



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

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Lechner, A., Keckeis, H., Schludermann, E., Loisl, F., Humphries, P., Glas, M., Tritthart, M., and Habersack, H. Shoreline configurations affect dispersal patterns of fish larvae in a large river. – ICES Journal of Marine Science, doi:10.1093/icesjms/fst139.

Received 4 February 2013; accepted 30 July 2013.

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). Therefore, 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 (Hinrichsen *et al.*, 2001; Houde, 2002; Dickey-Collas *et al.*, 2009). 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 (Huret *et al.*, 2007; Savina *et al.*, 2010; Basterretxea *et al.*, 2012). 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), windforcing (Dalley *et al.*, 2002) or temperature (Peck *et al.*, 2009), and a suite of active behavioural 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).

Although many marine studies have included individual-based models and particle tracing approaches to model the dispersal of young fish (see review in Peck and Hufnagel, 2012), the corresponding

efforts in the world's large rivers are rare (Korman *et al.*, 2004; Wolter and Sukhodolov, 2008; Schludermann *et al.*, 2012).

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 hyporhithral 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 analysed (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 is essential) 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 free-embryos and larvae, as well as the highly dynamic environment of the spawning sites, dispersal of ichthyoplankton in large rivers is often referred to 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 (Stoll and Beeck, 2012; Lechner *et al.*, 2013), 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 washout 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. Therefore, 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).

In this study 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 with 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 (Figure 1). The stretch between river kilometres 1890 and 1893.8 provides shoreline situations with distinctly different hydrogeomorphological 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 and 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.

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. In all, 10 females (2093 g eggs in total) and 14 males (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. Thereafter, 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 with 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 s.d. = $11.7 \pm 0.7^\circ\text{C}$) hatched on day 22 post-fertilization and were in the second larval stage (mean standard length \pm s.d. = 11.7 ± 1.9 mm) at release (12 d post-hatching). Embryos in the warmer flume ($14.8 \pm 3.3^\circ\text{C}$) hatched 8 d earlier and were already in the fourth larval stage at release (12.7 ± 1.8 mm).

According to Penaz (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 diphycerkal caudal fin. At this stage, *C. nasus* larvae show a positive phototaxis and fill the posterior chamber of their swimbladder. In the fourth larval stage (L4), fish already possess a two-chambered swimbladder, 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).

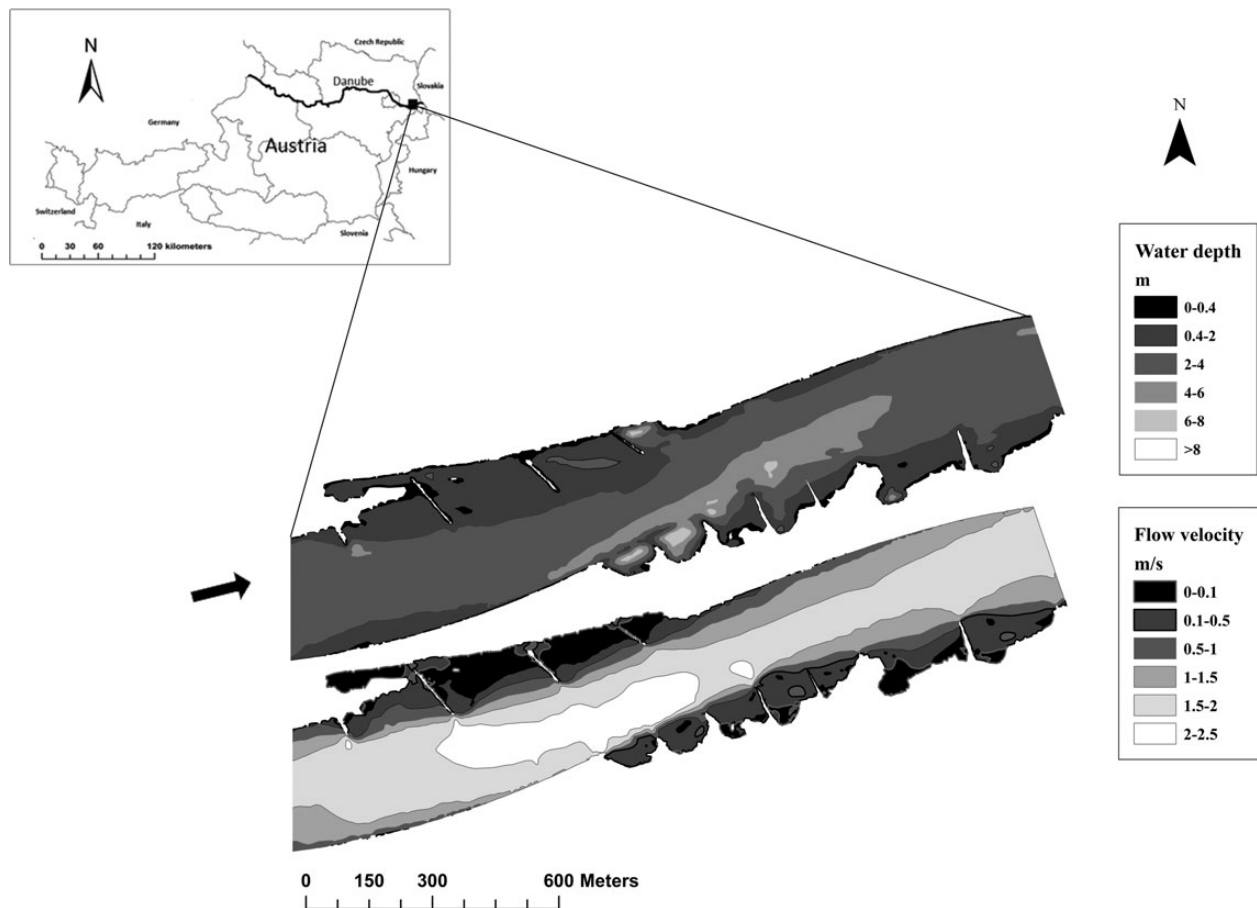


Figure 1. Overview of the study area with flow velocity and depth profiles for a discharge of $1143 \text{ m}^3 \text{ s}^{-1}$. Flow direction is indicated by the arrow.

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). Therefore, 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 d (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.

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

Table 1. Total numbers of released nase larvae differentiated for shorelines, developmental stages (L2–L4), and release points (inshore, IR; offshore, OR).

Shore	Stage	Release	Code	Number
Gravel bar	L2	IR	1-0-0	11 585
		OR	1-1-0	14 202
	L4	IR	1-0-0-1	12 558
		OR	1-1-0-1	10 116
Rip-rap	L2	IR	1-0-1	14 428
		OR	1-1-1	12 428
	L4	IR	1-0-1-1	7 062
		OR	1-1-1-1	14 812
Σ				97 191

Mark sequences in the otoliths are shown as binary code, where numbers indicate days with staining (1) and no-staining (0) and (–) indicate two-dimensional intervals.

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 (19:30–20:30 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: $0.93\text{--}0.95 \text{ g cm}^{-3}$, white-coloured 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 1 (day 2) and 4 (day 5) days post-release on each shore. A combination of stationary driftnets and point abundance sampling (PAS) was applied to survey larval

drift and settlement patterns (Figure 2). Drift sampling aimed to capture larvae that were washed downstream or entered the current. Triplets of conically shaped driftnets (0.5 m diameter, 1.5 m long, 500 μ m 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

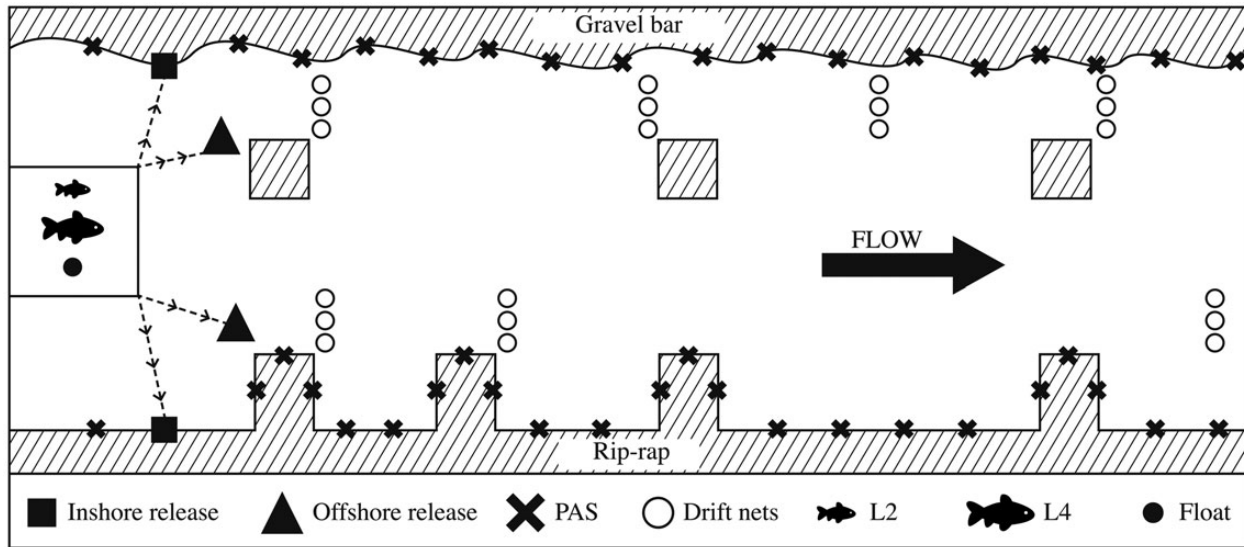


Figure 2. Sampling design. Shaded squares along the gravel bar represent remains of former groynes.

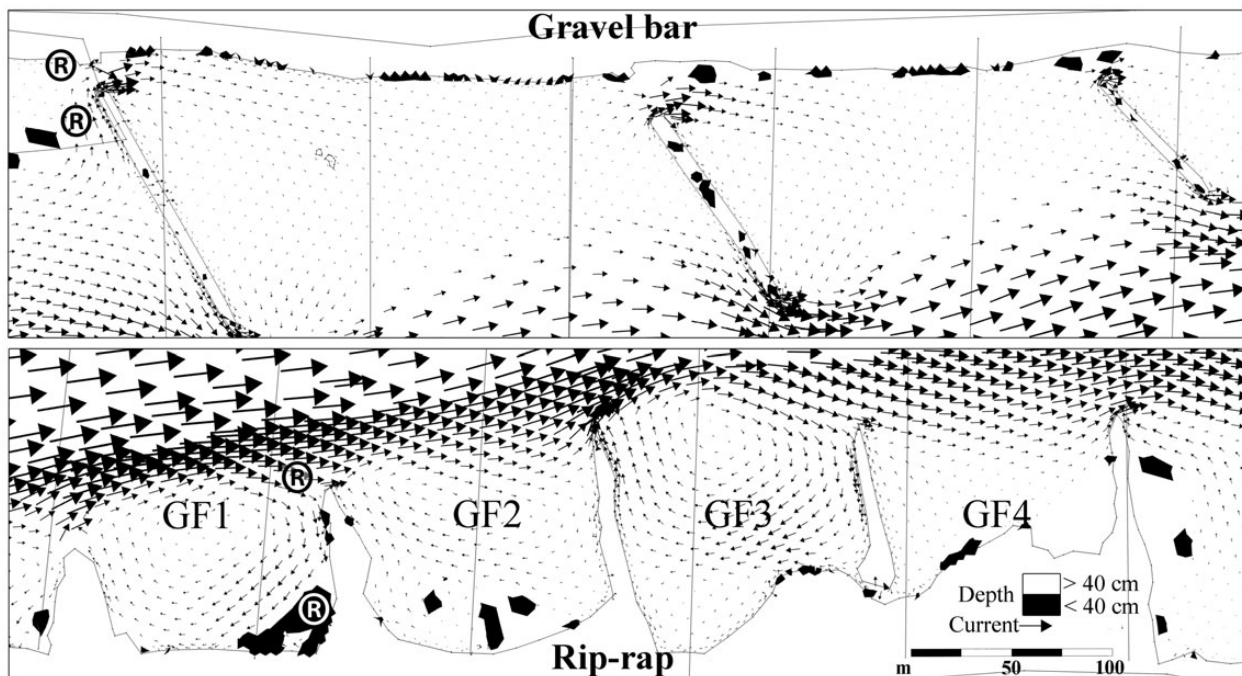


Figure 3. Flow patterns on both shores are illustrated by arrows. Arrow size is proportional to current speed and directly comparable between shores. Shallow areas, preferred by fish larvae, are shown as black areas. Consecutive groyne fields along the rip-rap are labelled (GF1–GF4).

for 30 min in hourly intervals for a total of 5 h. A flowmeter (2030R, General Oceanics[®], Miami) was attached to the lower third of each net entrance to measure the volume of filtered water.

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 and Copp, 1990). Using a dipnet (0.4 m diameter, 400 μm mesh size), a figure-8 sweep pattern was carried out, covering an area of $\sim 0.75 \text{ m}^2$ (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 the criteria of developmental stage and body length (mean body length at release $\pm 5 \text{ mm}$; 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 (CrystalbondTM, Aremco[®], New York) polished with abrasive paper 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 analysis).

Data analysis

Recapture rates (RRs) were calculated ($N_{\text{rec}}/N_{\text{rel}}$; 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, RRs were standardized by the volume of filtered water. The measured RR_Vol refers to the number of individuals per 1000 m^3 . For PAS, RR_Vol is given in individuals per 0.75 m^2 . 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 analysed performing systematic pairwise comparisons of DRs and SRs (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 analysed using the fully three-dimensional 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 (Launder and 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 scanings 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. Thereafter, 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 run-off 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 kilometres 1892.3 and 1893.4) using Acoustic Doppler 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;

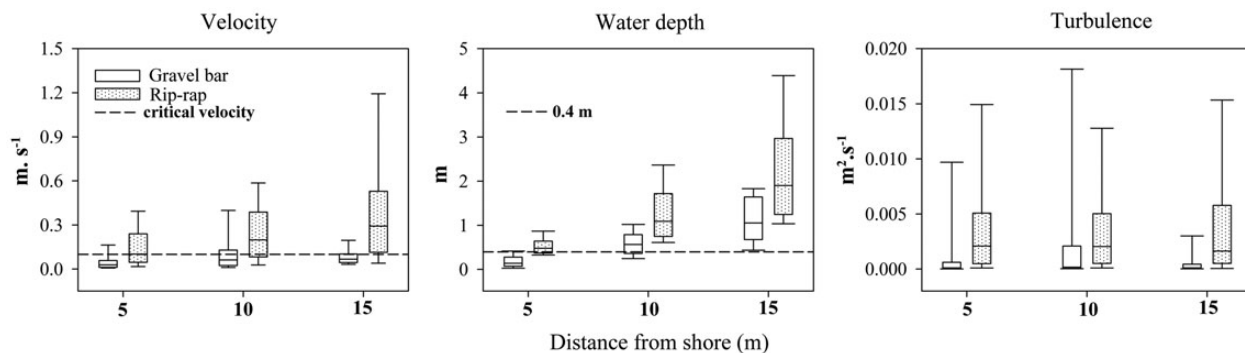


Figure 4. Lateral gradients of flow velocity, water depth, and turbulence at both shorelines. Values were derived from the hydrodynamic model (RSim-3D) by calculating the variables every 2 m on modelled lines (0.5, 5, and 15 m offshore) extending from the release point to the downstream end of the sampling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

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 (Figure 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 m s^{-1} even 15 m offshore (Figure 4). 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 $\sim 671 \text{ m}^2$ 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 (Figure 3). The recirculating flow patterns varied between adjacent groyne fields (GF1–GF4) relative to current strength, current direction, and vortices profile (Figure 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 (Figure 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 $\sim 153 \text{ m}^2$ of suitable nursery areas per 100 m shoreline length (and a total of 2785 m^2 , Table 2).

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 RR of 3.14%. Most larvae were caught in the stationary driftnets (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 DRs of all groups (L2, L4, F; IR, OR) tended to be greater at the gravel bar (Figure 5). Here, DRs of all larvae combined were significantly higher than at the rip-rap (Figure 6). Furthermore, overall larval DRs at the gravel bar explicitly outran those of floats at the same shore (Figure 6). No distinct differences between overall DRs of larvae and floats were observed within the rip-rap

Table 2. Total length of investigated shoreline, total area of suitable nurseries, and nursery area per 100 m shoreline length are given for both shores.

	Gravel bar	Rip-rap
Shoreline length (m)	540	1 816
Total nursery area (m ²)	3 627	2 785
Nursery area/100 m shoreline (m ²)	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

Additionally, mean numbers of settling individuals in nurseries along 100 m shoreline- stretches on each sampling day are given.

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

Shore	Day	Method	Samples	Individuals	Numbers				Mean RR Vol \pm s.d.				Total larvae
					IR		OR		IR		OR		
					L2	L4	L2	L4	L2	L4	L2	L4	
Gravel bar	1	D	33	2 152	187	107	713	1 145	0.6400 \pm 1.2346	0.3615 \pm 0.7320	1.9618 \pm 6.1172	4.5177 \pm 16.8591	1.7668 \pm 5.4495
		PAS	8	72	28	9	10	25	0.0297 \pm 0.0703	0.0089 \pm 0.0122	0.0087 \pm 0.0166	0.0305 \pm 0.0572	0.0183 \pm 0.0336
	2	D	59	89	20	43	8	18	0.0233 \pm 0.0785	0.0464 \pm 0.1267	0.0067 \pm 0.0239	0.0279 \pm 0.0699	0.0256 \pm 0.0477
		PAS	25	65	21	24	11	9	0.0072 \pm 0.0123	0.0077 \pm 0.0193	0.0031 \pm 0.0076	0.0037 \pm 0.0095	0.0056 \pm 0.0089
		D	57	52	22	8	14	8	0.0469 \pm 0.1543	0.0148 \pm 0.0544	0.0254 \pm 0.0687	0.0223 \pm 0.0829	0.0273 \pm 0.0604
Rip-rap	1	PAS	14	16	2	10	2	2	0.0011 \pm 0.0042	0.0057 \pm 0.0213	0.0009 \pm 0.0034	0.0013 \pm 0.0048	0.0024 \pm 0.0064
		D	54	152	35	5	58	54	0.1460 \pm 0.5345	0.1038 \pm 0.6884	0.3670 \pm 1.4228	0.1377 \pm 0.4134	0.1937 \pm 0.6039
	2	D	58	15	2	5	3	5	0.0027 \pm 0.0150	0.0301 \pm 0.1427	0.0089 \pm 0.0491	0.0089 \pm 0.0286	0.0344 \pm 0.1136
		PAS	27	117	8	5	55	49	0.0021 \pm 0.0094	0.0027 \pm 0.0117	0.0163 \pm 0.0845	0.0123 \pm 0.0599	0.0089 \pm 0.0415
		D	49	2	2	0	0	0	0.0031 \pm 0.0163	0.0000 \pm 0.0000	0.0000 \pm 0.0000	0.0000 \pm 0.0000	0.0009 \pm 0.0048
Total	GB	PAS	23	5	0	0	3	2	0.0000 \pm 0.0000	0.0000 \pm 0.0000	0.0010 \pm 0.0037	0.0006 \pm 0.0030	0.0005 \pm 0.0013
		D	149	2 293	229	158	735	1 171	0.1690 \pm 0.6362	0.1041 \pm 0.3774	0.4469 \pm 2.9581	1.0201 \pm 8.0599	0.4119 \pm 2.6361
RR	D	PAS	47	153	51	43	23	36	0.0092 \pm 0.0305	0.0073 \pm 0.0186	0.0034 \pm 0.0091	0.0076 \pm 0.0258	0.0068 \pm 0.0160
		D	161	169	77	56	80	80	0.0509 \pm 0.3153	0.0457 \pm 0.4075	0.1263 \pm 0.8372	0.0494 \pm 0.2471	0.0689 \pm 0.3592
PAS	D	PAS	69	439	29	47	177	145	0.0014 \pm 0.0064	0.0037 \pm 0.0187	0.0259 \pm 0.1473	0.0182 \pm 0.0904	0.0131 \pm 0.0653

Results refer to day of release (1) and subsequent samplings 1 (2) and 4 d (5) later.

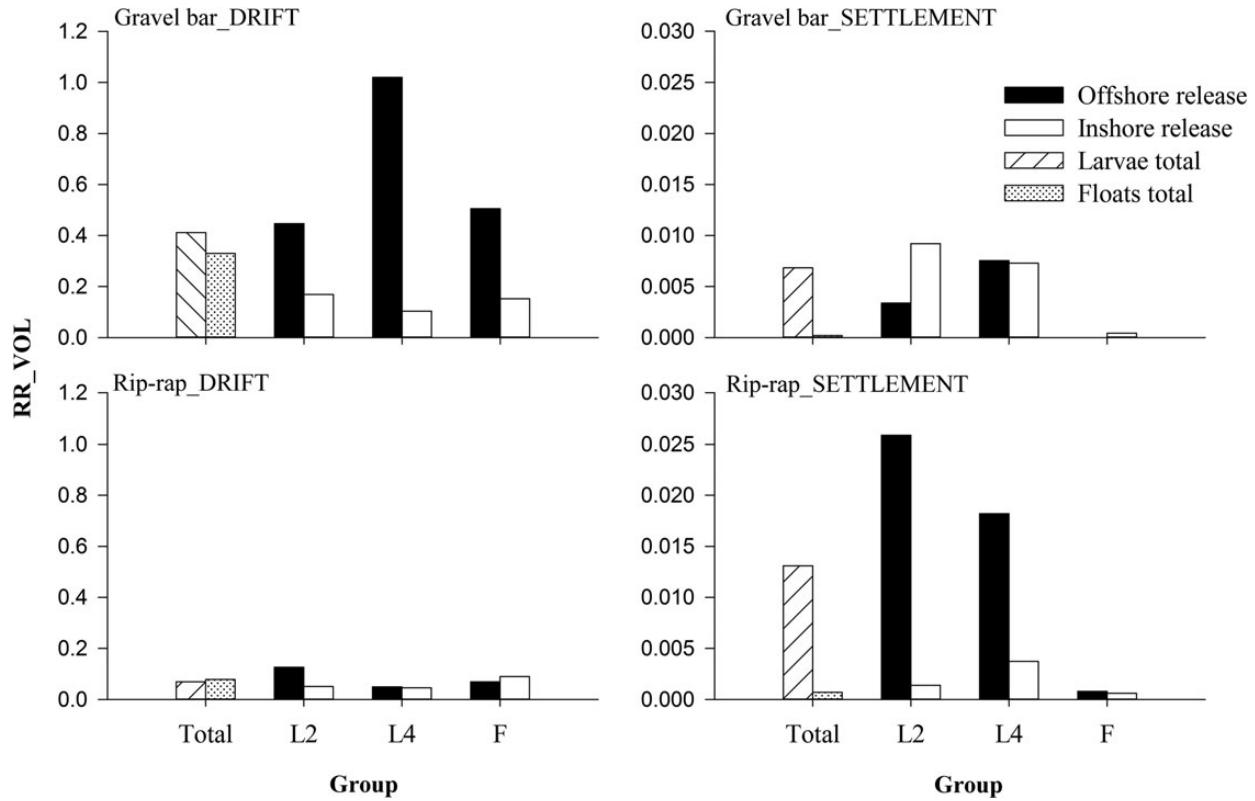


Figure 5. Mean recapture rates (RR_vol) of drifting and settling larvae for both shorelines relating to the total amount of recaptured larvae and floats (F) and single groups (L2, L4) and release points (inshore, offshore).

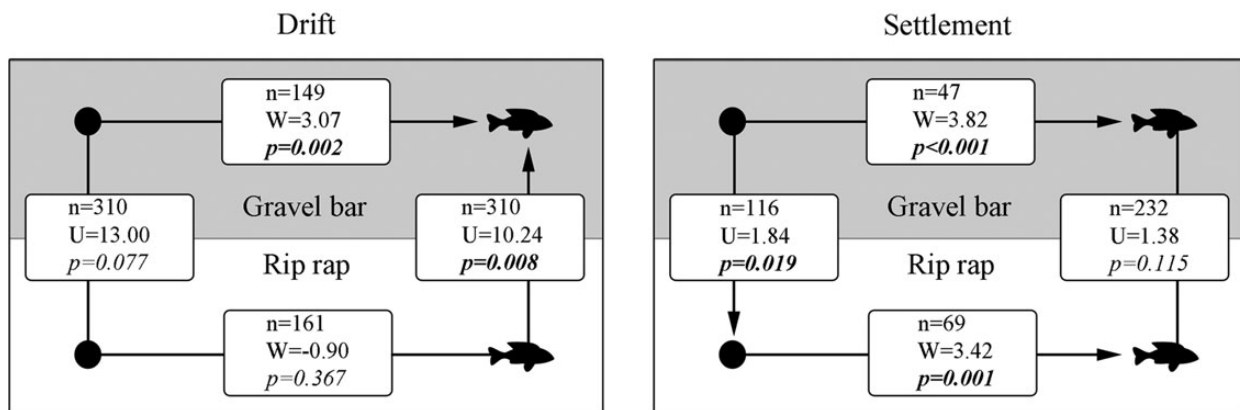


Figure 6. Differences between DRs and SRs of larvae (🐟) and floats (filled circles) within (Wilcoxon test) and between (U-test) the shorelines. The arrows point towards superior mean values. Significant results in bold letters. Significance level was (Bonferroni) adjusted to 0.025.

(Figure 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 (Figure 5). No clear distinctions between DRs of all groups, originating from the same release points, were detected within each shore (Figure 5).

No inter-shore differences in overall larval SRs could be detected (Figure 6), and only SRs of IR-L2-nase proved to be higher at the gravel bar (Table 4). However, overall larval SRs significantly exceeded float retention at both shores (Figure 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 (Figure 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 with the rip-rap (Figure 5). Overall more floats ($p = 0.019$) were retained at the rip-rap (Figure 6).

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,

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	L2	<i>n</i> = 116 <i>U</i> = 1.27 <i>p</i> = 0.002					<i>n</i> = 116 <i>U</i> = 1.61 <i>p</i> = 0.967	L2	Rip-rap
	L4		<i>n</i> = 116 <i>U</i> = 1.39 <i>p</i> = 0.031			<i>n</i> = 116 <i>U</i> = 1.55 <i>p</i> = 0.568		L4	
	F			<i>n</i> = 116 <i>U</i> = 1.748 <i>p</i> = 0.105	<i>n</i> = 116 <i>U</i> = 1.78 <i>p</i> = 0.025			F	

Significance level was (Bonferroni) adjusted to 0.01. Significant results in bold letters.

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	<i>n</i> = 47 <i>W</i> = 3.19 <i>p</i> = 0.001	<i>n</i> = 69 <i>W</i> = 0.71 <i>p</i> = 0.474	<i>n</i> = 47 <i>W</i> = 2.36 <i>p</i> = 0.018	<i>n</i> = 69 <i>W</i> = 2.84 <i>p</i> = 0.004	
L4	<i>n</i> = 47 <i>W</i> = 2.81 <i>p</i> = 0.005	<i>n</i> = 69 <i>W</i> = 1.07 <i>p</i> = 0.283	<i>n</i> = 47 <i>W</i> = 2.52 <i>p</i> = 0.012	<i>n</i> = 138 <i>W</i> = 2.47 <i>p</i> = 0.01	

Significance level was (Bonferroni) adjusted to 0.01. Significant results in bold letters.

respectively, were caught within 5 h after release (Figure 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 on at the gravel bar. Overall trends for drifting floats were similar to larvae, although at lower orders of magnitude at the gravel bar. Temporal characteristics of larval settlement also revealed a decreasing trend, with higher SRs on days 1 and 2 at the rip-rap, and conversely on day 5 with higher SRs at the gravel bar (Figure 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 2 d of observation.

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 (Figures 8a and 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 (Figure 8b), lower DRs of L4-nase (IR and OR) were detected at all four sampling stations (Figure 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 (Figures 8c and 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 with 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, and OR larvae were dominant in GF2 (Figures 8a and 9a).

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 (Figure 9b). Drift activity of L2-nase was restricted to SS1 and SS2 (with large numbers of OR individuals; Figure 8b). Except 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 (Figures 8b and 9b).

Day 5: low DRs of IR-L2-nase were observed only at SS1 (Figures 8c and 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).

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

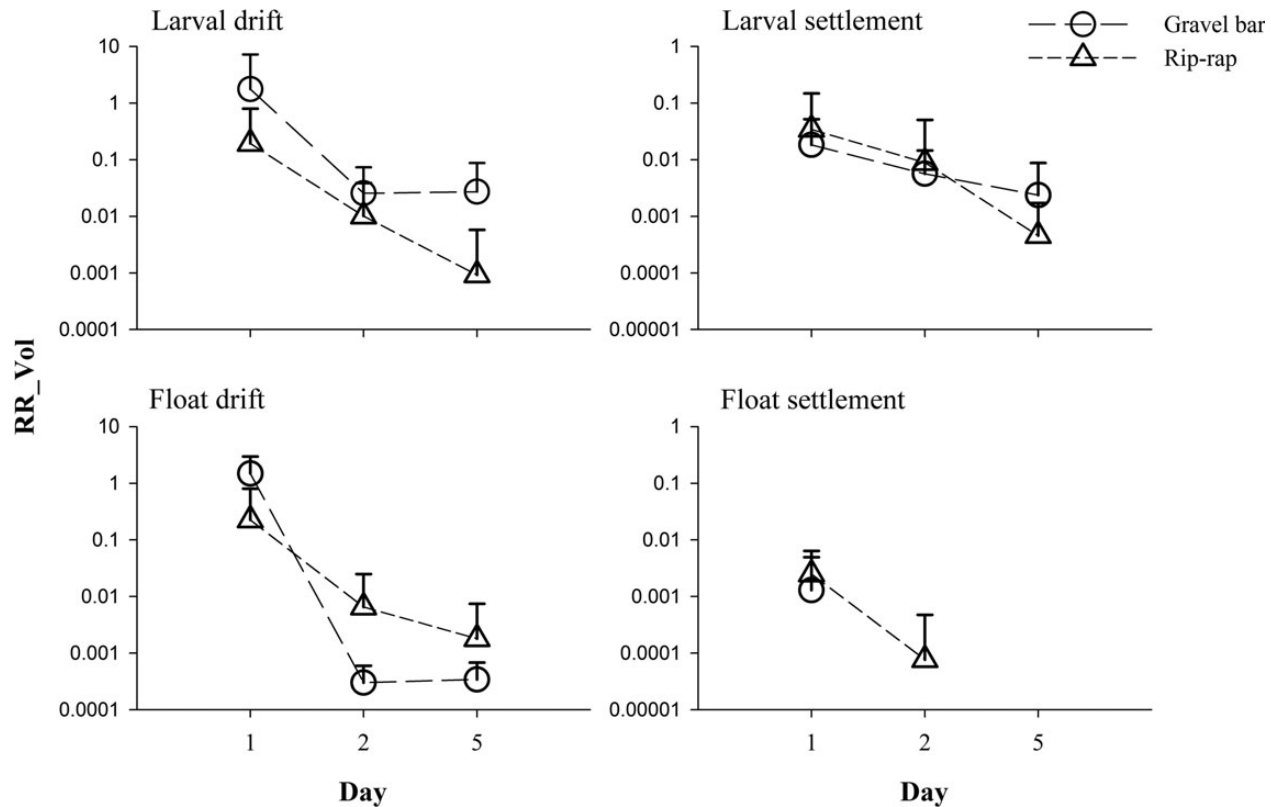


Figure 7. Temporal characteristics of drift and SRs at both shorelines. Values are plotted on a logarithmic scale.

investigated shorelines compared with passive float retention reflected larval swimming ability and behaviour. 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 with 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 (Uijttewaal *et al.*, 2001; Schwartz and Kozerski, 2003) and could therefore have enhanced passive larval introduction. The exchange rates between single groyne fields vary, depending on the flow patterns within the fields (Figure 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 (Uijttewaal *et al.*, 2001; Tritthart *et al.*, 2009). 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 the 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 (Figures 8 and 9a). Trajectories of those larvae were short and led from the swift flowing areas at the OR points into driftnets 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 washouts 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 (Figures 1 and 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 driftnets 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 days 2 and 5. The longitudinal connectivity at the rip-rap, within the investigated shore-length, was distinctly lower than at the gravel bar. To explore and colonize new nursery habitats,

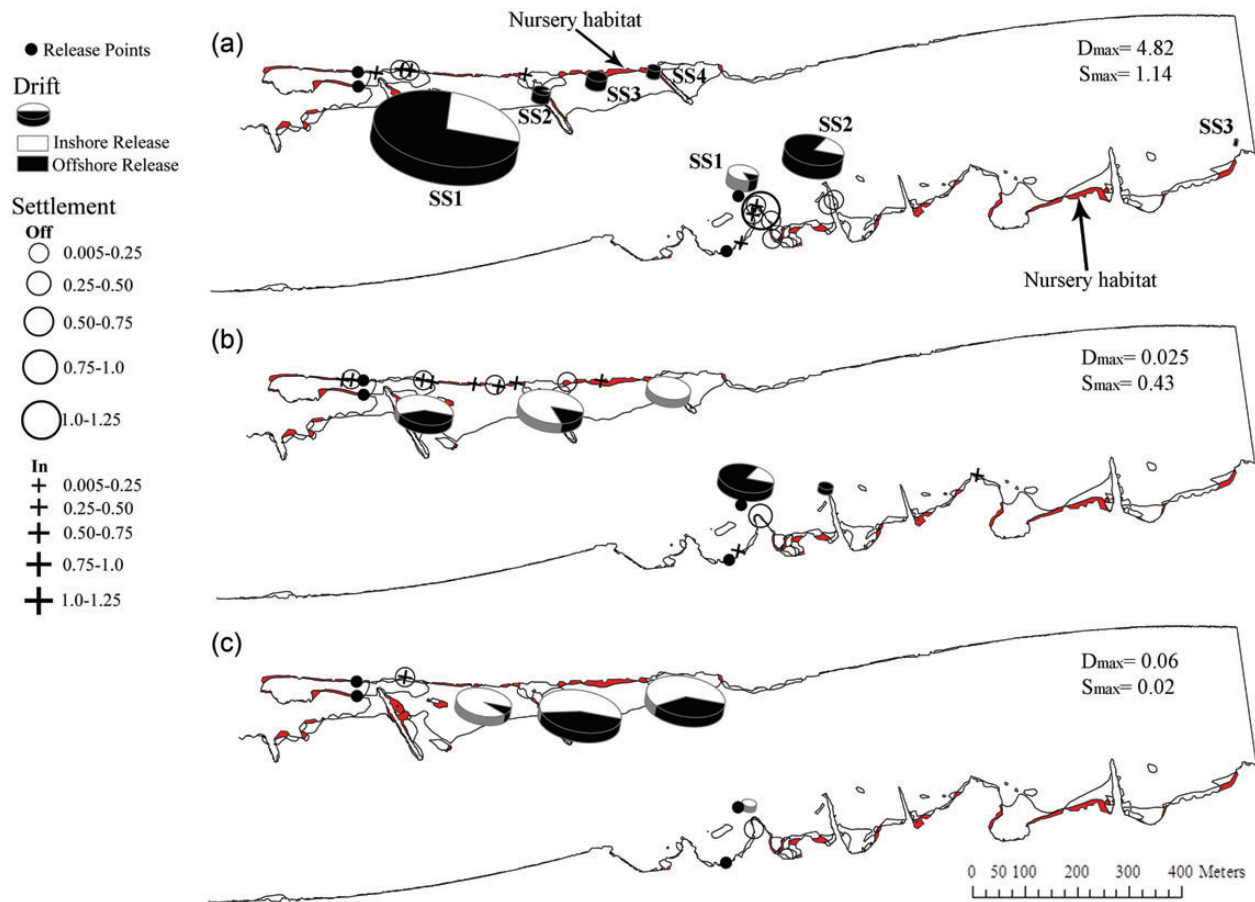


Figure 8. DRs (pies) and SRs (symbols) of L2-nase at all sampling stations (SS1–SS4) are shown for the day of release (a) and subsequent samplings on day 2 (b) and day 5 (c). Pie sizes refer to the maximum mean DR on a given day. For comparisons between days, maximum values of mean DRs (D_{max}) are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

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 SRs of IR and OR larvae served as a base to analyse 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. As a consequence, 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 patchily 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 in 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 behaviour 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 centre 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 (Gühr, 2002; Wolter et al., 2004; Kucera-Hirzinger et al., 2009), 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

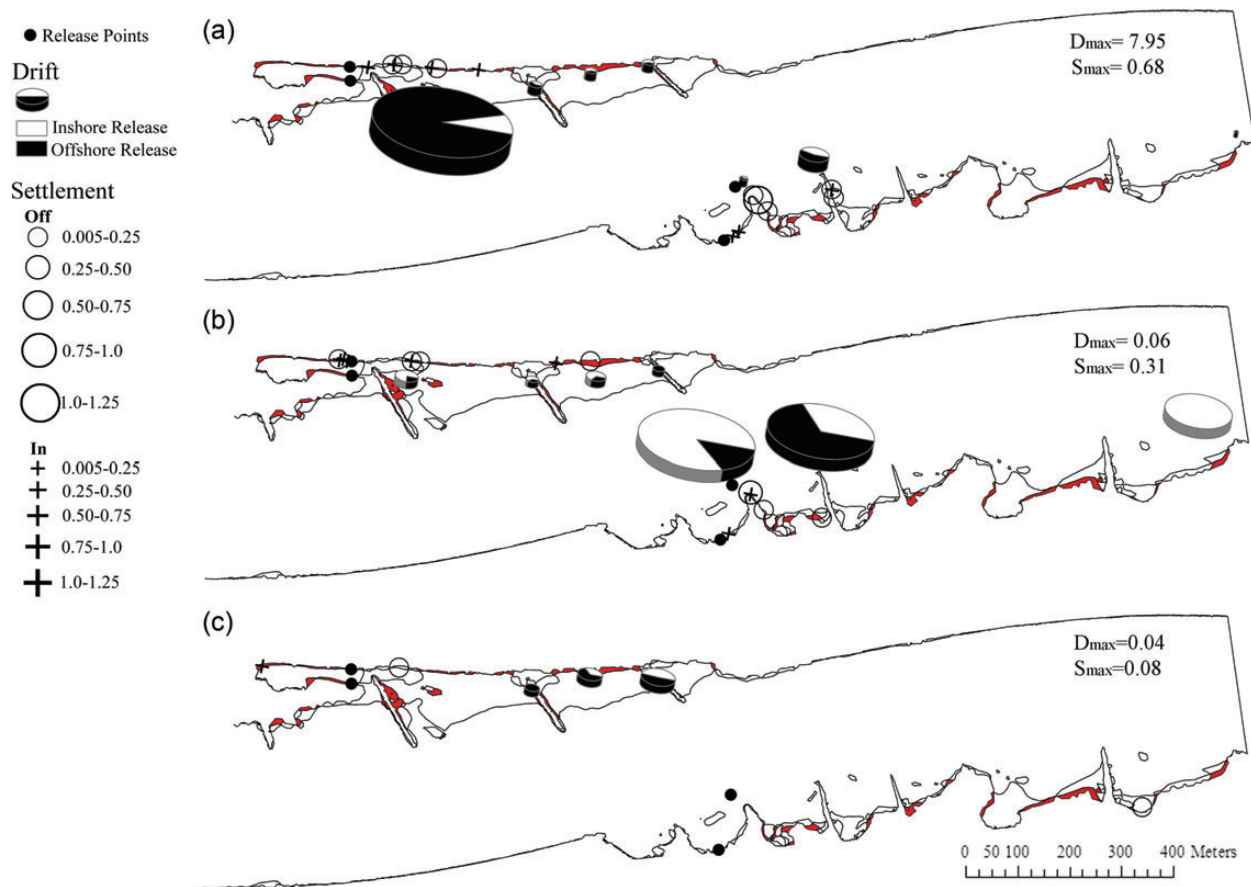


Figure 9. DRs (pies) and SRs (symbols) of L4-nase at all sampling stations (SS1–SS3) are shown for the day of release (a) and subsequent samplings on day 2 (b) and day 5 (c). Pie sizes refer to the maximum mean DR on a given day. For comparisons between days, maximum values of mean DRs (D_{max}) are given. Maximum SRs (S_{max}) are given too. Red areas along the shorelines show suitable nurseries according to [Keckeis et al. \(1997\)](#).

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, next to suitable inshore nursery habitats, presumably providing a safe route for larval dispersal. Larval DRs 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.

Acknowledgements

The authors would like to thank P. Abel, M. Jung, S. Singer, W. Obruca, N. Savio, B. Zens, R. Krusch, M. Gruber, M. Humphries, and G. Össer for their help in the field and in the laboratory. M. Stachowitsch improved the English. Gabriel Singer improved the statistics. M. N. Martinz improved the first author's life. The study was financed by the Austrian Science Fund (FWF; www.fwf.ac.at) project no. P 22631-21 B17.

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Handling editor: Claire Paris