Species-specific fish larvae drift in anthropogenically constructed riparian zones on the Vienna impoundment of the River Danube, Austria: Species occurrence, frequencies, and seasonal patterns based on DNA barcoding

Paul Meulenbroek1 | Silke Drexler1 | Daniela Huemer1 | Stephanie Gruber1 |
Susanne Krumböck2 | Pablo Rauch1 | Christian Stauffer2 | Viktoria Waidbacher1 |
Sabine Zirgoi1 | Matthias Zwettler1 | Herwig Waidbacher1

1 Vienna—Institute of Hydrobiology and Aquatic Ecosystem Management, University of Natural Resources and Life Sciences, Vienna, Austria
2 Vienna—Institute of Forest Entomology, Forest Pathology and Forest Protection, University of Natural Resources and Life Sciences, Vienna, Austria

Correspondence
Paul Meulenbroek, Vienna—Institute of Hydrobiology and Aquatic Ecosystem Management, University of Natural Resources and Life Sciences, Gregor-Mendel-Straße 33, A-1180 Wien/Vienna, Austria.
Email: paul.meulenbroek@boku.ac.at

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Abstract
As a result of river regulations over several centuries, followed by restoration measures in recent decades, most of the River Danube shoreline is man-made, primarily riprap, but some reconstructed gravel banks and riparian side arms. We investigated the effects of these different structures on fish larval dispersal over a 20-km stretch in Vienna via the use of drift nets. The habitats examined were created 18 years ago when the impoundment of the Danube hydropower station Vienna/Freudenau was constructed. About 15,000 fish larvae were trapped, and a subsample was determined to species level by DNA barcoding. In total, 26 different species were detected, including 10 species that are endangered or in danger of extinction. When species composition was considered, cyprinids become dominant at sites downstream of gravel bars, whereas in riprap sections, the majority of the larvae consist of invasive Gobiidae. Side arm habitats provide spawning and nursery grounds for additional species. Furthermore, clear species-related seasonal patterns were observed with peak densities and multiple spawning periods of some species being recorded. The largest peak of Percidae occurred in the first half of May, followed by Cyprinidae at the end of May and Gobiidae in mid-June.

KEYWORDS
artificial side arms, Danube, DNA barcoding, fish larvae, gravel bar, restoration, riprap

1 | INTRODUCTION

Fish assemblages in large rivers are highly diverse communities (Karr, 1981; Schiemer, 2000). This applies to the River Danube, where in the area of Vienna alone, 56 species were recorded in 2014 (Waidbacher, Drexler, & Meulenbroek, 2016). The conservation of riverine fish fauna is a great challenge due to the high level of degradation of river ecosystems as a consequence of the extensive utilization for navigation, hydroelectricity production, and flood control (Dudgeon et al., 2006; Morley & Karr, 2002; Schiemer, 2000).

The Danube was originally a braided river with highly diverse habitats and an absence of engineered bar protection (Hohensinner, Sonnlechner, Schmid, & Winiwarter, 2013). On the contemporary river, especially in densely populated areas, channelization shapes...
the appearance of the river, and the majority of the shorelines are dominated by riprap (Haidvogl, Guthyne-Horvath, Gierlinger, Hohensinner, & Sonnlechner, 2013; Schiemer & Waidbacher, 1992). These habitat modifications significantly affect the integrity and diversity of freshwater biota (Allan & Flecker, 1993; Karr, Toth, & Dudley, 1985; Richter, Baumgartner, Powell, & Braun, 1996).

The construction of the run-of-river power station Kraftwerk Wien/Freudenau between 1992 and 1998 was the last large-scale river engineering works undertaken on the Austrian Danube and included several environmental compensatory measures. The previously straight shoreline was reconstructed by creating backwaters, coves, gravel banks, and pools. Subsequently, further attempts have been made to restore the shorelines and provide ecologically functional habitats. These restored sections provide habitats for a wide range of fish species and different life stages (Straif, Waidbacher, Spolwind, Schönauer, & Bretschko, 2003). Within the present study, the artificial shoreline configurations were sampled with drift nets to evaluate their contributions to fish larval dispersal in the River Danube. Species composition of early life stages of fish indicates spawning ground quality within the upstream sections of the river (Humphries & Lake, 2000; Pavlov, 1994). This knowledge is of exceptional importance, as functional spawning grounds and nursery habitats are considered to be limiting factors for riverine fish populations in the contemporary River Danube (Jungwirth, Haidvogl, Hohensinner, Waidbacher, & Zauner, 2014; Jungwirth, Haidvogl, Moog, Muhar, & Schmutz, 2003). In view of these conditions, a clear species identification is essential but also challenging because during the early life history of fish, morphology changes quickly and significantly during development (Balon, 1981) from preflexion larvae to postflexion through to the pre-juvenile stage. As a result misidentification of species is likely for both rare and common taxa (Ko et al., 2013). In the last decade, DNA barcoding has become the method of choice for definition of different groups of biota (Hebert & Gregory, 2005). DNA barcoding uses a short genetic marker in an organism’s DNA to identify it as belonging to a particular species. Thus, DNA barcoding was chosen for identification of fish larvae as it is currently the most reliable and reproducible method (Pegg, Sinclair, Briskey, & Aspden, 2006; Ward, Zemlak, Innes, Last, & Hebert, 2005). The current study is the first time DNA barcoding has been used to confirm the identification of River Danube fish larvae to species level in Austria.

However, relatively few surveys have been conducted to demonstrate the functionality of such an approach worldwide (Bernhardt et al., 2005; Geist & Hawkins, 2016; Lechner et al., 2013; Palmer et al., 2005; Pander & Geist, 2013; Pander, Mueller, Knott, Egg, & Geist, 2017). In view of these conditions, the present study focuses on species-specific fish larval drift associated with different shore structures in a highly modified section of the River Danube, upstream of the hydropower plant (hpp) Freudenau/Vienna.

Three different constructed shoreline configurations: gravel bars, riparian side arms, and monotonous riprap sections, were studied over 2 years to gain information about (a) the functioning of spawning areas upstream of the sampling points; (b) species-specific differences in their contributions to fish larval dispersal; and (c) seasonal variation in drift densities.

Following the principles of ecological spawning guilds (Balon, 1975, 1990), lithophilic gravel bar spawners (e.g., *Chondrostoma nasus* and *Barbus barbus*) should increase in number in samples collected downstream of the gravel bars. The same applied to speleophilic species (e.g., *Neogobius melanostomus* and *Cottus gobio*) downstream of riprap areas.

## METHODS

### 2.1 Study sites

The study was conducted between the hpp Wien/Freudenau and hpp Greifenstein. In total, nine sites were sampled, including three gravel bars (nos 1–3), four riprap sections (nos 4–7), and two artificially
TABLE 1  Overview of sampling locations (1–9) and hpp

| Name               | No. | Type          | River km | Distance to hpp Freudenau (km) | Habitat length (km) | Mean flow velocity (m s⁻¹) |
|--------------------|-----|---------------|----------|--------------------------------|---------------------|---------------------------|
| hpp Freudenuau      | —   | —             | 1,921.05 | 0.0                            | —                   | —                         |
| Habitat C          | 8   | Side arm      | 1,926.10 | 5.0                            | 0.90                | 0.0–0.2                   |
| Impoundment C      | 4   | Riprap        | 1,927.00 | 6.0                            | 7.00                | 0.1–0.3                   |
| Habitat D          | 9   | Side arm      | 1,927.30 | 6.3                            | 0.25                | 0.0–0.2                   |
| Impoundment D      | 5   | Riprap        | 1,927.60 | 6.5                            | 6.40                | 0.1–0.3                   |
| Kuchelau           | 6   | Riprap        | 1,935.70 | 14.7                           | 2.30                | 0.3–0.5                   |
| Donauinsel         | 1   | Gravel bar    | 1,936.00 | 15.0                           | 2.00                | 0.3–0.5                   |
| Hügelland          | 2   | Gravel bar    | 1,938.10 | 17.1                           | 3.70                | 0.3–0.5                   |
| Kritzendorf        | 3   | Gravel bar    | 1,943.80 | 22.8                           | 1.50                | 1.0–1.8                   |
| Free Flow          | 7   | Riprap        | 1,946.00 | 25.0                           | 3.20                | 1.0–1.8                   |
| hpp Greifenstein    | —   | —             | 1,949.18 | 28.1                           | —                   | —                         |

Note. Habitat length indicates upstream extent of the sampled shoreline habitat. hpp: hydropower plant.

defined: Gobiidae/Cottidae (drop shape in dorsal view; often big roundish ventral fin visible), Cyprinidae p. (pigmented; fragile, elongated, body shape), Cyprinidae n.p. (not pigmented; fragile, elongated body shape), Percidae (more massive body shape, often two dorsal fins visible), and Undefined (e.g., damaged and fragments of larvae). Fish were caught in all larval stages, and juveniles were excluded. Following processing, a sample of 671 larvae was analysed using DNA barcoding to species level (Hebert, Cywinska, & Ball, 2003). The selection criteria were the abundance of each “similarity group” recorded at a sampling site for each calendar week and the potential number of species per group/family. The latter represents the proportion of potential species hidden in the five “similarity groups” (Cyprinidae p. and n.p.: 32 species; Gobiidae/Cottidae: 5 species; Percidae: 9 species; Undefined: 56 species; compared with Waidbacher et al., 2016). This number of individuals for barcoding was then randomly selected.

The most commonly used DNA barcode region for animals is a segment of the mitochondrial gene cytochrome oxidase 1 (COI; Hebert, Penton, Burns, Janzen, & Hallwachs, 2004). DNA was extracted using the GenElute Mammalian Genomic DNA miniprep kit (Sigma-Aldrich, St. Louis, USA) following the manufacturer’s instructions. Primers FishCo1-F and FishCo1-R (Baldwin, Mounts, Smith, & Weigt, 2009) were used to amplify approximately 650 bp from the 5′ region of the mitochondrial COI gene. The 20-μl polymerase chain reaction mixtures included 800 μM of dNTPs, 0.3 μM of each primer, and 0.1 μL peqGOLD Taq-DNA polymerase (peqGOLD/VWR, Erlangen, Germany) 1× reaction buffer Y (2 mM MgCl₂) and 50 ng DNA template. The thermal regime consisted of an initial step of 3 min at 94°C followed by 35 cycles of 30 s at 94°C, 45 s at 51°C, and 60 s at 72°C, followed in turn by 7 min at 72°C. Polymerase chain reaction products were sent for sequencing to Eurofins Genomics (Ebersberg, Germany) where Sanger sequencing was undertaken. Chromatograms were checked by eye using Chromas Lite 2.1.0.0 for the presence of ambiguous peaks so that only clear sequences were used for further analyses. Sequences were edited using GeneRunner 5.0.69.0. A BLAST search was performed using the nucleotide blast algorithm “blastn” in BLAST (Zhang, Schwartz, Wagner, & Miller, 2000).
2.4 Data analyses

The mtDNA verified information of the 671 individual species identifications was then proportionally calculated for the entire dataset of the 14,555 individuals caught from the sample sites across the morphological group affiliation. This was done to all seasonal and spatial aspects of species-specific patterns to be analysed (Tukey, 1977). All data presented in the result section are based on the genetic verified species level information. For the asymmetric confidence ranges (Figures 2 and 3), a random sample of all genetically analysed specimens was selected for the calculations ($\alpha = 0.1$). The affiliation to guild follows Schiemer and Waidbacher (1992) and Zauner and Eberstaller (1999) and was slightly expanded for *N. melanostomus*, which is considered as a speleophilic species (Kottelat & Freyhof, 2007).

3 RESULTS

We collected a total of 14,555 fish larvae, representing 26 species, from nine sampling points on the River Danube. The invasive Gobiidae—Round Goby (*N. melanostomus*: 30%) and Bighead Goby (*B. barbus*: 17%) dominated the samples, followed by Asp (*Aspius aspius*: 7%), Nase (*C. nasus*: 6%), Pike Perch (*Sander lucioperca*: 5%), Roach (*Rutilus rutilus*: 4%), Racer Goby (*Babka gymnotrachelus*: 4%), and Barbel (*B. barbus*: 3%). All other species were rare, accounting for less than 3% of the total.

3.1 Spatial variability

There were clear spatial distribution patterns for the family/species recorded (Figure 2): Sites downstream of gravel bars were dominated by Cyprinidae (61–65%) and similar proportions of Percidae (13–18%), Gobiidae (11–17%), and Cottidae (8–13%). Early life stages of fish caught in the side arms had a similar distribution but with higher confidence ranges. In contrast, at riprap sections, the majority of larvae consisted of speleophilic Gobiidae (47–53%) and Cottidae (23–29%). Cyprinidae (13–20%) and Percidae (7–13%) occurred less frequently in catches. However, there were also minor differences between the sampling sites along one shoreline (Figure 2; Table 2). The riprap “free flow” located furthest upstream comprised a greater proportion of Gobiidae and Cottidae, accounting for 90% of all larvae caught. A total 15 species were identified at this site including Schraetzer (*Gymnocephalus schraetzer*), which was exclusively recorded at this sampling point. Riprap “Kuchelau” displayed similar proportions of the species with Round Goby (*N. melanostomus*) being dominant but a slightly higher proportion of Cyprinid and Percid species. The third and fourth riprap sections examined within the impoundment were clearly different to the other sites, with smaller proportions of Gobiidae and Cottidae and a higher proportion of Cyprinidae and Percidae. Gobies still comprised the majority of the drifting larvae at these sites, but the Round Goby was largely replaced by the Bighead Goby (*P. kessleri*). In addition, great abundances of Pike Perch (*S. lucioperca*) and Roach (*R. rutilus*) were recorded. At all riprap sampling sites, some early life stages of Whitefish (*Coregonus sp.*) were confirmed, as well as the third non-native invasive Goby, the Racer Goby (*B. gymnotrachelus*).

The larvae recorded from sampling sites located on gravel bars were dominated by Cyprinids and Percids. Thirty per cent of all larvae recorded from the gravel bar site “Kritzendorf” were Nase (*C. nasus*). Numbers of Percidae like Zingel (*Zingel zingel*), Streber (*Zingel streber*), and Pike Perch were high. White-eye bream (*Ballerus sapa*) were only recorded at this upstream gravel bar site. There was a notable absence of Gobiidae. Three kilometres downstream at gravel bar “Hügelland”, 75% of all larvae caught were Cyprinids with a dominance of Barbel (*B. barbus*) and Nase. Unique at this site was the detection of the introduced Stone Moroko (*Pseudorasbora parva*). The third constructed gravel bar at “Donauinsel” on the left river bar differs from the other two with lower proportions of Percidae and Cyprinidae and higher proportions of Gobiidae. Over 50% of the larvae still comprise cyprinids, mostly Nase, Barbel, and Asp, around one third were Round Gobies, and a small proportion of Percidae was recorded.

In the side arm habitats, very few Gobiidae and Cottidae were caught. The majority or individuals recorded were Cyprinids. Roach were dominant in “Habitat C,” where remarkably some Carp (*Cyprinus carpio*) and Pike (*Esoc lucius*) larvae were also recorded; the latter being...
exclusively recorded in this habitat. The second side arm “Habitat D” was distinctive due to the occurrence of Bleak (Alburnus alburnus) and Chub (Squalius cephalus) along with high proportions of Perch (Perca fluviatilis) and Asp. Figure 3 illustrates that each of the shoreline types is dominated by one spawning guild; Gravel bars display high proportions of lithophilic species, riprap sites were dominated by speleophilic species, whereas the side arms supported high portions of phytophilic and phyto/lithophilic taxa.

3.2 Seasonal variability

The magnitude of drift density and the start and duration of the drifting period varied among families and species. Species-related seasonal patterns with peak densities from April to July were clearly observed in 2014. The highest peak of Cottidae occurred in the second half of April and Percidae in the first half of May. Drifting of Cyprinidae had a longer duration with the highest peak at the end of May, and Gobiidae were most abundant in mid-June (Figure 4).

There was high variation in temporal occurrence of species within the different families. Although sampling started in the beginning of April, the first larva caught was a Pike on April 16, 2014, and in the following week, five other species were recorded during their drift (Nase, Asp, Leuciscus sp., Whitefish, and Bullhead). The Bullhead drift was of relatively short duration and high intensity, and it was the first species to disappear from the catches. In the last days of April, and at the beginning of May, four species of Percidae began to drift (Zingel, Streber, Perch, and Pike Perch). The other members of this family started to drift later; first larvae of Volga Pike Perch (Sander volgensis) followed one week later, but the majority were caught in the first half of June. The Schraetzer represents a single detection at the end of

| TABLE 2 Relative distribution (%) of all species and families caught separated for each sampling sites |
|-----------------------------------|-----------------------------------|-----------------------------------|-----------------------------------|
| **Riprap** | **Gravel bar** | **Side arm** |
| Riprap | Kuchelau | Impoundment (2×) | Donauinsel | Hügelland | Kritzendorf | Habitat C | Habitat D |
| Cottidae | 30.23 | 31.50 | 9.56 | 13.10 | 2.94 | 14.90 | 1.19 | 71.96 |
| Cottus gobio | 30.23 | 31.50 | 9.56 | 13.10 | 2.94 | 14.90 | 1.19 | 71.96 |
| Cyprinidae | 8.07 | 12.14 | 34.17 | 47.50 | 73.54 | 61.35 | 61.35 | 71.96 |
| Abramis brama | 0.15 | 0.06 | 0.61 | 4.13 | 1.61 | 6.03 | 7.11 | 1.19 |
| Alburnus alburnus | 2.59 | 8.99 | 13.89 | 11.04 | 1.62 | 12.05 | 3.57 | 35.98 |
| Aspius aspius | 3.54 | 2.53 | 13.94 | 11.04 | 1.62 | 12.05 | 3.57 | 35.98 |
| Barbus barbus | 1.57 | 1.78 | 0.48 | 10.36 | 26.07 | 61.35 | 61.35 | 71.96 |
| Blicca bjoerkna | 4.83 | 4.83 | 4.83 | 4.83 | 4.83 | 4.83 | 4.83 | 4.83 |
| Chondrostoma nasus | 1.18 | 6.24 | 2.52 | 17.32 | 17.05 | 30.14 | 1.19 | 14.22 |
| Cyprinus carpio | 2.06 | 2.06 | 2.06 | 2.06 | 2.06 | 2.06 | 2.06 | 2.06 |
| Leuciscus sp. | 0.15 | 0.15 | 0.15 | 0.15 | 0.15 | 0.15 | 0.15 | 0.15 |
| Pseudorasbora parva | 4.81 | 4.81 | 4.81 | 4.81 | 4.81 | 4.81 | 4.81 | 4.81 |
| Rhodeus amarus | 0.95 | 0.95 | 0.95 | 0.95 | 0.95 | 0.95 | 0.95 | 0.95 |
| Rutillus rutillus | 0.59 | 0.69 | 10.59 | 0.00 | 11.42 | 8.31 | 42.32 | 17.99 |
| Rutillus virgo | 0.45 | 0.35 | 0.35 | 0.35 | 0.35 | 0.35 | 0.35 | 0.35 |
| Squalius cephalus | 0.15 | 0.15 | 0.15 | 0.15 | 0.15 | 0.15 | 0.15 | 0.15 |
| Esocidae | 0.67 | 0.67 | 0.67 | 0.67 | 0.67 | 0.67 | 0.67 | 0.67 |
| Esox lucius | 0.67 | 0.67 | 0.67 | 0.67 | 0.67 | 0.67 | 0.67 | 0.67 |
| Gasterosteidae | 0.10 | 0.33 | 0.33 | 0.33 | 0.33 | 0.33 | 0.33 | 0.33 |
| Gasterosteus aculeatus | 0.10 | 0.33 | 0.33 | 0.33 | 0.33 | 0.33 | 0.33 | 0.33 |
| Gobiidae | 60.07 | 50.69 | 37.92 | 37.39 | 5.88 | 7.33 | 7.33 | 7.33 |
| Bobka gymnotrachelus | 8.57 | 4.03 | 4.15 | 4.15 | 4.15 | 4.15 | 4.15 | 4.15 |
| Neogobius melanostomus | 51.51 | 42.79 | 4.48 | 30.84 | 5.88 | 7.33 | 7.33 | 7.33 |
| Ponticola kessleri | 3.88 | 29.29 | 6.55 | 6.55 | 6.55 | 6.55 | 6.55 | 6.55 |
| Percidae | 1.33 | 5.36 | 17.54 | 2.01 | 17.64 | 23.75 | 18.83 | 19.05 |
| Gymnocephalus cernua | 0.02 | 0.02 | 0.02 | 0.02 | 0.02 | 0.02 | 0.02 | 0.02 |
| Gymnocephalus schraetser | 0.02 | 0.02 | 0.02 | 0.02 | 0.02 | 0.02 | 0.02 | 0.02 |
| Perca fluviatilis | 0.15 | 0.87 | 3.37 | 5.78 | 5.78 | 2.28 | 2.28 | 14.29 |
| Sander luciperca | 0.83 | 4.24 | 11.07 | 1.79 | 6.09 | 11.66 | 16.08 | 4.76 |
| Sander volgensis | 0.10 | 1.06 | 1.06 | 1.06 | 1.06 | 1.06 | 1.06 | 1.06 |
| Zingel streber | 0.12 | 0.33 | 0.33 | 0.33 | 0.33 | 0.33 | 0.33 | 0.33 |
| Zingel zingel | 0.20 | 0.13 | 1.72 | 0.22 | 5.78 | 6.45 | 6.45 | 6.45 |
| Salmonidae | 0.20 | 0.30 | 0.48 | 0.20 | 0.30 | 0.48 | 0.20 | 0.30 |
| Coregonus sp. | 0.20 | 0.30 | 0.48 | 0.20 | 0.30 | 0.48 | 0.20 | 0.30 |

Note. \( n = 14,555 \) caught larvae; species designation is based on mtDNA verified information of 671 individuals.
June. The drifting period of Cyprinids lasted the longest time; at the end of April, Roach, Leuciscus sp., Asp, Danube Roach (Rutilus virgo), Nase, and Bream (Abramis brama) appeared, followed by Bleak and Chub at the beginning of May. Bitterling, Carp, and Barbel appeared in samples only in June. The seasonal distribution of the invasive gobies varied; the Racer Goby was first sampled at the beginning of May when its highest drift density occurred. The Bighead Goby followed in the second half of May, whereas the Round Goby was mainly recorded during June. In the second week of July, low abundances of only three species were caught: Barbel, Chub, and Round Goby. Furthermore, the duration of drifting varied among species. Most species appeared for 3 to 4 weeks, whereas some (Roach, Perch, Pike Perch, Danube Roach, Nase, and Bream) showed an extended drifting period of up to 8 weeks. Additionally, Roach, Bream, Chub, Round Goby, and Pike Perch exhibited multiple drifting peaks.

4 | DISCUSSION

Artificially constructed shorelines provide functional spawning grounds in large rivers (Pander & Geist, 2016), which can be assessed by the occurrence of early life stages of fish (Pavlov, 1994). Species-specific information is necessary to evaluate their particular contributions to fish larval dispersal within a river. Through the inclusion of species information, for example, it became apparent that gravel bars provide suitable spawning grounds for lithophilic species, whereas the side arms were rich in phyto- and lithophytophilic species (Figure 3). The effects of gravel bars (Cyprinidae dominated) and riprap sections (Gobiidae dominated) on family composition of fish larvae caught in drift samples were clear and also reported in other studies on the River Danube (Lechner, Schludermann, Keckeis, Humphries, & Tritthart, 2010). However, the present study indicates that differences within one shoreline type may also occur. These differences are even stronger when compared at the species level (Table 2).

One of the main reasons for the successful invasion of Gobiidae is that the majority of the shorelines are fixed by riprap (Ahnelt, Banarescu, Spolwind, Harka, & Waidbacher, 1998; Borcherding et al., 2013; Brandner, Auerswald, Schäufele, Cerwenka, & Geist, 2015). This observation is also supported by our results, as the sections investigated were clearly dominated by early life stages of these species, especially by the Round Goby (N. melanostomus), the most abundant drifting fish larvae and the second most frequently caught species today on the Austrian Danube (Waidbacher et al., 2016). The dominance of these shoreline configurations accelerated the expansion of this neobiota by providing spawning grounds and suitable habitats for all life stages (Brandner et al., 2015; Roche, Janač, & Jurajda, 2013). Consequently, a potential measure to reduce its abundances is to remove riprap where possible. In addition, such structural alterations affect the hydraulics of inshore areas, which may have dramatic effects on the dispersal and viability of native fish populations (Lechner et al., 2014; Schiemer, Keckeis, & Kamler, 2002).

Our results are in line with other studies (Lechner et al., 2013; Ramler, Ahnelt, Nemeschkal, & Keckeis, 2016) that report that the near natural shores provide substantially more suitable larval habitats for native fish fauna than anthropogenically stabilized shores.

One noteworthy finding is that the abundance of Bighead Goby increased compared with Round Goby from the head of the impoundment (0%) to the central impoundment (75% of Gobiidae). This might be due to changing habitat characteristics such as the reduction of flow velocity, reduced sediment loads, and constant water levels (Jungwirth et al., 2003; Ward & Stanford, 1983), which facilitated and increases the reproductive success of Bighead Goby.

Although the exact origin of the larvae caught remains unclear, our findings still indicate that some larvae drifted long distances and some probably hatched just upstream of our sampling points. An example of long-distance drifters, which were detected, was Whitefish larvae (Coregonus sp.), which were evenly distributed across the entire investigation area. There have been debates regarding the existence of a self-sustaining Whitefish population in the Danube for a long time (Holcik, 2003). In many fish surveys on the River Danube, only adults have been recorded, probably derived from stocking activities in impoundments upstream for recreational fishery purposes (Holcik, 2003; Jungwirth et al., 2014). The repeated capture of Whitefish larvae demonstrates that these spawned in the River Danube, although the evidence for the successful completion of the complete reproductive cycle is questionable as all the larvae were dead and there are no reports of juvenile Whitefish being recorded in the study area.

Within our study sites, there was a gradual increase in the number of species recorded on the course of the river, indicating drift for several kilometres downstream. This is also supported by the results of Gravel bar “Donauinsel,” which differed from the sites due to the presence of high proportions of typical riprap species, probably originating from the 10-km-long riprap stretch just upstream of the 2-km-long gravel bar. The undercut slopes in this area are characterized by high current speeds and turbulence, which probably exceeds swimming capacities of recently hatched larvae (Webb & Cotel, 2011; Wolter & Sukhodolov, 2008) and therefore results in greater drift distances (Corbett & Powles, 1986). However, the differences between gravel bar and riprap sections located in series are particularly pronounced, indicating nearby sources of the fish larvae. For the purpose of ecological river management, there is a pressing need for further research to determine drift distances of different species, in order to detect spawning grounds so that sites downstream can be designated as protected areas (Lechner, Keckeis, & Humphries, 2016).
Regardless of the drifting mode of the fish larvae (Pavlov, 1994; Pavlov, Mikheev, Lupandin, & Skorobogatov, 2008), we found evidence that (a) early life stages of fish drift into anthropogenically built side arm areas, (b) spawning activities occur within these systems, and (c) there is drift of larvae downstream of these areas indicating that they are point sources for fish larval dispersal. If there was only a unidirectional drift into the side arms, the composition of both, Habitats C and D, and the sampled riprap outside would be very similar. However, we recorded high proportions of phytophilic and litho/phytophilic species in the side arm areas, which may be anticipated given they contain high proportions of organic material and macrophytes available for spawning. They are hotspots of biodiversity in the impounded area of Vienna, and their functioning and colonization by fish and benthic invertebrates were described by Chovanec et al. (2002), Straif et al. (2003), and Waidbacher et al. (2016). This suggests that the creation of such specific habitat structures as part of restoration measures can increase the competitiveness of native species valued in conservation and is in line with other recent studies (Lechner et al., 2013; Pander, Mueller, & Geist, 2015; Pander, Mueller, Sacher, & Geist, 2016). The demonstration of the reproductive success of carp (C. carpio) within one of the artificially built side arms is particularly noteworthy, given that self-sustaining wild carp populations in the River Danube are considered particularly rare (Schiemer & Waidbacher, 1998).

In total, the 26 verified species represent nearly half of all species that have been sampled in this area between 2013 and 2015 (Waidbacher et al., 2016). This does not necessarily mean they do not reproduce here, as they may either spawn at other sites or avoid drifting. This may be the case for Bleak and Chub, which are abundant as juveniles and adults (Waidbacher et al., 2016) but are rarely caught or recorded at the larval stage as they have a negative propensity to drift (Reichard & Jurajda, 2007). Further research centred on the River Danube fish fauna is necessary, and the application of a classification proposed by Humphries and King (2003) characterizing the relevance and propensity to drift will improve interpretation of data.

Seven of the detected species recorded in this study are considered endangered (A. aspius, Cottus gobio, B. barbus, C. nasus, E. lucius, Rhodeus amarus, and Leuciscus sp.), and a further three species (C. carpio, R. virgo, and Z. streber) are in danger of extinction within the Austrian River Danube (Schiemer, Jungwirth, & Imhof, 1994; Schiemer & Spindler, 1989). On a European scale, six species (A. aspius, Cottus gobio, Rhodeus amarus, R. virgo, G. schraetser, and Z. streber) are listed in Annex II of the Flora-Fauna-Habitat Directive (Der, 1992). The reproduction and records of larvae of numerous protected and endangered species highlight the importance of these anthropogenically constructed inshore restoration structures.

All of the species recorded displayed a specific drift period. Similarly to the findings of Zitek, Schmutz, and Ploner (2004) and Janáč, Šlapanský, Valová, and Jurajda (2013), repeated occurrences of early larval stages in drift were observed. This indicates repeated spawning events for some species as the appearance in drift is directly linked to the timing of reproduction (Brown & Armstrong, 1985). In both years of the investigation, records started with 2 weeks of zero catches, clearly highlighting the start of larval drift in the middle of April.

Seasonality and duration of drifting were generally specific for each species. Most species appeared for 3 to 4 weeks, whereas some displayed an extended drifting periods of up to 8 weeks. Other studies in this area have recorded similar seasonal patterns, even though most of them did not cover the entire drifting season and therefore missed the peaks of either the early drifters (e.g., Bullhead in April) or those last to drift (Lechner et al., 2010, Ramler et al., 2016, Zitek, Schmutz, & Ploner, 2004). In the last 2 weeks of July, only a small number of Chub, Round Goby, and Barbel were recorded, indicating the end of drifting for most species. Other studies have reported drifting periods through to September, especially for the invasive Round Goby (Borcherdinger et al., 2016, Janáč et al., 2013, Meulenbroek et al., in prep).

The knowledge generated on the seasonal variability of drifting linked to spatial variation can be used to help inform conservation measures. For example, navigation or other activities could be modified in areas were fish reproduction of endangered species occur during their drifting season, as these practices have negative effects on the survival rates of fish larvae (Pavlov et al., 2008; Wolter & Arlinghaus, 2003).

5 CONCLUSION

This study indicates that the artificial shoreline areas investigated, riprap, gravel bar, and side arms are potentially used as spawning grounds for riverine fish species. Furthermore, these different shoreline configurations determine the species composition of fish larval dispersal in the River Danube with a species-specific periods of drifting. The relevance of the habitat mitigation measures examined (gravel bar and riparian side arms) highlights the apparent reproductive success of numerous protected and endangered species. The results of this study therefore provide the basis for effective conservation and management of riverine fish populations. Furthermore, the effect of monotonous riprap shorelines on the spatial distribution and potential spread of the invasive Gobiidae is clearly documented.

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