and from a further 10 samples of the side arm when it was flowing, on each sampling date, and are expressed as individuals per m^2 . After determination of the individual release origin using the otolith mark patterns, abundances of in- and offshore released larvae were determined for each sampling point and date. Distances between sampling points and source were calculated using GIS, and travel distance for each recaptured larva was determined. For each sampling date, median travel distances and 25th and 75th percentiles were calculated. The characteristics of microhabitats (depth, velocity and shore slope) with and without retained larvae were compared using a Man-Whitney U-test.

All data analyses were performed with ArcGIS 9[®] (ESRI, Redlands, CA), RSim-3D (Tritthart 2005), SPSS 16.0[®] (SPSS Inc., Chicago, IL), Sigma Plot 10.0[®] (SYSTAT Software Inc., Chicago, IL) and R[®].

Results

In total, of the 40,000 released nase larvae, 3,026 were recaptured with drift nets and 24 by PAS, representing an overall recapture rate of 7.56% (Table 1).

Larval drift: temporal and spatial components

Larval drift patterns were monitored over a 6-week period. However, the vast majority of recaptured larvae (3017 or 7.54% of released larvae) was found in the drift nets on the day of release, the remainder (9 or 0.02%) the day after and none after that (Table 1). Combining data from both release stations, an overall mean ($\pm 1SD$) of $135.8 \pm 152.6 \text{ Ind.} \cdot 100 \text{ m}^{-3}$ were collected in the inner nets, and $46.4 \pm 54.8 \text{ Ind.} \cdot 100 \text{ m}^{-3}$ were collected in the outer nets, but the difference was not statistically significant (Student t-test of transformed data, $t_{44}=1.94$, $P=0.06$). Ignoring distance from release stations, maximum drift densities were observed in the inner nets in the first 30 min, whereas maximum drift densities were observed in the outer nets 60 min after release, (ANOVA, $F_{16,65}=28.7$, $P<0.001$; Post-hoc test after Scheffé: two homogenous subsets at $P=0.05$).

With regard to the origin of released larvae, the densities of inshore-released larvae in all nets decreased steadily with time ($y=ae^{-bx}$; $a=464.30 \pm 46.49$, $b=0.037 \pm 0.003$; $r^2=0.99$, $P<0.001$), whereas those of offshore-released larvae were low initially, increased to a maximum between 30 and 60 min after release and then declined again ($y = ae^{-0.5(\frac{x-x_0}{b})^2}$; $a=93.86 \pm 2.92$, $b=16.53 \pm 0.59$, $x_0=62.32 \pm 1.04$; $r^2=0.99$, $P<0.05$) (Fig. 3).

The proportion of in- and offshore-released larvae in the drift samples varied with time and distance from release (Fig. 4). The proportion of inshore-released larvae was highest soon after release; most noticeably within 40-80 m downstream of release, where inshore-released larvae comprised up to 90% of the total catch. However, by the time larvae reached 120 m from release, inshore-released larvae comprised approx. 60% of all larvae. With time, densities of inshore larvae decreased throughout the study site and the proportion of in- and offshore-released larvae became similar (Fig. 4). On the day of, and the day after, release, inshore-released individuals formed the majority of larvae collected in the drift nets (63% and 76% of total catch, respectively).

Larval drift: hydro-morphological triggers

The offshore releasing station was significantly deeper, had higher current velocity and shear stress, but lower turbulence than the inshore station at the time of release of larvae (mean discharge of the Danube: $Q=1930 \text{ m}^3 \cdot \text{s}^{-1}$; Kruskal-Wallis test, $\chi^2_{1,50}=36.77$, $P<0.001$; Table 2). Larval drift densities were plotted against a contour map of modelled current velocity (Fig. 4), as velocity is often identified as a trigger for downstream dispersal (Pavlov 1994, Reichard et al. 2004). In general, current velocity showed a constant decline towards the shore. The values of the stations where larvae were released confirmed this (Table 2). According to the hydrodynamic model, sub-critical values (sensu Flore et al. 2000) were found along the shoreline, where PAS sampling was conducted (Fig. 4). However, all drift nets were deployed in areas with supra-critical current velocities. Observed larval drift densities were also higher in inshore nets.

Because larvae moved between offshore and inshore areas, data for both release stations were pooled for a detailed analysis of the hydro-morphological characteristics, and drift densities of both nets were related to the median and the IQR of the modelled hydraulic variables of the whole region between nets (50 m, 100 m, and 200 m) for Study 1.

Residuals of drift densities were significantly negatively related to medians of tested hydrodynamic variables in a radius of 10 m from the net (velocity gradient ($P=0.048$), turbulence ($P=0.023$) and shear stress ($P=0.024$), and were best described by significant polynomial functions; however, drift densities peaked at intermediate current velocities ($P=0.011$) (Fig. 5 a-d). Residuals of drift densities also showed significant negative relationships with the variation in hydrodynamic variables, expressed as IQR (turbulence ($P=0.003$) and shear stress ($P=0.006$)) (Fig. 5 e-f). Thus, drift densities were always greatest where the median or variance for all variables, except velocity, were lowest.

GLM analysis and stepwise AIC indicated that a model including median velocity, interquartile range of turbulence, median shear stress, interquartile range of shear stress and velocity gradient was significant ($F_{5,25}= 3.546$, $P=0.015$) and explained 29.8% of the variance in residual drift densities of released nase larvae (Table 3). Hierarchical partitioning analysis showed that velocity gradient contributed almost 25%, the interquartile range of shear stress approx. 22% and velocity approx. 18% to the overall model.

Larval drift: particle tracing – random walk

The random-walk describing passive displacement was used to represent larval drift patterns. Of the 50 particles in total that were released virtually at the larval release stations in the particle tracing experiment, none reached the shore (Fig 6a). The mean time particles took to pass the study site on the gravel bar was 6 min. Particle tracing paths were straight, with a uniform displacement pattern, passing along the shore. No mixing between inshore- and offshore-released particles was observed. When particles moved closer to the shore, their travel times increased, due to the increased turbulence associated with the river bed.

Larval retention: temporal component

Point abundance sampling collected 24 nase larvae over a period of 6 weeks, representing just 0.06% of the 40,000 larvae released (Table 1). Of these, 22 larvae were collected upstream of the release stations and 2 downstream, in the Johler side-arm, once it was connected at higher discharge on 24 April 2008. On each sampling occasion, larvae were collected in 4-8% of PAS samples (). Larvae were between stages L2 and L6 (Peñáz 1974). The highest abundances of retained larvae per sampling date were always upstream of the release stations, although many more than the number collected in PAS were collected drifting downstream of the release stations. The mean distance between the release stations and the collection point of larvae was constant over the investigation period (travel distance = -50 m), except for the sample date when the Johler sidearm downstream of the releasing location was connected, when the mean distance increased to 175 m.

One day after release, inshore-released larvae made up a most of the total catch (6 out of 7 individuals) in the PAS samples. However, over the 6-week period, inshore- and offshore-released larvae were collected in similar numbers ($n_{\text{inshore}}=11$ vs. $n_{\text{offshore}}=13$).

Larval retention: hydro-morphological relationships

Larvae were collected in microhabitats characterised by significantly deeper water, steeper slopes and lower flow velocities than points with no larvae (Mann-Whitney-U-test, water depth: $U_{24,167}=1198.5$, $P<0.001$; velocity: $U_{24,167}=1509.0$, $P=0.049$; shore slope: $U_{24,167}=1205.5$, $P=0.002$; sediment heterogeneity: $U_{24,167}=1991.5$, $P=0.929$).

Larval retention: particle tracing – random walk

The random walk approach was also used to display upstream larval dispersal patterns derived from the PAS data. Because the random walk component can only produce upstream movements on a very short time scale, which is insufficient for larvae to swim significant distances upstream, additional particle tracing experiments were conducted on an inverted

flow field. This was achieved by multiplying the three velocity vector components (u , v , w) in any calculation node by (-1), corresponding to the assumption that if larvae move upstream actively, they do so by orienting themselves on the flow streamlines. In the particle tracing experiment, only inshore-released particles passed the PAS sampling points where larvae were found (Fig 6b). However, in the larval release experiment, offshore released larvae were also found in catches along the shore.

Drifting vs. retained larvae

One day after release, larvae were found in the drift nets and in the PAS samples along the shore. At this time, significantly smaller nase larvae (total length, mean \pm 1SD: 11.80 \pm 0.55 mm) were found in the drift than were collected by PAS (total length: 14.04 \pm 1.57 mm; Student t-test: $t_{df=1,14}=4.74$, $P<0.001$), although they were at the same larval stage.

Discussion

If the nase larvae had all drifted passively through the reach during the experimental release, this would have taken approximately six minutes, as indicated by the particle tracing experiment. Instead, larvae were captured in drift nets for up to two hours after release, indicating movement was not entirely passive. This was despite current velocities at the release stations being above the critical thresholds for nase larvae at this developmental stage (Flore et al. 2000). Only a relatively small proportion of larvae were recaptured, although recapture rates compare favourably with other similar studies (Bartl & Keckeis 2004, Schludermann et al. unpubl., Steffensen et al. 2010).

Whereas the densities of inshore released nase declined from high values initially (30 min) to low values (120 min), as might be expected if nase were entrained immediately in the

current, densities of offshore-released nase were greatest at 60 min. This indicated that nase did not drift immediately, but delayed moving until either they could no longer hold position or 'chose' to drift. Furthermore, the path taken by all larvae, released offshore and inshore, did not follow that predicted from the particle tracing experiments based on the hydrodynamic model. The fact that offshore-released larvae were caught in inshore nets and comprised 50% of those larvae retained in the study site and the observed relationship between drift densities and velocity gradients, reinforces an active movement during dispersal, and mostly towards the shore. This finding was also observed by Robinson et al. (1998) for the larvae of native fish in the Little Colorado River, and showed that there was an active component to their drift, but that once larvae reached the shore, they acted like passive particles, as their dispersal pattern mainly overlapped those of passive particles. Higher drift densities near-shore were also observed by Peñáz et al. (1992) in the Upper River Rhone and Reichard et al. (2004) in the River Dyje.

Analyses showed that in combination, a range of hydraulic variables could explain about 30% of the variance in time-corrected nase densities captured in drift nets in the present study. Simple regressions indicated that there was a trend for the highest larval densities to be found at intermediate and relatively constant velocities and low and constant turbulence. This implies that larvae were drifting in moderately fast currents that were relatively stable. Fish larvae show varying responses to velocity when drifting, with the densities of some species positively correlated (barbel, Copp et al. 2002; Kootenai white sturgeon, Kynard et al. 2007), and others negatively correlated with velocity, or at least associated with slower velocities (nase, Persat & Olivier, 1995; several North American species, Robinson et al. 1998). Larvae generally drift on the edges of rivers rather than in the middle (Gallagher & Conner 1980, Kynard et al. 2007, Reichard et al 2004). Studies examining relationships between larval densities and other hydraulic variables besides velocity in rivers are less common but also show apparently contradictory patterns. For example, Gallagher & Conner (1980) noted that

larvae of a range of species were more abundant in near-shore zones with high turbulence, whereas Pavlov et al. (2008) cited studies showing that fish can detect relatively small differences in adjacent turbulence and, because critical velocity declines with increasing turbulence, may select zones of lower turbulence when drifting. For marine fish larvae, turbulence seems to be important for feeding: feeding is enhanced in turbulent waters because of greater retention times and therefore greater access to zooplankton (MacKenzie 2000). Stoll et al. (2010) found similar patterns in the littoral zones of lakes, although in this case, turbulence re-suspends food items and so makes them more available for capture and ingestions. For riverine fish larvae, however, the relationship is less clear. It is unlikely that access to food would have been a primary motivating factor during our short-term dispersal experiment, and more likely that turbulence would have been directly affecting their dispersal path. Observations in flume tanks have suggested that larvae can get temporally disorientated when exposed to turbulent flow (Chun et al. 2011), but that this only lasts for a relatively short period (Kaminskas, Humphries and Keckeis personal observation).

The shoreline of the gravel bar where the experiment was conducted is shallow, but with highly variable current velocities, shear stress and turbulent kinetic energy. Larval densities tended to be higher at intermediate levels of velocity and turbulence, whereas at low and high levels of these variables, larval densities were lower. This implies that under low-velocity conditions, larvae can possibly hold position, whereas under high-velocity conditions they are swept away or show an avoidance-reaction (see also Pavlov, 1994). Stoll et al. (2008) proposed a sheltering behaviour to reduce hydrodynamic stress for larvae in shallow, littoral habitats with high near-bottom velocities. They observed repeated hiding of YOY dace in their enclosure experiments during wave events. Several studies have noted a behavioural component in drift, related to current velocity: Copp et al. (2002) found a positive relationship between barbel drift density and velocity, whereas Persat & Olivier (1995) observed avoidance of emerged nase larvae to strong flow conditions. Certainly there is good evidence

to show that most riverine fish larvae are rheotactic, and can apparently locate current speeds that allow them to maintain position (Pavlov et al. 2008).

Results from the particle tracing experiments showed that released particles had longer travel times in the inshore areas, because of relatively low current velocities and high turbulence. If larvae act like passive particles, the likelihood of them being retained in inshore areas is thus higher than in offshore areas. Presumably, the probability of encountering suitable microhabitats to fulfil their bioenergetic demands may be higher under heterogeneous current patterns than under uniform, but high current velocities (Flore et al. 2000, Hill and Grossman 1993).

Those nase larvae in the present study that were retained in the study site were collected predominantly from sheltered inshore areas (e.g. dead zones). Furthermore, many were collected from upstream of the release stations and some used a side-arm of the main channel, once it was connected. The latter is common for other species and river systems elsewhere in the world (Martin and Paller 2008, Peirson et al. 2008, Robinson et al. 1998), however, the former was unexpected, and has only rarely been documented (Roussel and Bardonnet 1999), but not in a natural river, and deserves further attention.

The mechanisms for how fish larvae find nursery or rearing habitats are not known. Robinson et al. (1998) argued that larvae swim lateral to currents, after hatching, to seek out suitable low velocity habitats. However, the clumped distributions of larval fish, which are often found in freshwater systems (e.g. Wintersberger, 1996), apparently reflect passive dispersal. Furthermore, high mortality rates support this hypothesis (Bartl and Keckeis 2004, Reichard et al. 2004, Robinson et al. 1998). Based on our findings, and in agreement with Robinson et al. (1998) we propose that fish larvae in rivers move towards the shore and are then able to maintain position or to move upstream because of sub-critical velocities in these inshore areas and a heterogeneous velocity pattern.

Most fish larvae show rheotaxis (Jurajda 1998, Reichard and Jurajda 2007, Reichard et al. 2004). Pavlov (1994) has hypothesized, however, that once threshold velocities are reached, this rheotaxis is neutralised and passive downstream transport takes place. Our results partly support Pavlov's contention, since retained larvae were significantly larger than drifters, and swimming ability generally increases with length (Flore et al. 2000).

Particle tracing experiments generally showed similar patterns to the observed larval paths in the present study. Inshore-released particles were never 'retained' along the shoreline. Retention of passive particles was only observed at a dead zone at the far end of the gravel bar. Since offshore-released particles never reached the shore by a totally passive dispersal process, whereas offshore released larvae did, this provides strong evidence for an active component of larval dispersal. On the basis of a 2D hydrodynamic model, Korman et al. (2004) found that particles assigned rheo- and geotactic characteristics showed higher retention rates than neutral ones.

In the particle tracing experiments conducted on an inverted flow field, we showed that inshore released particles would pass microhabitats where fish larvae were found. This strongly supports the rheotaxis of fish larvae, because particles move perpendicular to lines of equal energy potential according to Eq. (1). Larval dispersal patterns seem to be based to some extent on the same basic principle. However, the velocities along the flow path would have been beyond the swimming capabilities of nase larvae, and so it is uncertain whether they swam directly upstream, using the substrate elements as refugia at times, or moved inshore and swam upstream at lower velocities. This is something that requires further research.

In Conclusion, we have clear evidence that larval dispersal is not solely a passive process, but has a strong active component. Released larvae clearly moved towards the shore, where the larvae encountered slower currents, more stable patterns of velocity and turbulence. This was contrary to the entirely passive pathway taken by particles in a tracing experiment

conducted at the same study site, where offshore released particles were never retained, and inshore- and offshore-released particles did not mix. Larval dispersal patterns were also dependent on the hydraulic characteristics of the release points. The detailed mechanisms of larval dispersal, however, remain unclear, as individual behaviour was not investigated in this study.

An improved understanding of dispersal patterns of the young stages of fish is crucial for successful restoration and management of rivers (James et al. 2002). In most temperate rivers, deterioration in the connectivity of key habitats, such as spawning and nursery areas, has led to a decline in typical riverine biota, as migration routes and exchange processes with the river's hinterland are interrupted (Keckeis et al. 1996, Kirchhofer 1996, Lusk and Halačaka 1995). Thus, larval dispersal can be used to explore the connectivity between spawning and nursery habitats and as a tool to assess overall ecological integrity. Connectivity between appropriate habitats must be considered as an integral component of future restoration programs in Europe. The need for basic knowledge of dispersal patterns and mechanisms is clear, and should be the focus of further study.

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Tables

Table 1. Sampling dates, observed discharge and modelled discharge, sampling methods (drift, point abundance sampling [PAS]) used on each date, the number and location of nase larvae collected by each method, and observed larval stage (after Peñáz 1974) and age (dph). Note: 'down' = downstream from release stations, 'up' = upstream from release stations. * marks discharges with side-arm connection.

Date	Observed discharge (m ³ •s ⁻¹)	Modelled discharge (m ³ •s ⁻¹)	Drift	PAS	Drift		PAS		Larval stage	Age (days ph)
					no.	Loc.	no.	loc.		
21. Apr. 2008	1926	1930	x		3017	down	---		L2	10
22. Apr. 2008	2209	2230	x	x	9	down	7	up	L2	11
24. Apr. 2008	3241*	3000	x	x	---		2	down	L2	13
29. Apr. 2008	2424*	2500	x	x	---		11	up	L3	18
06. May 2008	2253	2230		x			3	up	L3/L4	25
13. May 2008	2233	2230		x			---			
20. May 2008	2740*	2500		x			---			
27. May 2008	2344	2500		x			1	up	L6	46

Table 2. Hydro-morphological characteristics of the two release stations. The median, the 25th and 75th percentiles, minimum, maximum and range of the water depth, current velocity, turbulence and shear stress are derived from the hydrodynamic model.

	Inshore release station				Offshore release station			
	Water depth (m)	Current velocity (m•s ⁻¹)	Turbulence (m ² •s ⁻²)	Shear stress (N•m ⁻²)	Water depth (m)	Current velocity (m•s ⁻¹)	Turbulence (m ² •s ⁻²)	Shear stress (N•m ⁻²)
Median	0.80	0.47	0.0125	3.13	1.32	0.69	0.0085	3.58
25 th percentile	0.78	0.47	0.0122	3.09	1.32	0.69	0.0085	3.55
75 th percentile	0.81	0.48	0.0127	3.16	1.33	0.69	0.0086	3.62
Minimum	0.76	0.47	0.0120	3.06	1.31	0.68	0.0084	3.52
Maximum	0.83	0.48	0.0129	3.20	1.33	0.70	0.0086	3.65

Table 3. Parameters of the GLM analysis and stepwise AIC. Given are the values (estimate±SE), T-values (T) and significance (P) for the single variables.

	Estimate±SE	T	P
Intercept	-1.307 ± 0.484	-2.699	0.012
med velocity	3.673 ± 1.164	3.156	0.004
IQR turbulence	43.584 ±17.807	2.448	0.022
med shear stress	-0.315 ± 0.104	-3.032	0.006
IQR shear stress	-0.128 ± 0.048	-2.677	0.013
velocity gradient	12.193 ± 4.025	3.029	0.006

Figure captions

Fig. 1. Location of study site in the River Danube (upper graph) and study area (lower graph), indicating the location of potential spawning habitats (white circles) and of settled larvae (black circles) as observed in a previous study. The releasing stations in the present study are given by the two black squares. The shading represents the depth contours at the long term average discharge. Data derived from Keckeis et al. (2007).

Fig. 2. Study area and location of the release stations (black squares) of drift sampling points immediately after release (study 1: grey triangles), of randomly deployed nets in the following weeks (study 2: white triangles) and of point abundance sampling (black triangles).

Fig. 3. Comparison of the immediate temporal drift pattern (drift density \pm 1SD) for inshore-released (black) and offshore-release (white) larvae within the first two hours after release.

Fig. 4. Contour maps of flow velocity and standardised larval drift densities for different sampling intervals immediate after release (30, 60, 90, 120 min). Shading represents the different values of velocity thresholds (Flore et al 2000). The squares represent the release stations, circles the larval drift densities. Their size is relative to density; adjacent numbers are actual densities. White segments of circles = inshore, black segments =offshore released larvae.

Fig. 6. Relationships between larval drift densities (residuals) and the median and the variability of abiotic factors (IQR), respectively, for random sampling points. a) median of velocity: $y = -1.84 + 3.36x - 1.23x^2$, $r^2 = 0.27$, $P = 0.011$, $F_{(2,28)} = 5.28$; b) median of velocity gradient: $y = 0.30e^{-0.03x}$, $r^2 = 0.13$, $P = 0.048$, $F_{(1,29)} = 4.26$; c) median of turbulent kinetic energy: $y = 0.016 + 0.004/x$, $r^2 = 0.17$, $P = 0.023$, $F_{(1,29)} = 5.74$; d) median of shear stress: $y = 0.40 - 0.02x$, $r^2 = 0.16$, $P = 0.024$, $F_{(1,29)} = 5.67$; e) IQR of turbulent kinetic energy: $y = 0.32 - 7.20x$, $r^2 = 0.26$, $P = 0.003$, $F_{(1,29)} = 10.24$; f) IQR of shear stress:

$y=0.33 - 0.03x$, $r^2=0.23$, $P=0.006$, $F_{(1,29)}=8.63$). Boxplots represent the variation of time-dependent larval drift densities at the different random sample points.

Fig. 7. Spatial distribution of the values and the vectors of the current velocity slightly above the river bed at the study site at mean discharge ($Q=1930\text{m}^3\cdot\text{s}^{-1}$). Plotted are the (a) Calculated particle paths (yellow lines) starting from the release stations (red circles) derived from the random-walk approach ($n=50$) and position of drift nets (white circles). (b) Particle paths (yellow lines) derived from the random-walk approach applied in an inverted flow field ($n=50$) and location of recaptures of released larvae (grey symbols) by PAS. Data are derived from the 3D hydrodynamic model.