

Hydraulic forces impact larval fish drift in the free flowing section of a large European river

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ABSTRACT

Dispersal of fluvial freshwater fish larvae occurs commonly in heavily regulated rivers. Studies increasingly indicate that drifting young fish have an active component to their movement and so are capable of coping with the dynamic hydraulic forces typical of rivers. We investigated hydraulic–drift relationships of the young stages of fish over one breeding season along a gravel shore of the Austrian Danube using stationary drift nets from the first occurrence until the end of the seasonal peak (April–June 2008). Observed densities of families and developmental stages were related to the hydraulic parameters flow velocity (in three spatial directions), turbulent kinetic energy and water depth, derived from a three-dimensional hydrodynamic model of the sampling site. We detected distinct responses of drifting young fish to several hydro-physical factors under conditions (low light level, over-critical currents), which were considered to cause washouts and passive drift. In general, drift densities decreased with water depth and flow velocity. Weak swimmers (e.g. bull head *Cottus gobio* and early-stage cyprinid larvae) avoided turbulent flows, as their abilities to orientate and hold position may be limited. Early larval as well as early juvenile stages of cyprinids used lateral currents directing to the bank, potentially to drop out of the flow and reach inshore areas. Our study indicates that there are family-specific and stage-specific responses to hydraulic variables and that fish actively disperse, probably to minimize mortality and maximize successful dispersal. Copyright © 2013 John Wiley & Sons, Ltd.

KEY WORDS freshwater fish larvae; dispersal; Danube; turbulence; hydrodynamic modelling

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INTRODUCTION

Dispersal is a key event in the early life history of many fishes that enhances gene flow and species diversity, and promotes community stability (Zimmer *et al.*, 2009; Schwalb *et al.*, 2010). Fish larvae typically disperse by current-mediated drifting, to settle in areas with optimal temperature, current speeds and food availability (Keckeis *et al.*, 1997; Schiemer *et al.*, 2003) and to avoid competition and cannibalism at spawning sites (Humphries, 2005). They also disperse to find rich, relatively safe nursery habitats or environments (Pavlov, 1994). But this movement, especially at such a young, relatively vulnerable stage, is accompanied by high mortality (Harvey, 1987; Reichard *et al.*, 2002b). The trade-off between risks and benefits of dispersal has been the impetus for debate over the mechanisms of downstream transport for some time (Gale and Mohr, 1978; Pavlov *et al.*, 1978; Pavlov, 1994; Persat and Olivier, 1995; Robinson *et al.*, 1998; Reichard *et al.*, 2002a; Reichard and Jurajda, 2004; Zitek *et al.*, 2004a, 2004b; Pavlov *et al.*, 2008; Schludermann *et al.*, 2012).

Seasonal patterns of larval fish drift abundance and composition in rivers are driven ultimately by the timing of reproduction (Humphries and Lake, 2000; Baumgartner *et al.*, 2008), which is in turn influenced by circadian rhythms, photoperiod and temperature (Reichard *et al.*, 2002b; Sonny *et al.*, 2006). Proximally, drift abundance and composition are influenced by ontogeny and individual behaviour (Copp and Cellot, 1988). Drift may be ‘active’, and so linked to behavioural ‘choices’ to move to satisfy particular physiological needs, or ‘passive’, where movement is out of the individual’s control because of a lack of ability to maintain position (Reichard and Jurajda, 2007). Aside from a few studies, which highlight the accidental component of larval fish drift (Corbett and Powles, 1986; Wolter and Sukhodolov, 2008), most studies now recognize that there is a major active component to drift (Pavlov *et al.*, 2008).

Assuming that dispersal has evolved to avoid or adapt to variable or fluctuating environments (Stevens *et al.*, 2011), it seems logical that the drift-related behaviour of fish larvae (and other organisms, for that matter) in lotic habitats has been influenced by hydrologic and hydraulic processes. Indeed, positive and negative correlations between drift densities and discharge and flow velocity are common (Johnston *et al.*, 1995; Araujo-Lima and Oliveira, 1998; Reichard *et al.*, 2001; Copp *et al.*, 2002;

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Zitek *et al.*, 2004b; Daufresne *et al.*, 2005). However, prevailing characterizations of flow velocity as a one-dimensional, unidirectional vector pointing in the direction of flow do not describe the dynamic flow features that fish larvae encounter in a large river. These features also include spatial and temporal velocity gradients, which form eddies and vortices in the water column and thereby create turbulence. Turbulent flows affect fish behaviour and physiology by challenging stability of posture and swimming trajectories, decreasing swimming speeds and increasing costs of locomotion (Utne-Palm and Stiansen, 2002; Liao, 2007). Fish can detect turbulence (Pavlov *et al.*, 2008; Webb and Cotel, 2011) and are able to minimize its negative impacts by choosing ranges appropriate to their ecology, motivation and physical state (Lupandin, 2005). Fish may even use the energy of vortices to aid swimming (Webb and Cotel, 2011). However, studies on fish larvae in this context are scarce, and the influence of turbulence on young fish dispersal has not been investigated so far.

The present study aimed to investigate the links between the drift of free embryos, larvae and juvenile fish and hydraulics in the River Danube. Specifically, we examine how densities and spatial distributions of drifting fish are affected by turbulence, vertical, horizontal and longitudinal components of flow velocity and water depth, and whether our results indicate that fish show hydraulic preferences. The relevance of these results to ongoing and future river restoration projects is discussed.

MATERIALS AND METHODS

Study area

The study was conducted in one of the few remaining free-flowing stretches of the Austrian Danube, downstream of Vienna. Even though affected by regulation, the 50-km river reach was declared a National Park in 1996 to preserve its near natural alluvial landscapes. The habitat diversity of the alluvial system favours the high species richness in this river part (53 native fish species according to Schiemer and Spindler 1989). The sampling was conducted along a 300-m-long gravel bar located between river kilometres 1885.50 and 1885.20 (E 16°55'05", N 48°08'47") immediately upstream of the Johler-Arm (Figure 1). This side arm of the Danube is connected to the main channel at an average of 105 days per annum. The width of the river at the study site was about 300 m. The average depth of the river during the sampling period was approximately 2 m. Specific discharge values for this river section are 915 (regulated low flow), 1930 (mean flow) and 5300 m³ s⁻¹ (annual flood).

Sampling

In total, 250 samples were collected in weekly intervals from 21 April to 24 June 2008 on ten occasions (Figure 2). We used conical drift nets (0.5-m diameter opening, 1.5-m length, 0.5-m mesh size) with a removable reducing jar (1 l) at the cod end. A flowmeter (General Oceanics®, Miami) was attached

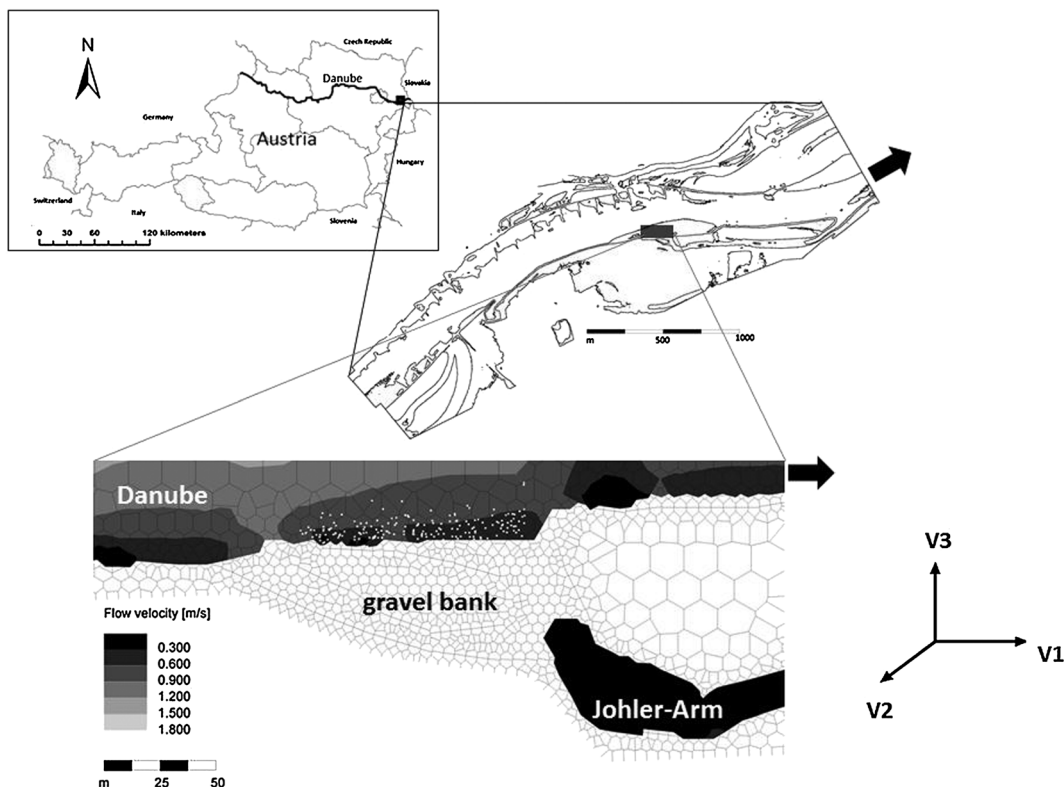


Figure 1. Location of the study site in the River Danube (upper map) and study area (lower map). At the bottom, drift net positions (white points) are shown in a velocity map of the gravel bar with computation cells of the hydrodynamic model. The three-dimensional coordinate system shows the spatial directions of velocity vectors used in the analysis.

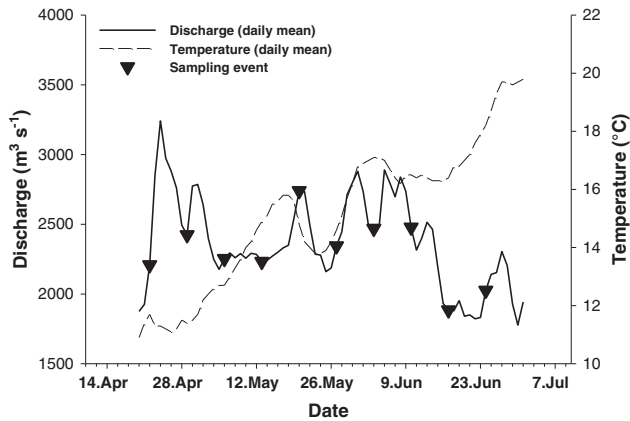


Figure 2. Daily means of discharge (solid line) and water temperature (dotted line) in the Danube with marked sampling dates (triangles).

to the lower third of the net entrance to measure the volume of filtered water. The nets were fixed to iron rods driven into the riverbed and sampled the top 0.5 m of the water column. Positioning of the nets followed a randomized block design with 5×20 m sections comprising the blocks. Section 1 was located at the most upstream part of the reach, at the transition from a sheltered bay to the gravel bar. Section 5 was located at the most downstream part of the reach at a depositional area, adjacent to the inlet of the Johler-Arm. The other Sections were located in between. As fish drift is largely nocturnal (Reichard *et al.*, 2001), sampling started at dusk (1930–2030) and continued for 3 h at 30 min intervals. At the start of each sampling occasion, one net was randomly positioned laterally and longitudinally within each of the five sections and left for 30 min. After 30 min, each net was retrieved, the contents of reducing jar washed into a sample jar, fish larvae were overdosed with Tricaine (MS-222, Sigma-Aldrich[®], St.Louis) and preserved in 96% ethanol, and the net was randomly re-positioned in the section. The maximal distance from the shoreline was 14 m and encompassed a substantial range of current speeds, turbulence and water depths (Figure 1). Exact net positions were mapped with a mobile dGPS (GS 20, Leica[®], St.Gallen). Water depth and temperature (Flo-Mate 2000, HACH[®], Colorado) were measured at each sampling point. Daily discharge data for the River Danube was provided by the nearest gauging station of the Austrian waterways authority (via-donau).

Sampling processing and data analysis

Samples were sorted in the laboratory under a dissecting microscope and the standard length (SL) of each fish

measured to 0.1 mm using vernier callipers or an ocular micrometer. Fish were identified to family. All Cyprinidae and Percidae were assigned to nine embryonic (E1–E9), six larval (L1–L6) and two juvenile (J1, J2) developmental stages according to Penaz (2001). Whereas the onset of exogenous feeding marks the transition between embryonic and larval stages, a lengthy transitional status, where provisional larval structures are replaced by definitive ones of the adult phenotype, indicates the change between larval and juvenile stages. Morphological changes during ontogeny often go along with changes in the organism-to-environment interactions. Larval stage analysis was not applied for the families Gobiidae because they have direct development (Penaz, 2001) and for Cottidae because of their different development. Drift density was expressed as number of individuals 100 m^{-3} of filtered water. Timing and seasonal dynamic of fish drift is a function of the spawning time and therefore strongly influenced by water temperature (Reichard *et al.*, 2002b; Zitek *et al.*, 2004b). To extract the effects of abiotic parameters on drift patterns, we tried to minimize seasonal effects by fitting a function to the overall drift data and the data of each family and developmental stage. Further correlation and regression analysis were calculated using the residuals from these curves (DD_{Res}).

At each sampling point, values for turbulent kinetic energy and current velocity in different spatial directions and water depths (Table I) were derived from a three-dimensional hydrodynamic model of the sampling site. The software model RSim-3D (Tritthart and Gutknecht, 2007) solves the Reynolds-averaged Navier Stokes equations by means of the finite volume method on a polyhedral computation mesh and employs the standard $k-\epsilon$ model (Lauder and Spalding, 1974) for turbulence closure. With the use of sets of bathymetric measurements originating from hydrographic surveys and laser scans conducted between the years 2003 and 2008, the model was set up for a river reach of 4 km in length (river-km 1888.0 to 1884.0). The computation mesh consisted of 208 416 three-dimensional cells with a typical point spacing of 20 m at the centre of the river and a progressive mesh refinement towards the bank, resulting in a resolution of 3 m in near-shore areas, such as the one where the present study was conducted. Calibration was performed on the basis of water level measurements as well as flow velocities in three spatial directions and turbulence intensities measured using acoustic Doppler velocimeter and acoustic Doppler current

Table I. Hydraulic predictors of drift density.

Variable	Description	Mean and range
Velocity layer	Flow velocity in the depth layer of the model the drift net was exposed in (m s^{-1})	0.87 ± 0.22
V1	Depth averaged velocity at the sampling points directing towards the main flow path of the River Danube (m s^{-1})	0.82 ± 0.21
V2	Depth averaged velocity at the sampling points directing 90° away from the shoreline (m s^{-1})	0.03 ± 0.07
V3	Depth averaged velocity at the sampling points directing to the zenith (m s^{-1})	-0.0003 ± 0.003
Turbulence	Turbulent kinetic energy at the sampling points ($\text{m}^2 \text{ s}^{-2}$)	0.02 ± 0.01
Water depth	Water depth at the sampling points (m)	0.65 ± 0.2

profiler techniques. With the employment of different data sets of measured values, the model was successfully validated. Details of the calibration and validation procedure can be found in Tritthart *et al.* (2009).

Boosted regression trees (BRTs) were used to investigate the major hydraulic parameters of drift density. The principle of BRTs is to combine and fit several models to optimize predictive performance and give insights into complex relationships (Elith *et al.*, 2006; Leathwick *et al.*, 2006; Elith *et al.*, 2008; Buston and Elith, 2011). The effect of multiple hydraulic factors was tested for each family and stage (Tables I and II). Analyses were not conducted for several stages within cyprinids (L5, J2) and all stages within percids because of the small sample size ($n < 30$). We used a learning rate of 0.001–0.002, bag fractions of 0.70–0.80 and tree complexity of 2–3 splits. Because of the small data sets ($n < 100$) a fivefold cross validation (CV) was used (Clapcott *et al.*, 2010). Here, the data is split fivefold, four of which are used for model development, and the fifth used for model validation. This provides the advantage of allowing the final model to be fit using the full data set. Partial response plots (pr-plots) were constructed to show the relative effect of abiotic predictor variables on the drift density. Relative influence of all predictors in a model can be accumulated to 100%. Partial plots were constructed for models, which had a CV deviance explained of >10 (Table II). Pr-plots are shown for predictors with relative influence higher 5%. BRT models were fitted in R (v.2.15.1, <http://www.R-project.org>; R Development Core Team 2006) using the ‘gbm’ library (Ridgeway, 2004) plus additional code written by Elith *et al.* (2008). One-way-ANOVAs and correlations were calculated with SPSS 16.0 (IBM Corp., Armonk, NY, USA). Seasonal curves of drift densities were fitted in Sigma Plot 12.0.

RESULTS

Water temperatures in the River Danube increased from 11.7 to 18.2 °C and mean daily discharge ranged from 1885 to 2740 m³ s⁻¹ over the sampling period (Figure 2). The means of water depth and turbulence at the sampling sites were 0.65 ± 0.2 m and 0.02 ± 0.01 m² s⁻¹, respectively. The spatial components of flow velocity differed by many orders of magnitude, with currents in the vicinity of the main flow being highest (0.82 ± 0.21 m s⁻¹) (Table I).

A total of 5235 free embryos, larval and juvenile fish were caught over the 10-week sampling period. This represented an overall total drift density of 16.8 ± 27.5 Ind. 100 m⁻³. Gobiidae (14.5 ± 23.7 Ind. 100 m⁻³) and Cyprinidae (7.0 ± 13.2 Ind. 100 m⁻³) were the most abundant families collected (Figure 3). Drift densities of Percidae and Cottidae were lower: 0.6 ± 1.4 Ind. 100 m⁻³ and 0.4 ± 1.2 Ind. 100 m⁻³, respectively. The families Esocidae, Gasterosteidae and Siluridae were represented by single individuals only. Significant stage-dependent drift patterns were observed for percids (Figure 4, ANOVA; $F_{1, 6} = 14.62$; $p < 0.001$) and cyprinids

Table II. Model inputs for the boosted regression trees and hydraulic predictors of drift densities for all families and developmental stages L1–L4 and L6–J1 for Cyprinidae. Numbers in bold show the explained deviance of models with a CV deviance explained >10 . Numbers above are the relative contributions of predictor variables for each model.

Model inputs	Gobiidae	Cyprinidae	Cottidae	Percidae	CL1	CL2	CL3	CL4	CL6	CJ1
N	92	181	36	70	113	102	92	34	37	33
Number of predictors	6	4	6	5	6	6	5	6	6	6
Learning rate	0.001	0.001	0.002	0.001	0.001	0.001	0.001	0.001	0.001	0.001
Tree complexity	2	3	2	3	3	3	3	2	2	2
Predictors					Relative contribution (%)					
V1	9.90		31.80	13.40	4.40	19.00		2.60	6.80	10.30
V2	2.40	36.70		1.00	22.00	23.10	16.10	2.50	6.40	17.00
V3	15.00	14.00	13.30	13.00	9.60	9.70	14.60	21.20	7.90	6.50
Velocity layer	44.70	21.60	10.30	10.90	17.00	21.20	11.50	2.00	52.50	38.30
Turbulence	17.60	27.80	12.00	11.30	38.30	14.70	15.20	6.50	2.70	24.50
Water depth	10.40		31.70	51.40	8.60	12.40	42.60	65.20	23.70	3.50
Deviance explained (%)	6.60	13.63	46.01	37.80	30.79	51.70	30.87	18.63	35.40	56.00

HYDRAULIC FORCES IMPACT LARVAL FISH DRIFT

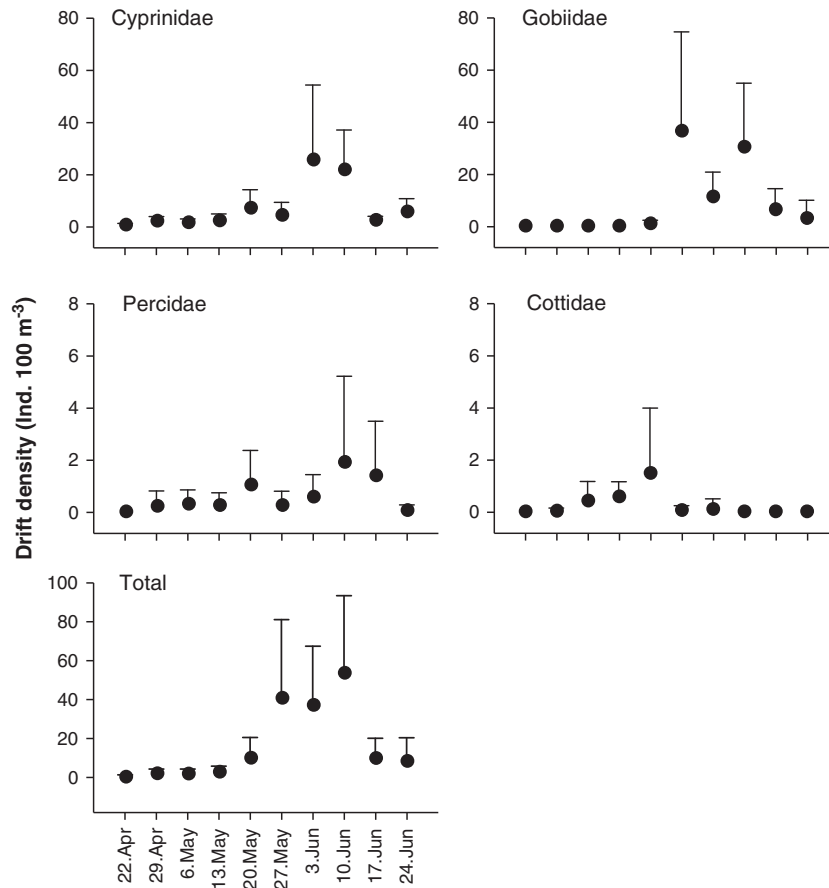


Figure 3. Seasonal patterns of larval fish drift in the River Danube in 2008. Shown are mean drift densities + 1 standard deviation.

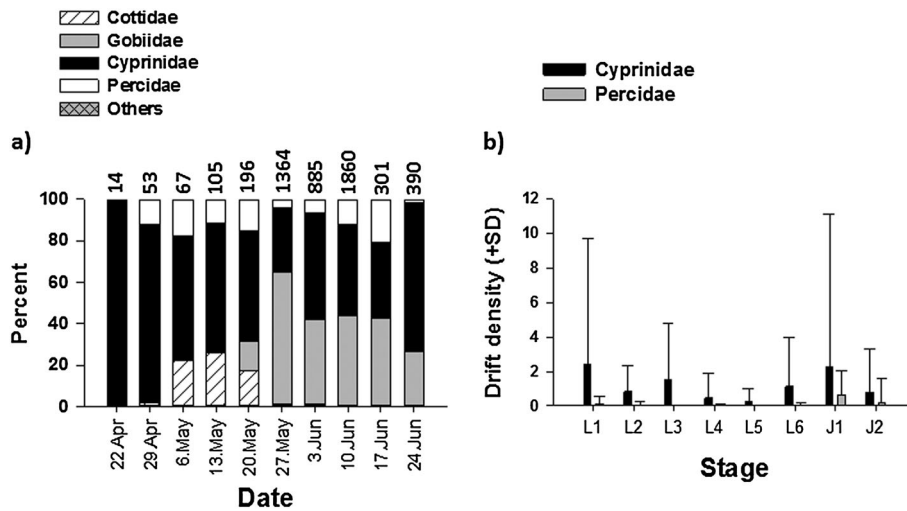


Figure 4. Taxonomic composition (%) of larval fish drift in the Danube (a) with total numbers of captured individuals for each date (above bar) and (b) drift densities of the separate developmental stages within the families Cyprinidae and Percidae. Drift data are log transformed.

(Figure 4, ANOVA; $F_{1, 7} = 10.49$; $p < 0.001$). Percids predominantly drifted as juveniles (J1) and cyprinids during early larval stages (L1, L2, L3) and also at the transition from the last larval stage (L6) to the first juvenile stage (J1). (Figure 4, Duncan tests for *post-hoc* comparisons). A unimodal seasonal drift pattern was found in the River Danube, peaking at the start of June (Figure 3). The densities of Cyprinidae, Percidae and

Gobiidae all peaked at this time, whereas that of the Cottidae peaked 2 weeks earlier.

Hydraulics–drift relationship

Families. Significant effects of hydraulic factors on drift densities were observed for cottids and percids. Poorly fitting models explaining hydraulic–drift relationships for

Cyprinidae and Gobiidae (Table II) means that results for these families are not further discussed.

Important predictors of drift dynamics for cottids were current velocity (in line with flow and vertically), water depth and turbulence (Table II). Cottids predominantly drifted in shallow low-flow areas with negligible turbulence (Figure 5). Noteworthy is the effect of a vertical current resulting in greater drift densities of cottids. The drift of larval and juvenile perch along the gravel shore was mostly restricted to areas with water depths of 0.5 m and below (Figure 6). High currents ($>1 \text{ m s}^{-1}$) and zones of low turbulence seemed to be avoided by these fish, but stage-specific responses may have more relevance than patterns of all individuals, regardless of stage.

Developmental stages. The BRT models failed to explain significant variance in the drift densities of cyprinid stages

L1, L3 and L4. The main hydraulic predictors for the drift densities of second-larval-stage (L2) cyprinids were flow velocity in all directions, velocity in the water-depth-layer where the drift net was exposed, and turbulence (Figure 7). Most L2-larvae were collected in areas with a lateral velocity gradient towards the shore (negative values for V2). The plots for Vel_lay and V1 furthermore indicate that young cyprinids drifted mostly in low ($<0.6 \text{ m s}^{-1}$) and intermediate ($0.8\text{--}1.0 \text{ m s}^{-1}$) currents. Turbulent flows were avoided at this early life stage. The nature of the influence of water depth and vertical velocity gradient on drift density was unclear.

Drift densities of larval cyprinids in the transition to the juvenile stage (CL6) were observed to decline, as velocities in the centre of the exposed drift nets and the water depth increased (Figure 8). The relative contribution of other predictor variables was low, and no clear relationships were found.

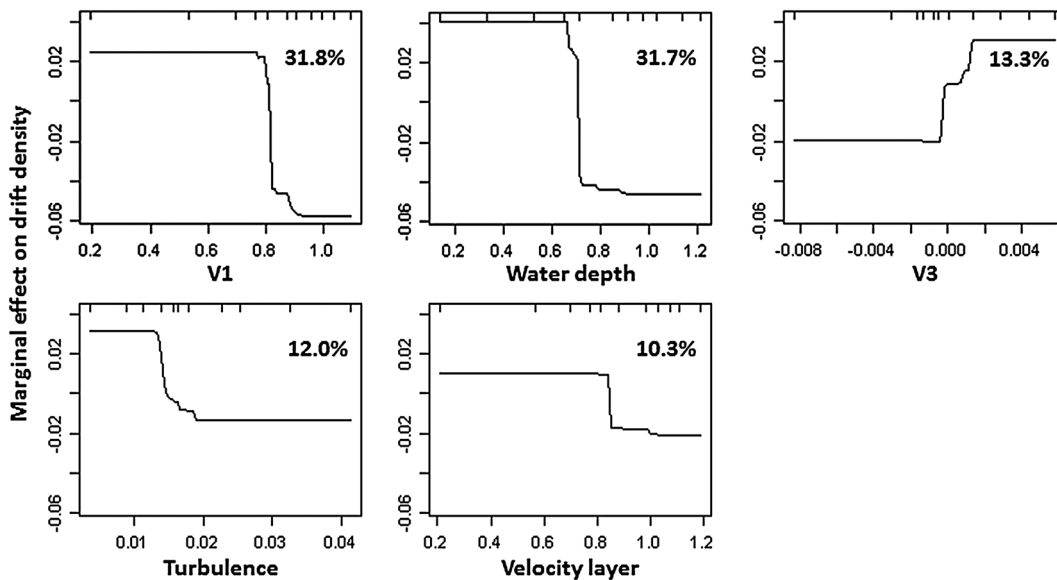


Figure 5. Partial dependence plots for the most influential hydraulic parameters ($>5\%$), which predict drift densities of Cottidae. Dashes at the top of each plot represent the measured observations of the predictor variable.

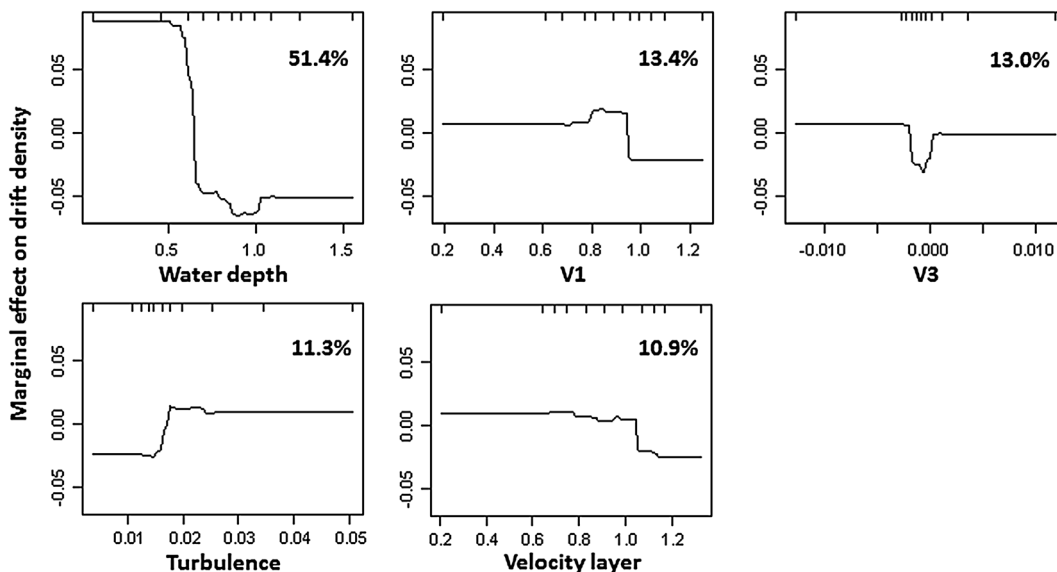


Figure 6. Partial dependence plots for the most influential hydraulic parameters ($>5\%$), which predict drift densities of Percidae. Dashes at the top of each plot represent the measured observations of the predictor variable.

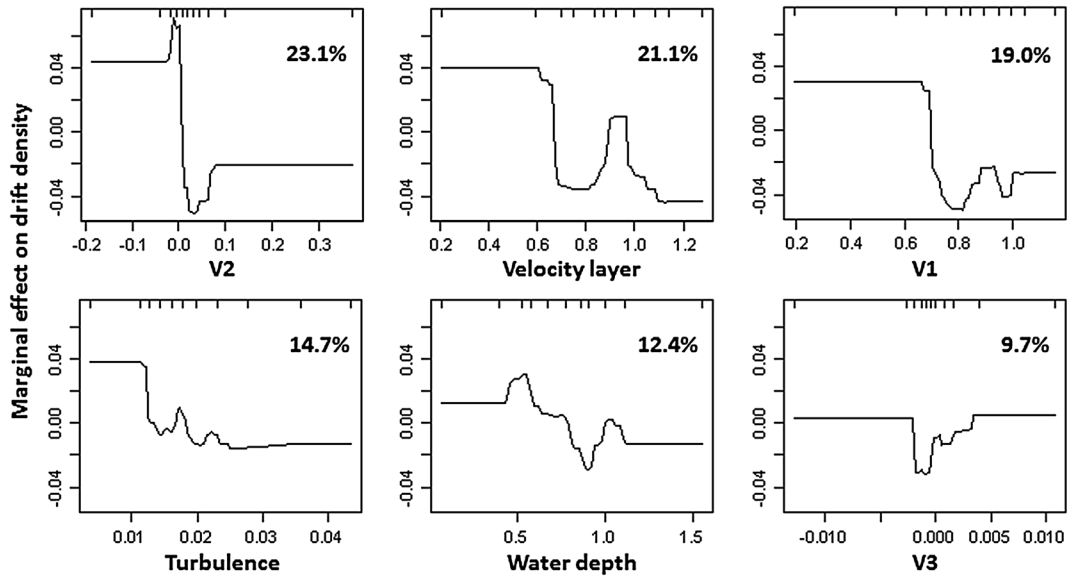


Figure 7. Partial dependence plots for the most influential hydraulic parameters (>5%), which predict drift densities of L2-Cyprinidae. Dashes at the top of each plot represent the measured observations of the predictor variable.

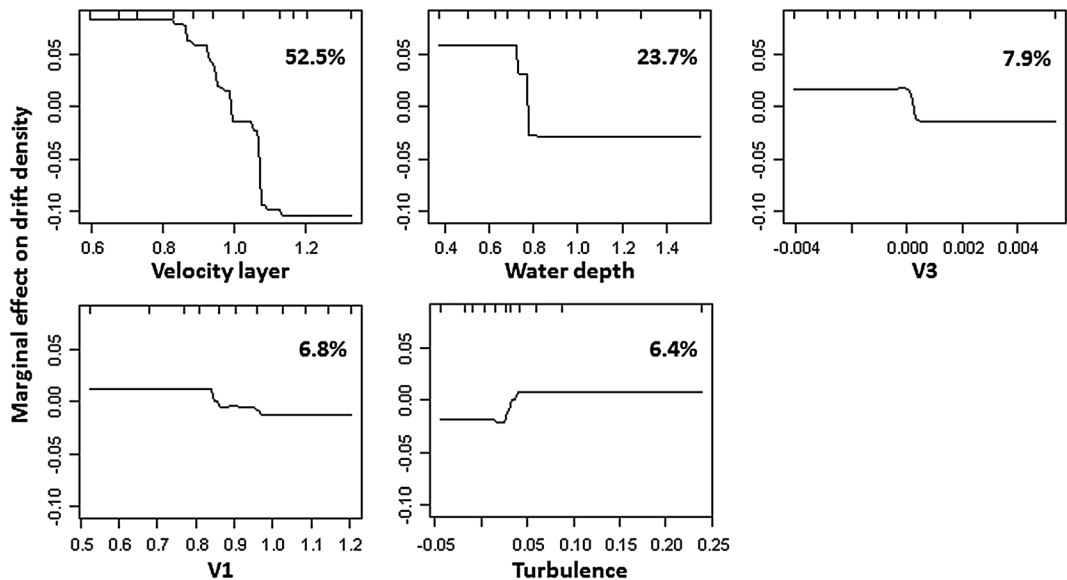


Figure 8. Partial dependence plots for the most influential hydraulic parameters (>5%), which predict drift densities of L6-Cyprinidae. Dashes at the top of each plot represent the measured observations of the predictor variable.

The main hydraulic predictor for the abundance of drifting and dispersing juvenile cyprinids (CJ1) was the flow velocity in the centre of the drift nets (Figure 9.). Above current speeds of 1.0 m s^{-1} , densities of juveniles declined. On the other hand, fewer juvenile individuals were caught in low-turbulent areas. Higher drift densities of juveniles were detected in regions with a water flow towards the shore.

DISCUSSION

Drift composition and seasonal patterns

Our results show that the main channel of the River Danube is important as a spawning and nursery ground for the riverine fish fauna. The reasons for species-specific and

family-specific differences in drift density may include spawning success, recruitment, size of the spawning population, availability of local spawning areas, drift avoidance, timing of sampling and density effects, and are not the focus of this paper and are discussed elsewhere (Pavlov, 1994; Humphries and Lake, 2000; Reichard *et al.*, 2002b; Zitek *et al.*, 2004b).

Ichthyoplankton drift in the River Danube was dominated by gobies (Figure 4a: 53.3% of total drift density, 41.8% cyprinids, 3.4% percids, 1.5% cottids), which is surprising, as this group is composed of only four species (from overall 57, Jungwirth *et al.*, 2003), and there is a large overlap in spawning season between these gobiid species, and 24 cyprinid and 8 percid species (Schiemer and Spindler, 1989; Jungwirth *et al.*, 2003). Goby species include the endemic tubenose goby (*Proterorhinus marmoratus*), and

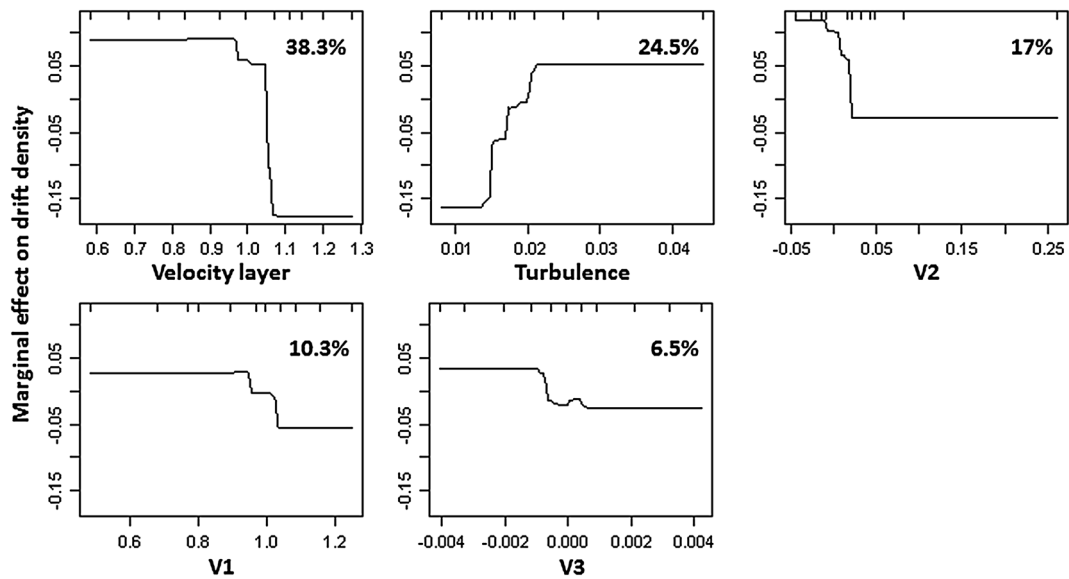


Figure 9. Partial dependence plots for the most influential hydraulic parameters (>5%), which predict drift densities of J1-Cyprinidae. Dashes at the top of each plot represent the measured observations of the predictor variable.

the ponto-caspian invaders, bighead goby (*Neogobius kessleri*), racer goby (*Neogobius gymnotrachelus*) and round goby (*Neogobius melanostomus*) (Wiesner, 2005). All species potentially contributed to the families' drift density because all can spawn multiple times from April onwards (Hauer, 2007). Their successful dispersal may be due partly to continuous spawning and partly to their drifting behaviour (Zitek *et al.*, 2004a).

The abundance of certain developmental stages in the drift may be evidence for an active entry into the drift (Pavlov *et al.*, 2008), the susceptibility of particular stages to entrainment by the current (Reichard and Jurajda, 2007) as a result of physio-morphological deficits (wash-out effects, Brown and Armstrong, 1985) or innate behavioural reactions that distribute fish in the open water (non-specific behavioural reactions, *sensu* Pavlov, 2008). Stage-specific drift patterns of cyprinids and percids in the river Danube agree with those of other studies. Reichard and Jurajda (2007) found most of the seven cyprinid species in the rivers Morava and Kyjovka drifting at the third larval stage and at the transition from the last larval to the first juvenile stage. These authors propose that fish actively entered the drift, triggered by a coincidence of improved swimming performance and behavioural/physiological aspects (i.e. habitat shifts, density dependent response to competition). In a similar study in the Marchfeldkanal, a high proportion of drifting cyprinids were in their first larval stage (Zitek *et al.*, 2004a), possibly as a result of a proportion of a clutch that got washed away from spawning substrates or left their refuge for other reasons: the larvae of several common species in the Danube (*Abramis brama*, *Alburnus alburnus*, *Chondrostoma nasus*, *Gobio* spp, *Rutilus rutilus*) exhibit vertical movements towards the surface during the first larval stage to fill their swim bladder (Zitek *et al.*, 2004a). High drift densities of percids in their juvenile stage have also been described in other rivers and may be related to active food migrations (Mion *et al.*, 1998; Pavlov *et al.*, 2008).

Hydraulic–drift relationships

We found that there were family-specific and stage-specific responses of drifting individuals to the prevailing hydraulic conditions in the study area. These results are noteworthy as they were detected during night and in areas with overcritical currents. Loss of visual orientation in the dark and the inability to resist fast currents were long assumed to be the driving forces behind passive dislodgement, where disorientated fish get washed downstream, and served as an explanation for peaks in nocturnal drift and higher drift densities during floods (Harvey 1987; Pavlov 1994). Even though Reichard *et al.* (2002a) has stated that entry into the drift may be related to the amount of ambient light and is an active 'decision', our results also indicate that fish larvae may be capable of orientating at low visibility using hydraulic gradients during downstream transport.

Although current speeds at the sampling site exceeded maximal sustainable velocities (water velocity at which fish cannot maintain their position in the water column, Flore and Keckeis, 1998) and burst swimming speeds (maximum speeds maintained just for seconds, Wolter *et al.*, 2004), in 99.2 % of all cases, we found correlations between drift densities and hydraulic forces. Therefore, we conclude that young fish are capable of orientating themselves in the water column while using the current as means of transport, even if unable to swim directly into the current (i.e. active–passive drift *sensu* Pavlov 1994). The assumption that larval distribution in large rivers is solely related to hydrodynamic forces (Pavlov *et al.*, 1978; Wolter and Sukhodolov 2008) is therefore rejected.

The main hydraulic predictors of drift densities in the present study were flow velocity and water depth. As the most important nurseries for young riverine fish are shallow near-shore areas (Scheidegger and Bain, 1995; Schiemer *et al.*, 2001b; Humphries *et al.*, 2002; King 2004), drift densities are usually higher along these shoreline habitats (Gale and Mohr

1978; Brown and Armstrong 1985; Oesmann 2003; Reichard *et al.*, 2004). We found no lateral drift gradient although many individuals were collected in shallow regions. Aside from habitat preferences, water depth may affect drift densities because habitat heterogeneity may be crucial for a fish's ability to orientate (Pavlov *et al.*, 2008). Being able to see the riverbed could be important so that drifting individuals can determine and adjust their position in the water column.

There was a clear trend towards lower drift densities in higher currents for all families, except percids, in the present study. Whereas other studies have detected no effect of velocity (Copp *et al.*, 2002; Reichard and Jurajda 2004) or the opposite (Iguchi and Mizuno 1991; Kynard *et al.*, 2007), results from the present study suggest that active mechanisms operate, whereby drifting fish larvae favour low-flow areas (bearing in mind that currents were generally over-critical).

Decreasing drift densities at higher levels of turbulence were detected for early larval stages of (L2)-cyprinids and for cottids. The bullhead (*Cottus gobio*) is the only species belonging to the family Cottidae in the Austrian Danube. This benthic fish has no swim bladder and is known as a weak swimmer, which moves by hopping along the riverbed (Tudorache *et al.*, 2008). A comparatively poor swimming performance is also a feature of second-larval-stage cyprinids, as they are characterized by a finfold instead of ventral and dorsal fins and yet have no rays in the diphyccercal caudal fin (Penaz, 2001). The critical swimming velocity that a fish can maintain declines in turbulent conditions (Pavlov *et al.*, 2008). Additionally, negative impacts of turbulent flows are directly linked to the fish's total length and affect small individuals at lower levels (Liao, 2007). Hence, it is plausible that individuals with limited swimming capacities and lacking attributes to stabilize position (i.e. fins, swim bladder) prefer non-turbulent flows for their transport. Pavlov (2008) noted that fish larvae are able to detect and orientate to benign turbulence patches, and may remain sensitive to turbulence cues under over-critical current conditions (Pavlov, personal communication), which was confirmed by our results.

More cyprinids at the transition from the last larval (L6) to the first juvenile stage (J1) and percids (most of them being J1) drifted at higher levels of turbulence. It is known that fish can reduce locomotory costs by using turbulent flow, providing their mechanisms of stability are sufficient for a given hydrodynamic environment (Liao, 2007). Morphological attributes of late larval (L6) and early juvenile (J1) stages may already match these attributes.

Only the drift of bullheads was influenced by a vertical velocity gradient in the present study. This species is normally benthic but was frequently caught in surface nets. A nocturnal ascent of drifting benthic larvae has been described elsewhere (Pavlov *et al.*, 1978) and may be to avoid benthic predators or collision with the substratum (Brown and Armstrong 1985). However, the use of upwelling currents to get there seems plausible.

Higher drift densities of early larval (L2) and juvenile (J1) cyprinids were collected in areas with slow currents orientated towards the bank. Drift of young fishes facilitates habitat shifts and the exploitation of high quality

microhabitats along the shore, where abiotic conditions match changing ontogenetic requirements (Pavlov 1994; Keckeis and Schiemer, 2002). The ability of fish to settle out of the flow may either be mediated by hydraulic forces alone, as modelled for newly hatched larvae with negligible swimming performance (Wolter and Sukhodolov 2008), or depend on a specific dispersal strategy, where larvae swim lateral to the currents and actively seek near-shore areas (Robinson *et al.*, 1998). The fact that we found individuals using velocity gradients orientated towards the shore indicates support for the second scenario.

CONCLUSION

Young riverine fish depend on heterogeneous inshore areas where a broad range of microhabitats, with gradual changes of abiotic factors, matches their changing requirements during ontogeny ('Inshore Retention Concept', Schiemer *et al.*, 2001a). As well as providing important nurseries, the inshore zones of large rivers are also important corridors for larval and juvenile dispersal (Reichard *et al.*, 2004). Our study has shown that ontogenetic and taxonomic differences are correlated with hydraulic conditions during drift and suggest that hydraulic heterogeneity along shorelines plays an important role in dispersal. Structural alterations to fluvial systems, which primarily affect inshore areas (straightening, embankments and impoundments) tend to reduce heterogeneity of habitats and flow patterns (Schiemer *et al.*, 2003). The effects of changes to the hydraulics of these inshore areas are uncertain. However, any changes may have dramatic effects on the dispersal of the young stages of fish and flow on to the viability of populations.

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