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Ecological Responses of Fish to Engineered Mitigation Measures at the Danube Hydropower Impoundment Vienna, Austria

Dissertation
at the University of Natural Resources and Life Sciences Vienna

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Vienna, April 2019

Dear Friend,

Go with the flow
Be thoughtful of those downstream
Slow down and meander
Follow the path of least resistance
for rapid success

Immerse yourself in nature,
trickling streams,
roaring waterfalls,
sparkles of light dancing on water
Delight in life's adventures around every bend
Let difficulties stream away

Live simply and gracefully in your own true nature
moving, flowing, allowing,
serene and on course
It takes time to carve the beauty of the canyon
Rough waters become smooth
Go around the obstacles
Stay current

The beauty is in the journey!

--- Ilan Shamir ---

--- *Chondrostoma nasus* ---

Content

Abstract

For several centuries, most of the Danube river shoreline has been modified mainly for navigation, flood protection, and hydroelectric power generation. These man-made shorelines, primarily ripraps, do not provide the essential requirements of riverine fish to build self-sustaining stocks. In recent decades, restoration measures have been taken to improve the situation with reconstructed gravel banks, riparian side arms, and lateral connections of backwaters or fish by-passes. Riverine fish are good indicators of the quality of habitat structure, as well as of the ecological integrity of river systems because of rather complex habitat requirements needed at different stages of their life cycles. A near-natural fish by-pass system, gravel banks, and riparian side arms were assessed for their functioning as fish habitats at different life stages of fish. The study was conducted 15 years after the implementation of theses mitigation measures. A total of more than 30,000 fish of 48 species, including several protected and endangered species, in all life stages, including eggs, larvae, juveniles, and adults, were sampled. The indicator species of the free-flowing River Danube are nase (*Chondrostoma nasus*) and barbel (*Barbus barbus*), which migrated into the near-natural fish by-pass and successfully spawned before returning. A heterogenic habitat configuration provided conditions for all ecological guilds, and consequently, increased biodiversity. The chosen solution of the constructed by-pass system exhibited similar functions as a natural tributary. Furthermore, the effect of constructed gravel bars and riparian side arms on species-specific fish larval dispersal (identified via mt-DNA barcoding) were investigated over a 20-km stretch of the River Danube in Vienna by sampling with drift nets. Cyprinids were dominant at sites downstream of gravel bars, whereas in the riprap sections, the majority of the larvae consisted of invasive Gobiidae. Side arm habitats were identified as multifunctional sites, providing spawning and nursery grounds for a variety of species. Finally, recommendations and management aspects are discussed.

Dissertation outline

The present dissertation is submitted as a cumulative dissertation that is built upon two peer-reviewed papers in scientific journals and one book chapter related to one common topic as stated in the title of the dissertation. All articles have been published and are included as original reprints. The additional text sets the frame for the scientific background and complements the objectives and findings of the papers. More specific aspects are provided in the original papers attached at the end of the dissertation.

[A 1] MEULENBROEK P., DREXLER, S., HUEMER, D., GRUBER, S., KRUMBÖCK, S., RAUCH, P., STAUFFER, C., WAIDBACHER, V., ZIRGOI, S., ZWETTLER, M. & WAIDBACHER, H., 2018a: 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. River Research and Applications 34, 854-862. -> (MEULENBROEK et al., 2018A)

[A 2] MEULENBROEK P., DREXLER, S., NAGEL, C., GEISTLER, M. & WAIDBACHER, H., 2018b: The importance of a constructed near-nature-like Danube fish by-pass as a lifecycle fish habitat for spawning, nurseries, growing and feeding: a long-term view with remarks on management. Marine and Freshwater Research 69, 1857-1869. -> (MEULENBROEK et al., 2018B)

[A 3] WAIDBACHER H., DREXLER, S.-S. & MEULENBROEK, P., 2018: Danube Under Pressure: Hydropower Rules the Fish, in: SCHMUTZ, S., SENDZIMIR, J. (Eds.), Riverine Ecosystem Management. Springer, Cham, pp. 473-489. -> (WAIDBACHER ET AL., 2018)

Figure 1 gives a graphical overview of topics and spatial scales addressed in these articles.

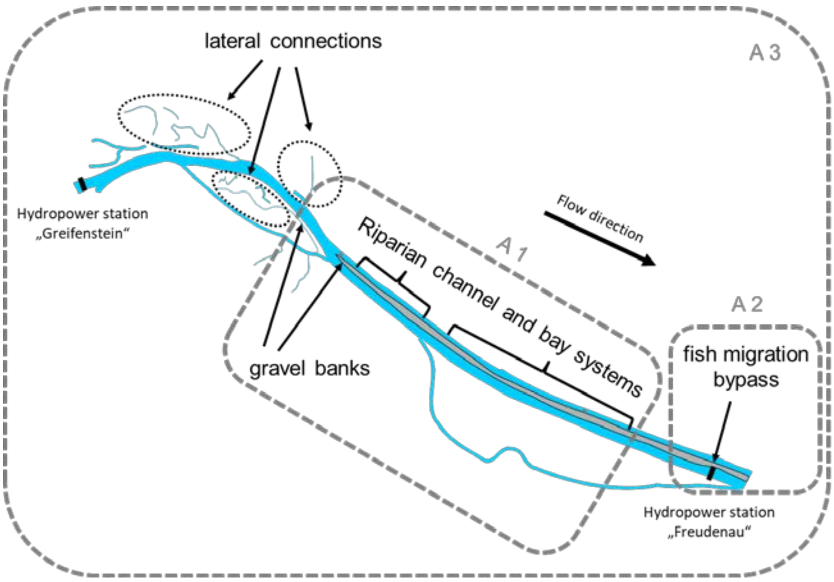

Figure 1. Location of different mitigation measurements at the impoundment "Freudenau" in the River Danube and the topics/spatial scale of the articles (A 1. (MEULENBROEK et al., 2018A), A 2. (MEULENBROEK et al., 2018B), A 3. (WAIDBACHER et al., 2018))

Synthesis

1. Introduction

1.1. The original river Danube and its fish habitats

Large rivers exhibit highly diverse fish communities (KARR, 1981, SCHIEMER et al., 2000). This also applies to the River Danube in Vienna, where 56 species were recorded in 2014 (WAIDBACHER et al., 2016). The upper part of the River Danube is topographically well defined by its high slope (0.43‰ in Austria) and high bedload transport. Large tributaries from the Alps considerably increase river discharge, which reaches a mean value of approximately 2,000 m^3/s eastward from Vienna (LIEPOLT, 1967, SCHIEMER & WAIDBACHER, 1992). In this section, the Danube was a braided river with highly diverse habitats and an absence of engineered bank protection (HOHENSINNER et al., 2013). It was characterized by large alluvial areas, especially in the plains of Eastern Austria. A variety of river arms offered a rich diversity of gradients of flow velocity, substrate, and riparian vegetation (Compare Figure 2: Years 1570 - 1849). This provided ideal conditions for the development of the typical Austrian Danube fish community (HOHENSINNER et al., 2004).

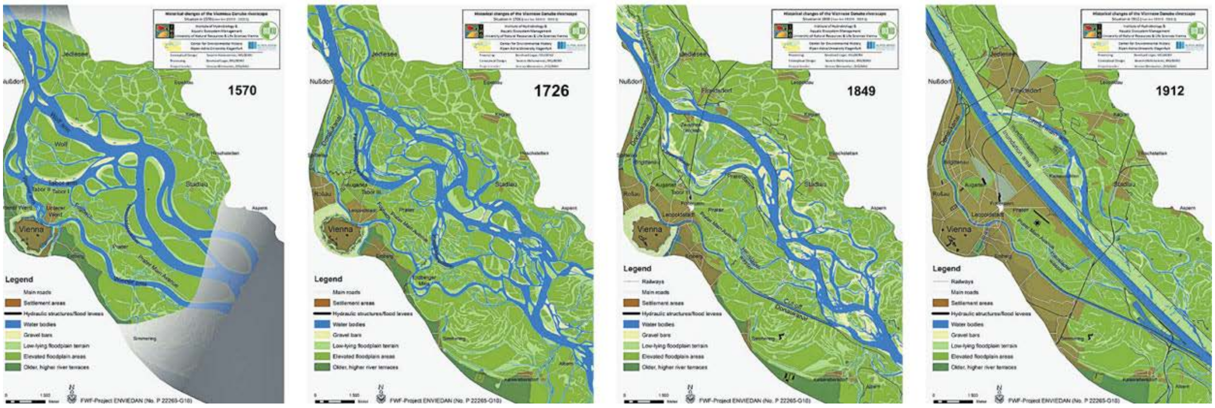

Figure 2. Reconstructed state of the Danube riverscape in Vienna in 1570, 1726, 1849, and 1912 (HOHENSINNER et al., 2013)

The diversity of the above-mentioned habitats is the basis for a rich species community as diverse niches for different fish species are available (JUNGWIRTH et al., 2000). The relevant biological requirements also change during the life cycle and during ontogeny (KARR, 1991, SCHIEMER, 2000). Several studies have documented these habitat changes by fishes within the main channel environment (COPP, 1990, SCHIEMER & ZALEWSKI, 1991, SCOTT & NIELSEN, 1989). The various guilds integrate a wide range of riverine conditions via migration (COPP, 1989, SCHIEMER, 2000, SCHIEMER & WAIDBACHER, 1992).

Apart from seasonal migration to different life cycle habitats, facultative and daily shifts are performed as well. These movements compromise visits to winter habitats (CUNJAK, 1988, 1996) and refugia under harsh environmental conditions, such as floods, draughts or other environmental disturbances (SCHLOSSER, 1995). Fish of all development stages also perform daily migration to different feeding habitats during the day (SCHIEMER & SPINDLER, 1989, SCHLOSSER, 1995), as well as to night and day habitats (CROOK et al., 2001, SEMPESKI & GAUDIN, 1995). The following basic scheme (Figure 3) gives an overview of these ontogenetical, seasonal, daily, and facultative habitat shifts of riverine fish.

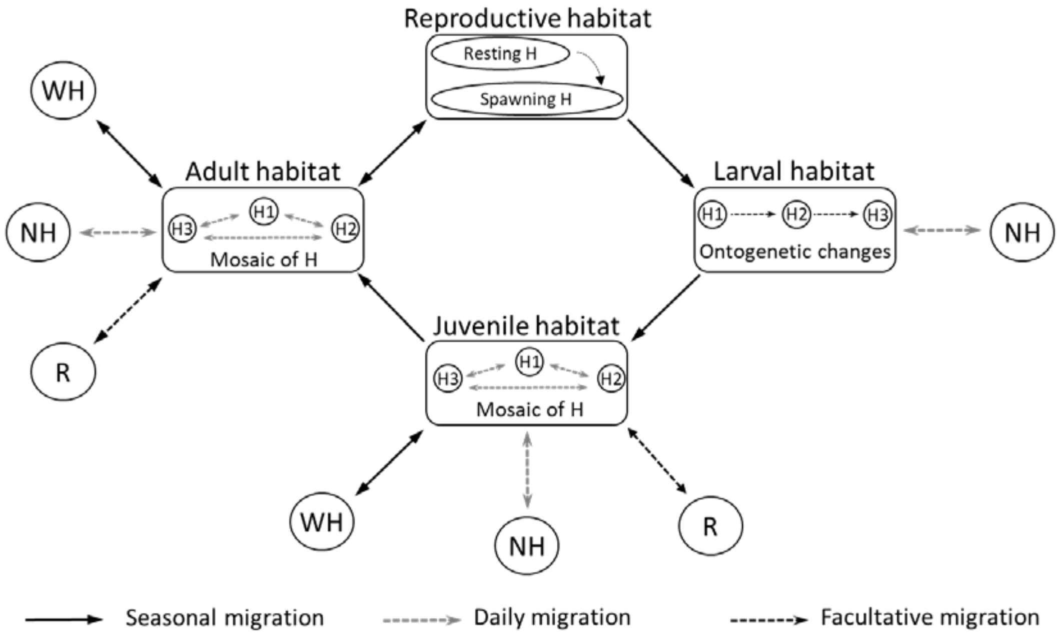

Figure 3. Basic scheme of seasonal and daily migration patterns of riverine fish, with emphasis on their life cycle and habitat use. Each box/cycle represents a specific habitat with certain characteristics: WH … Winter habitats, NH … Night habitats, R … Refuge from harsh environmental conditions, H … Habitat for feeding. Lines indicate seasonal, daily, and facultative migration between them (AFTER JUNGWIRTH et al., 2012, SCHIEMER & SPINDLER, 1989, SCHLOSSER, 1995) (adapted after MEULENBROEK et al., 2018C).

In conclusion, the availability of different habitat types provides the basis for
(1) different species and their habitat niches/requirements,
(2) changing requirements concerning species-specific demands for completion of the life cycle of each species (spawning ground, nursery, and feeding habitats),
(3) daily migration to night and feeding habitats, and
(4) facultative refugia, under harsh environmental conditions.

A prerequisite for migration between these different habitats is a functioning connectivity at different scales (MEULENBROEK et al., 2018C). Therefore, fish are good indicators of habitat structure, as well as of the ecological integrity of river systems because of their complex habitat requirements at different stages of life cycles (SCHIEMER, 2000, SCHIEMER & WAIDBACHER, 1992, SCHMUTZ & JUNGWIRTH, 1999).

1.2. River regulations and mitigation measures

As a result of river regulations and hydromorphological alterations for navigation, flood protection, hydroelectric power generation, as well as the disconnection of tributaries, especially in large rivers, such as the Danube, riverine habitats are degraded and fragmented (compare Figure 2) (DUDGEON et al., 2006, MORLEY & KARR, 2002, SCHIEMER, 2000). The construction of impoundments causes a disruption of the connection between the river and the lateral backwaters, a change in the shorelines, and a stabilization of the previously fluctuating water levels, as well as other impacts, thereby completely changing the ecological functions of river system (SCHIEMER & WAIDBACHER, 1992). These impoundments neither provide riverine conditions (reduced flow, increased depth, silty to muddy sediments resulting from increased sedimentation) nor lacustrine characteristics (low average annual temperature of the river, the lack of shoreline structures, no stratification, short retention times, and low plankton density). The original dominant riverine fish species could mainly be found in the last remaining free-flowing sections, or in the uppermost part of the impoundments (WAIDBACHER, 1989). The conservation of riverine fish fauna is a great challenge because of the high level of degradation of river ecosystems (DUDGEON et al., 2006, MORLEY & KARR, 2002, SCHIEMER, 2000). Particularly, the lack of functional spawning grounds, nursery habitats, and reduced connectivity are now considered to be limiting factors for riverine fish populations in the Danube (JUNGWIRTH et al., 2014, JUNGWIRTH et al., 2003, KECKEIS & SCHIEMER, 2002, PANDER & GEIST, 2010). According to the key objective of the European Water Framework Directive (WFD), all waterbodies in the EU need to achieve a “good ecological status,” defined as slight deviation from the biological community (fish, benthic invertebrates, and aquatic flora) that would be expected in conditions of minimal anthropogenic impact (EUROPEAN-PARLIAMENT, 2000). In the case of the 350 km-long Austrian Danube river, intensive human uses constrain the implementation of comprehensive rehabilitation programs to achieve good ecological status. For such “heavily modified waterbodies,” a basically similar approach applies, targeting the “good ecological potential” as a slight deviation from the “maximum ecological potential” (EUROPEAN-PARLIAMENT, 2000, JUNGWIRTH et al., 2005).

Additionally, unless a certain level of resilience of the system exists, restoration measures in such heavily modified river stretches are likely to need on-going management (PALMER et al., 2005). Pre- and (long-term) post-monitoring is essential for an adaptive restoration and management approach for improving running water ecosystems and for the sustainable functioning of the measures (DOWNS & KONDOLF, 2002, PALMER et al., 2007).

In light of the above-mentioned degradations and the need for action caused by the WFD and national laws, strategies have been developed to counteract and minimize negative impacts caused by the construction of new hydropower dams. In the last decades, only a small number of rehabilitation measures along the Austrian Danube were undertaken and their effect on the fish fauna is only partly documented (e.g. KECKEIS, 2014, SCHABUSS & RECKENDORFER, 2006, WAIDBACHER, 1989, WAIDBACHER et al., 2016, ZAUNER et al., 2016, ZAUNER et al., 2001).

During the construction of the latest Danube hydropower plant at "Freudenau" in Vienna between 1993 and 1998, efforts were made to maintain the ecological integrity of the river system by introducing several mitigating measures. These include improving the lateral connection between the river and the backwaters, creating large gravel areas, and increasing the diversity of the inshore riverbed structures to improve the quality of spawning substrates and nurseries for fish (WAIDBACHER et al., 2018, WAIDBACHER et al., 1996). However, several studies concluded that relatively few surveys have been conducted for large rivers to demonstrate the functionality of such approaches (BERNHARDT et al., 2005, GEIST & HAWKINS, 2016, LECHNER et al., 2013B, PALMER et al., 2005, PANDER & GEIST, 2013, PANDER et al., 2017).

2. Objective and definition of the research topic in the propounded articles

The primary research objectives in article [A 3] have been to demonstrate the complex scheme of impacts of the Danube hydropower impoundments on native fish associations, to give an overview of possible mitigation measures, and to summarize the ecological response, and sustainability of the constructed habitat improvements in Vienna/Freudenau 15 years after construction.

For article [A 1] and [A 2], we studied selected mitigation measures over two years in more detail and evaluated their functioning as habitats for selected life stages. Article [A 1] focuses on species-specific fish larvae drift associated with different shore structures. Three different constructed shoreline configurations: gravel bars, riparian channels, and monotonous riprap sections, were studied 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. In article [A 2], we studied the near-natural by-pass system in Freudenau-Vienna and its function as a "mitigation-habitat". We hypothesized that the fish by-pass would provide habitats for spawning, nurseries, growth, and feeding. Furthermore, the heterogenic configuration should provide conditions for different species compositions. Therefore, we sampled fish larvae, juveniles, and adult fish and analyzed species occurrences, as well as spatial and temporal differences of assemblage structure. Figure 1 in the Dissertation outline gives a graphical overview of topics and spatial scales addressed in the articles.

3. *Innovative methodical aspects*

Noteworthy is that the present study (MEULENBROEK et al., 2018B) **[A 2]** is the first that investigates habitat use of a by-pass at large rivers such as the Danube, considering all life stages of fish (eggs, larvae, juveniles, and adults) from a broad range of species (43) over two years. Juvenile and adult fish were sampled by point abundance electrofishing (COPP & PEŇÁZ, 1988). Drift nets similar to ZITEK ET AL. (2004) with two equilateral triangle openings were used to collect early life stages of fish. A detailed description of the applied and standardized methods can be found in the two attached publications (MEULENBROEK et al., 2018A, MEULENBROEK et al., 2018B) **[A 1 and 2].**

However, this is the first time that DNA barcoding has been used to identify riverine fish larvae and eggs to the species level.

Traditionally, larval fish identification has always used morphological characters, such as body shape, pigmentation, mouth position, meristic counts, and measurements. Most of the available literature on the identification of the early life stages of fish is limited to certain groups and certain larval stages (e.g. BALINSKY, 1948, PINDER, 2001, SPINDLER, 1988, URHO, 1996). Already the correct allocation to a specific larval stage reveals the first difficulties. Metamorphosis can be a threshold, or sometimes a longer interval, during which some larval stage-specific structures remain while some others appear. Many species share the same morphology and some can change quickly and significantly during the development from preflexion to postflexion larvae (BALON, 1990, COPP & KOVÁC, 1996). Furthermore, in large rivers with a high diversity of fish species the usage of multiple keys is not expedient. Additionally, as mentioned by KO et al. (2013), different larval fish taxonomists may have different capabilities, skills and experiences in identification, so even the same specimen can be identified inconsistently, which makes data comparison difficult. Other practical difficulties derive from damaged fish larvae, hybridization, body deformations caused by alcohol fixation, etc. Caused by these comprehensible limitations, large parts of the conducted studies in the literature on the early life stages of riverine fish either

a) analyze their results on family or genus level (e.g. LECHNER et al., 2013A, RAMLER et al., 2016),

b) experiment with artificially hatched fish from a known broodstock, (e.g. LECHNER et al., 2013B, SCHLUDERMANN et al., 2012), or

c) focus on aspects of single species or selected groups (e.g. COPP et al., 2002, KECKEIS et al., 1997, SCHIEMER et al., 2002).

Surprisingly most of the publications have non-transparent and difficult verifiable methods for their identification of the fish larvae. The given information ranges from, their own collection of comparative material, the usage of their own keys, based on experience, raising juveniles, based on the assumption of occurrences, or no information is given at all (e.g. BORCHERDING ET AL., 2016, COOPERMAN ET AL., 2010, DE GRAAF ET AL., 1999, FALKE ET AL., 2010, HUMPHRIES & LAKE, 2000, JANÁČ ET AL., 2013, REICHARD & JURAJDA, 2007, WOLTER & SUKHODOLOV, 2008).

A clear and reliable method for species identification is DNA barcoding which was developed in 2003 (HEBERT ET AL., 2003). The application to larval fish identification has become popular in recent years for marine environments (e.g. HUBERT et al., 2010, KO et al., 2013, PEGG et al., 2006) but has not arrived at river environments. The most commonly used DNA barcode region for animals is a segment of the mitochondrial gene cytochrome oxidase I (COI) (HEBERT ET AL., 2003). We used the primers FishCo1-F and FishCo1-R (BALDWIN ET AL., 2009), and for some individuals the cytochrome b primers KAI_F and KAI_R (KOTLIK ET AL., 2008). The total catch of more than 20,000 fish larvae was identified to family level and subsamples were analysed genetically (compare MEULENBROEK et al., 2018A, MEULENBROEK et al., 2018B) [A 1 and A 2]. Therefore, first reliable species-specific results on riverine fish larvae (and eggs) are presented.

4. *Literature review and discussion of the publications*

The introduction gave an overview of the variety of habitat requirements of riverine fish, the reason for their degradation, and the need for mitigation measures in the river Danube. In the following, basic schemes of impacts on the fish fauna, implementation of mitigation measures and their ecological response are discussed with regard to the findings of the publications. More details and specific aspects are provided in the publications and are attached at the end of the Dissertation.

4.1. Scheme of impacts of Danube hydropower impoundments on native fish

Fish communities are good indicators for the ecological integrity of river systems because a broad spectrum of abiotic variables of different spatio-temporal scales is linked to their complex habitat requirements that shift in the course of their lifecycles (JUNGWIRTH et al., 2000, SCHIEMER, 2000, SCHMUTZ & JUNGWIRTH, 1999). The changes in population structures and abundances induced by damming can be elucidated either by comparing the fish fauna in free-flowing sections with that of impounded areas or by a pre- and (long-term) post-monitoring. The first and at a large scale of such investigations in River Danube were done as part of an interdisciplinary study of the impoundment of "Altenwörth" in the mid-1980s (SCHIEMER & WAIDBACHER, 1992, WAIDBACHER, 1989) and at the impoundment of "Freudenau" in the mid- 2010s (WAIDBACHER et al., 2016).

WAIDBACHER et al. (2018) **[A 3]** recapitulates and adds new comparative results of these two investigations: The free-flowing section of the "Wachau" is characterized by a dominance of rheophilic species, such as barbel (*Barbus barbus*) and nase (*Chondrostoma nasus*), that occur at high abundances, followed by a distinct predominance of eurytopic species [e.g., roach (*Rutilus rutilus*) and bleak (*Alburnus alburnus*)] in the impounded section. The species composition between the uppermost part of the impounded river, with high flow velocity and coarse-grained sediments, and the central part of the impoundment, with reduced flow, and monotonous shoreline structures, is not very different. However, the population density declines noticeably in the main impoundment of the characteristic riverine species. An analysis of the size structure shows that close by the dam, only old age classes are represented. Flow velocity and the littoral substrates (mainly riprap) are not adequate to function as spawning sites and rearing areas for native riverine species.

MEULENBROEK et al. (2018A) **[A 1]** ads new insights on the impacts of Danube hydropower impoundments on native fish, as it compares species specific aspects of fish larval dispersal of riprap section in the impoundment and gravel bars in the head of the impoundment. The latter provides spawning for native lithophilic species, whereas the riprap shorelines are dominated by early life stages of invasive gobies,

especially the round goby (*Neogobius melanostomus*). The dominance of riprap shoreline configurations accelerated the expansion of this neobiota by providing spawning grounds and suitable habitats for all life stages (BRANDNER et al., 2013, ROCHE et al., 2013).
Our results are in line with other studies (LECHNER et al., 2013B, RAMLER et al., 2016) that report that the near natural shores provide substantially more suitable larval habitats for native populations (LECHNER et al., 2013A, SCHIEMER et al., 2002). However, in the present study, this is for the first time that species-specific differences at a large number of sites (9) and shoreline types (3) have been compared and interpreted.

4.2. Implementation of mitigation measures and the ecological response

To enhance the ecological situation in this degraded river system, and to fulfil the need for action caused by legal obligations, rehabilitation measures have to focus on the provision and improvement of type-specific river habitats like spawning and nursery grounds, which are considered to be limiting factors in the Danube nowadays (JUNGWIRTH et al., 2014, JUNGWIRTH et al., 2003, KECKEIS & SCHIEMER, 2002, PANDER & GEIST, 2010). Targeting this thematic background, WAIDBACHER et al. (2018) [A 3] presented restoration types that could be considered the most promising for achieving the objectives of the Water Framework Directive. Those are based on the results of research at the “Altenwörth” impoundment in the mid-1980s, containing the creation of:

(a) Dynamic gravel banks
(b) Dynamic sand habitats
(c) Shelters in times of flood events
(d) Possibility for upstream migration
(e) Lateral connections of water bodies
(f) Riparian bays and channel systems

Some of these recommendations were implemented during the construction of the hydroelectric power plant Vienna/Freudenau between 1992 and 1998 (compare Figure 1). This was the first time that a wide range of measures had been introduced to mitigate the impacts of the habitat alterations caused by construction. Additionally, a long-term post-monitoring enables an adaptive restoration and management approach for the sustainable functioning of the measures (DOWNS & KONDOLF, 2002, PALMER et al., 2007). In the following, the ecological response of selected measures is summarized and discussed.

4.2.1. Gravel banks

Gravel banks are essential for various life stages of most of the native rheophilic species (SCHIEMER & WAIDBACHER, 1992). In the head of impoundments, relative high water level fluctuations occur, and the creation of type-specific gravel bars by river widening or by re-establishment along the embankments or as islands within the main channel are viable options (JUNGWIRTH et al., 2005). Instream constructed gravel bars can be protected against major erosion into the main channel by the construction of an underwater riprap, or by setting up groyne fields to ensure its ecological function over a longer period of time (WAIDBACHER et al., 2018) **[A 3]**.

MEULENBROEK et al. (2018A) **[A 1]** represents the first study evaluating the contribution of different shoreline configurations (gravel bank, riprap, and riparian channel) on fish larval dispersal at the species-level in the Danube, based on mtDNA barcoding. There were clear spatial distribution patterns for the family/species recorded: Sites downstream of gravel bars were dominated by Cyprinidae (61–65%) followed by Percidae (13–18%), Gobiidae (11–17%), and Cottidae (8–13%). 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. The clear effects of gravel bars and riprap sections on family composition are also reported in other studies on the River Danube (LECHNER et al., 2010, RAMLER et al., 2016). However, the present study indicated that differences within one shoreline type also occur when species information is considered as well. The three investigated gravel bars exhibit different shares of species occurrences (e.g. *Barbus barbus* ranges from 0 % -30%) and several species were restricted to only one of the sites (e.g. *Zingel streber, Ponticola kessleri, Leuciscus* sp*., Blicca bjoerkna, Pseudorasbora parva,* or *Alburnus alburnus*). These species-specific differences have several implications and highlight the need for further research.
Possible explanations include that the gravel banks differ in their suitability for a successful reproduction for the different species or other factors that influence the year-to-year chance for the occurrence of certain species and their reproduction on a specific site. Nonetheless, it clearly indicates that the creation of multiple gravel banks increases the probability of creation of spawning grounds for a wide range of species.

4.2.2. Riparian channel and bay systems

Based on the location in the impoundment, two parts can be divided: one part exhibits no fine sediments and flow velocity (>1 m/s), where a riverine fish assemblage has developed and persists even after 18 years of impounding. In the second part, located closer to the hydropower plant, sediment deposition along the shoreline is not cleared and some reduced flow situations are present with macrophytes, beaver dams, reeds, and other structural elements. If deep enough these zones can act as shelters during flood events. Unfortunately, some of the created habitats completely dewater when the water level of the impoundment is lowered during a flood event and lose their functions (SCHMUTZ et al., 2014, WAIDBACHER et al., 2016). The constructed riparian bays are hotspots of fish and benthic invertebrate biodiversity in the central impoundment as shown by WAIDBACHER et al. (2018) [A 3], CHOVANEC et al. (2002) and STRAIF et al. (2003).

In addition, MEULENBROEK et al. (2018A) [A 1] evaluated the functioning of these systems as spawning and nursery grounds for riverine fish. The two riparian channels sampled had a length of 1.1 km and 0.4 km, respectively. The majority of larvae recorded were Cyprinids. The longer channel was dominated by roach (*Rutilus rutilus*), and remarkably some carp (*Cyprinus carpio*) and pike (*Esox lucius*) larvae were also recorded.

The second one was distinctive because of the occurrence of bleak (*Alburnus alburnus*) and chub (*Squalius cephalus*) along with high proportions of perch (*Perca fluviatilis*) and asp (*Leuciscus aspius*). However, in both side arms, we recorded high proportions of phytophilic and litho/phytophilic species, which could be explained by the high proportions of organic material and macrophytes available for spawning. Furthermore, we found evidence that

(a) early life stages of fish drift into human-built side arm areas,

(b) spawning activities occur within these systems, and

(c) there is a drift of larvae downstream of these areas indicating that they are point sources for fish larval dispersal.

These factors identify the multiple functions of these habitats in providing suitable nursery and spawning grounds for an essential variety of Danube fish species. In another study, MEULENBROEK et al. (IN PREP.) outlined that these shoreline improvements increase the total number of species and abundances significantly when compared with the monotonous riprap sections. In some instances, additionally, a lower number of non-native species was observed (Figure 4).

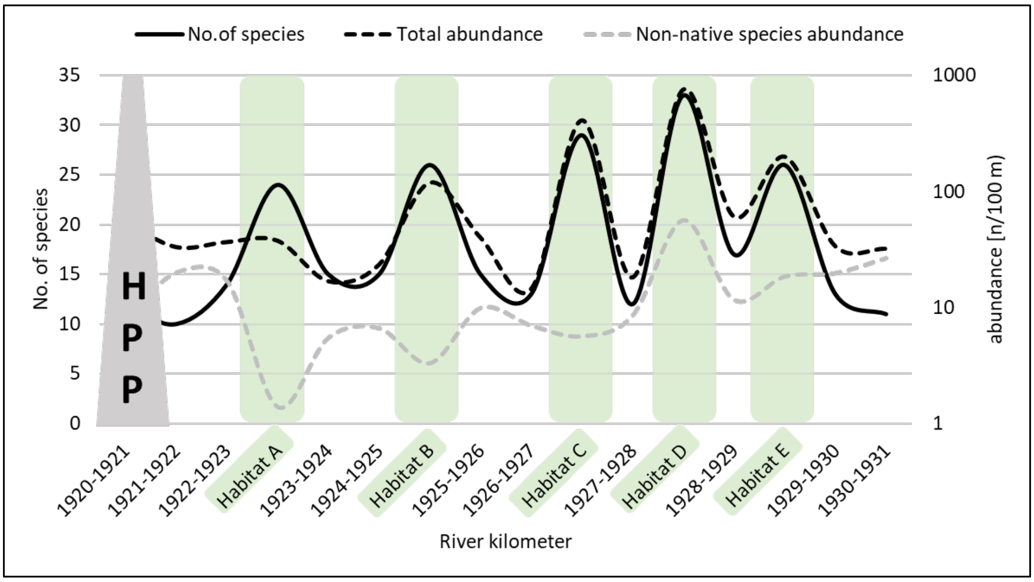

Figure 4. Number of species, total abundance [n/100m] and non-native species abundance [n/100m] along the shoreline of the impoundment Vienna, between river kilometer 1920 and 1931; the locations of the riparian channels are highlighted in green; location of hydropower plant (HPP) is indicated in grey (adapted after MEULENBROEK et al. (IN PREP.)).

Therefore, WAIDBACHER et al. (2018) **[A 3]** concluded that fish assemblages in the impoundment of "Freudenau" followed the same pattern as in other Austrian Danube impoundments if the riparian mitigation measures were not taken under consideration. This suggested that the creation of such specific habitat structures, as part of restoration measures can increase the competitiveness of native species valued in conservation.

4.2.3. Fish by-pass as a lifecycle fish habitat

The focus for the implementation of fish by-passes has mostly been driven to enable migration corridors. Investigations showed that a free passage, by itself, does not improve the ecological status of a river satisfactorily in many cases (HARREITER et al., 2015, REYJOL et al., 2014, SCHMUTZ, 2012). Taking into account that functioning habitats are limiting factors in the Danube, near-natural by-passes are preferred over technical solutions as they a) provide passage for a wider range of species, age classes, and sizes (CALLES & GREENBERG, 2007, JUNGWIRTH et al., 1998, TUMMERS et al., 2016), and b) are used as key habitats by riverine fish (CALLES & GREENBERG, 2007, EBERSTALLER et al., 1998, GUSTAFSSON et al., 2013, PANDER et al., 2013, PARASIEWICZ et al., 1998, TAMARIO et al., 2018).

However, the above-mentioned studies mostly focused on salmonids at by-passes in smaller rivers. Therefore, the present study (MEULENBROEK et al., 2018B) **[A 2]** is the first on a large river, such as the

Danube, that considers all life stages of fish from a broad range of species. Seasonal changes in abundances, species diversity, and spawning events are described. A total of 43 species colonize the by-pass of Freudenau with temporary and spatial fluctuations. Furthermore, we have shown that the heterogenic configuration (straightened-, meandering sections, stagnant sidearms, and pool pass) provides conditions for different ecological guilds, and consequently, increase biodiversity. The straightened section is characterized by a relatively low number of species (17). In early spring, the indicator species of the free-flowing Danube, nase (*Chondrostoma nasus*) and barbel (*Barbus barbus*), migrated into the fish by-pass in very high quantities and successfully spawned. Shortly afterwards, a massive drift of early life stages of riverine fish species was observed. The pool pass and the stagnant sidearm showed high shares of stagnophilic species, such as European bitterling (*Rhodeus amarus*), three-spined stickleback (*Gasterosteus aculeatus*), rudd (*Scardinius erythrophthalmus*), and tench (*Tinca tinca*). Our observations and the occurrence of the majority of the Danube fish species at different life stages, including various protected species, validates our hypothesis that the fish by-pass provides habitat for spawning, nursery creation, growing, and feeding for a wide range of species and highlights the importance of such constructed fish by-passes for their conservation (MEULENBROEK et al., 2018B) [A 2].

4.3. Sustainability, management aspects, and recommendations

All three Publications (MEULENBROEK et al., 2018A, MEULENBROEK et al., 2018B, WAIDBACHER et al., 2018) [A 1 - 3] emphasizes that such artificial systems need to be maintained and managed continuously to function sustainably. Additionally, recommendations are given to improve their ecological value. Especially long-term assessments of the functionality of restored riverine habitats are crucial to understand and assess their sustainability (PANDER & GEIST, 2016). MEULENBROEK et al. (2018B) [A 2] emphasized, in accordance with FAO (2002), that even though near natural by-passes are easier to maintain, these artificial systems need continuous management. Besides the maintenance of all technical facilities, ecological maintenance needs to be implemented. Currently, the power plant operator needs only to ensure free passage of fish by an official decision of the competent authority. This comprises mainly of the yearly removal of beaver dams and logs or driftwood jams (RENNER, 2012). However, geodetic research showed a deepening of the riverbed caused by continuous erosion because of a lack of gravel input from upstream. After 17 years of operation, the whole system deepened by an average of 24 cm, resulting in a loss of more than 3000 m³ of gravel to the main river (HAGEL & WESTERMAYR, 2016). This demonstrates the absolute need for gravel addition to ensure system stability and to fill up developed depressions, which can prevent some species from swimming upstream. Gravel addition could also create or improve suitable spawning grounds (PULG et al., 2013). In 2016, a high discharge occurred in the fish by-pass, shortly after migrating nase (*Chondrostoma nasus)* arrived, resulting in no catches of young-of-the-year fish and the loss of a whole year class. Higher discharge provides better passage, but it needs to be in accordance with the morphology of the fish by-pass (FAO, 2002). The critical swimming capacity (PLAUT, 2001) of different species and life stages needs to be considered. In the case of nase (*Chondrostoma nasus)*, the stability of the spawning habitats must be guaranteed for nearly four weeks for successful recruitment to occur (HAUER et al., 2007). Short periods of increased discharge are still recommended, as the interstitial spaces of the sediments have to be 'cleaned up.' This improves the habitat not only for egg and larvae development of fish but also for other organisms such as macroinvertebrates (DOLE-OLIVIER, 2011, DUDGEON et al., 2006) or biofilms (BOULTON, 2007). Such artificial disturbances should be implemented before the migration season and not at a particular date. The timing varies every year as it is related to water temperature, discharge, and other individual parameters (NORTHCOTE, 1984).

In the course of the investigations conducted for the study of MEULENBROEK et al. (2018A) [A 1], additional temporal and spatial changes of habitat structures through on-site surveys were measured in the riparian side arms and bays (PAYERL, 2015, WAIDBACHER et al., 2016). Succession happens in the riparian vegetation, as well as in the habitat morphology. Reeds grow from the banks into the open water resulting in a reduction of the surface area. Moreover, fine sediments accumulated in the time course of the respective bank structures. The degree of filling increases from 40% to 100% with upstream distance from the hydropower plant for the eight created riparian side arms. This demonstrates the need for continuous management actions to secure the positive ecological effects of constructed mitigation measures. Unless there is a certain level of resilience of the system, restoration measures in such heavily modified river stretches are likely to need on-going management (PALMER et al., 2005).

5. Conclusions

The Austrian stretch of river Danube (approximately 350 km) is shaped by hydromorphological alterations for navigation, flood protection, disconnection of tributaries, as well as hydroelectric power generation. The 10 hydropower stations/impoundments that have been implemented within the last 70 years significantly affect the fish fauna caused by habitat degradation and fragmentation (SCHIEMER, 2000, SCHIEMER & WAIDBACHER, 1992, WAIDBACHER, 1989). The findings of this dissertation have a number of important implications for future practice, as they add substantially to our understanding of possible mitigation measures and their ecological response. Because funding for river restoration is typically limited, long-term data on the effectiveness and functionality of instream restoration measures are crucial for choosing those most effective (PANDER & GEIST, 2016).

WAIDBACHER et al. (2018) [A 3] gives an overview on the lessons learned at other impoundments and summarizes the ecological measures to improve the biotic integrity of the affected river section of the latest Danube hydropower plant at "Freudenau." Large-scale habitats, including riprap secured gravel banks, creation of riparian channels and a by-pass system for fish migration were constructed together with the hydropower plant (1992-1998). About 15-18 years later, most species from the Austrian Danube were observed using the investigated man-made measures (gravel bank, riparian channel, and fish by-pass) as habitats for different life stages.

In the study of MEULENBROEK et al. (2018A) [A 1] is the first wherein DNA barcoding was used to confirm the identification of riverine fish larvae to species level. Therefore, the first reliable results on species-specific fish larval dispersal have shown that the different shoreline configurations determine the composition of drifting larvae. Studies in the early life stages of fish are valuable as their occurrence verifies the existence of suitable spawning grounds, that reproduction was successful, and that the conditions were suitable for the development of eggs (compare HUMPHRIES & LAKE, 2000). The correct identification to species level is a prerequisite to understanding which species are spawning where and when, their hatching and nursery grounds, and their possible migration patterns in their early life history stages. Consequently, this information can be used for ecological monitoring, environmental impact assessment, establishing protected areas and suggesting other possible conservation measures because many practices (e.g. navigation) have negative effects on the survival rates of fish larvae (KO et al., 2013, LECHNER et al., 2016, PAVLOV et al., 2008, WOLTER & ARLINGHAUS, 2003).

MEULENBROEK et al. (2018B) [A 2] concluded that the diversity of species and sizes of the colonized fish in the near natural by-pass, as well as the evident reproduction, correspond to a situation in a natural sidearm or tributary of the Danube. The reproduction success of numerous protected and endangered species highlight the relevance of habitat mitigation measures and their contribution to species conservation. Furthermore, it is shown that the heterogenic configuration provides conditions for different ecological guilds and life stages. However, such artificial systems need to be managed continuously to function sustainably. The spatial extent of the measures is limited in comparison to the degradation and disconnection of former habitats, and the habitat quality of these artificial systems may be lower than that of natural habitats. Nevertheless, they have high potential as a remediating or mitigating measure and this is clearly visible in the present Dissertation.

SCHMUTZ et al. (2014) stated that rehabilitation success depends mainly on its spatial extent and is most effective in accordance with river size. Their results showed that improvement of habitat is achieved by the construction of gravel banks and hook groynes at a scale of more than 3.8 km, by riparian channels at a scale less than 1.2 km. In contrast, one of our investigated gravel banks has a length of approximately 1.9 km and one of the riparian channels of only 0.4 km and already exhibits a clear positive ecological response. Out of 9 riparian channels, WAIDBACHER et al. (2016) even found the highest number of species in the smallest. This indicates that not only the size matters but also the complexity, connectivity, diversity, and arrangement of different mitigation measures influence success.

Taking into consideration that the Danube was originally a braided river with highly diverse habitats (HOHENSINNER et al., 2013), and the need of species- and life-stage specific habitats (as summarized in MEULENBROEK et al., 2018C), a systematic approach to the creation and connection of habitats is necessary to improve the ecological situation of such a modified system. Especially the provision of functioning spawning and juvenile habitats are two of the most essential tasks to strengthen the native fish fauna (JUNGWIRTH et al., 2014, KECKEIS & SCHIEMER, 2002, PANDER & GEIST, 2010) and achieve the requirements formulated in the EU–WFD (EUROPEAN-PARLIAMENT, 2000).

List of figures

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Received: 25 January 2017 | Revised: 17 May 2018 | Accepted: 18 May 2018
DOI: 10.1002/rra.3303

RESEARCH ARTICLE

WILEY

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

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Funding information
Verbund Hydro Power GmbH

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, Schönbauer, & 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, Haidvogel, 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.

2 | 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

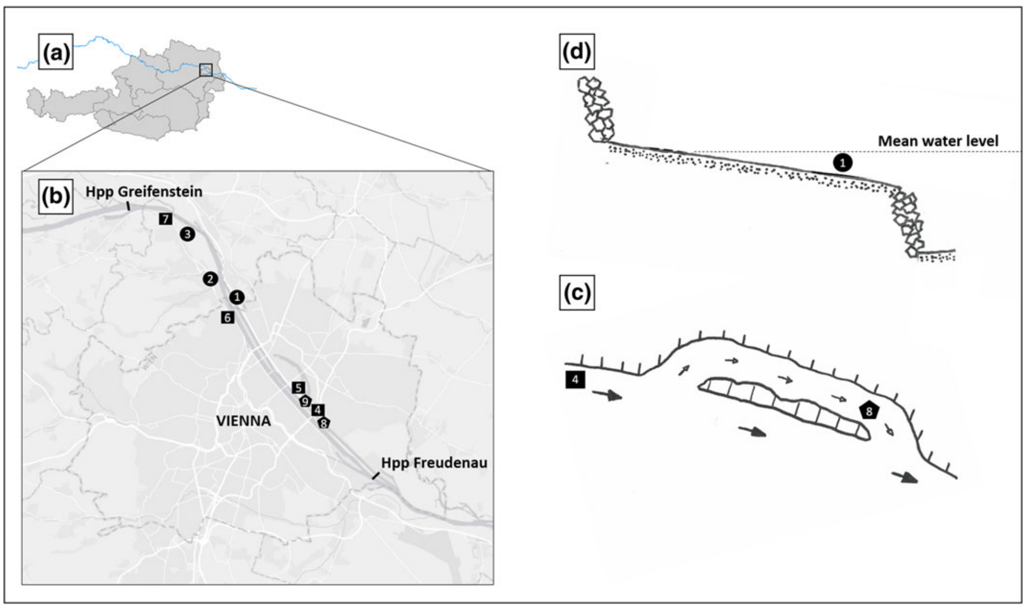

FIGURE 1 (a) Location of study area, (b) sampling sites, (c) illustration of one of the artificial side arms, and (d) illustration of the man-made gravel bar Donauinsel; circle: gravel bar (1: Donauinsel; 2: Hügelland; 3: Kritzendorf); square: riprap (4 and 5: central impoundment; 6: Kuchelau; 7: free flow); pentagon: side arms (8: Habitat C; 9: Habitat D); Hpp: hydropower plant [Colour figure can be viewed at wileyonlinelibrary.com]

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 Freudenau	—	—	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.

constructed side arms (nos 8–9) (Figure 1b). All sites were anthropogenically built or initiated (Figure 1; Table 1). The two side arms sampled (Figure 1; nos 8 and 9) comprise man-made inshore structures at the orographic left bar of the River Danube on the so-called "Danube Island" with a length of 1.1 km (Habitat C) and 0.4 km (Habitat D), respectively. A detailed description of the location and site is given by Chovanec, Schiemer, Waidbacher, and Spolwind (2002), Straif et al. (2003), and Waidbacher et al. (2016). The two gravel bars, "Donauinsel" (no. 1) and "Hügelland" (no. 2), have also been anthropogenically constructed. The riparian shoreline is fixed with riprap, whereas additional submerged riprap prevents the gravel bar from being eroded into the main channel (Figure 1d). The gravel bar furthest upstream (no. 3) was initiated by the construction of a groin field. The two riprap sections examined (nos 4 and 5) are located in the central impoundment upstream of the side arms. Riprap no. 6 is located in the upper part of the impoundment, and no. 7 is located in an almost free-flowing section.

2.2 | Field sampling

Early life stages of fish were sampled continuously from April to July 2013 on 39 occasions and on 24 occasions in 2014, approximately twice a week. Drift nets similar to Zitek, Schmutz, Unfer, and Ploner (2004) with two equilateral triangles with a side length of 37 cm per sampling device were used. Each net had a mesh size of 1 mm, a mouth opening of 592.8 cm^2 and a total length of 550 cm. The last 50 cm were detachable to allow the caught larvae to be emptied. Drift nets were exposed for 24 hr on each occasion.

2.3 | Identification of early life stage fishes and DNA barcoding

Fish larvae are difficult to morphologically determine to genus or species level (Ko et al., 2013). Therefore, trapped fish larvae were divided into "similarity groups" based on simple morphological features (e.g., body shape, pigmentation, and head proportion) by using specific keys and literature (Balinsky, 1948; Pinder, 2001; Spindler, 1988; Urho, 1996). A total of five groups linked to the family taxonomic level were 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 I (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 mixes included 800 µM of dNTP, 0.3 µM of each primer, and 0.1 U peqGOLD Taq-DNA polymerase (peqlab/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 (*Ponticola kessleri*: 11%) as well as the native Bullhead (*C. gobio*: 23%)—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.

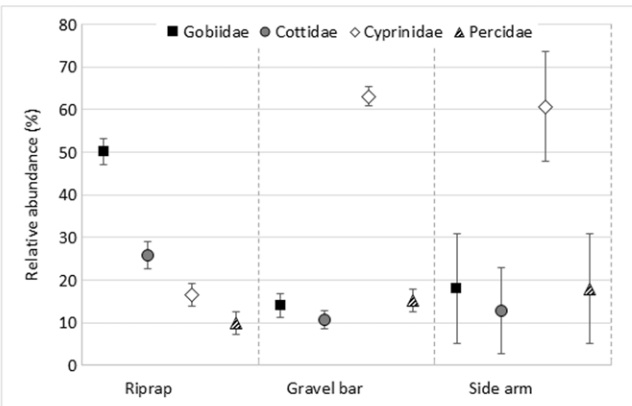

FIGURE 2 Confidence ranges of relative abundance of caught larvae on family level for all shoreline configurations; Gasterosteidae and Salmonidae were removed; n = 173 DNA-barcoded larvae

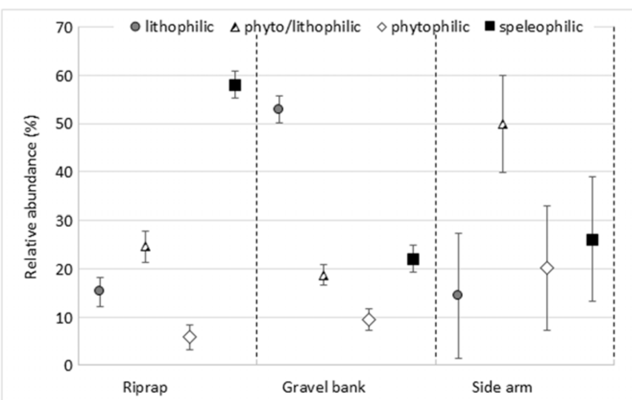

FIGURE 3 Confidence ranges on relative abundance of spawning guilds for gravel bar, riprap, and side arm; ostracophilics were removed; n = 170 DNA-barcoded larvae

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 schraetser*), 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 (*Esox lucius*) larvae were also recorded; the latter being

TABLE 2 Relative distribution (%) of all species and families caught separated for each sampling sites

	Riprap			Gravel bar			Side arm	
	Free flow	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	
Cottus gobio	30.23	31.50	9.56	13.10	2.94	14.90	1.19	
Cyprinidae	8.07	12.14	34.17	47.50	73.54	61.35	71.98	71.96
Abramis brama		0.15	0.06	4.13	1.61	6.03	7.11	
Alburnus alburnus				2.59				8.99
Aspius aspius	3.54	2.53	13.94	11.04	8.69	12.05	3.57	35.98
Barbus barbus	1.57	1.78	0.48	10.36	26.07		1.19	
Blicca bjoerkna						4.83		
Chondrostoma nasus	1.18	6.24	2.52	17.32	17.05	30.14	1.19	
Cyprinus carpio				2.06			14.22	
Leuciscus sp.	1.18	0.15	4.81		5.79			
Pseudorasbora parva					2.90			
Rhodeus amarus			0.95					
Rutilus rutilus	0.59	0.69	10.59	0.00	11.42	8.31	42.32	17.99
Rutilus virgo		0.45	0.35				2.38	
Squalius cephalus		0.15	0.48					8.99
Esocidae							0.67	
Esox lucius							0.67	
Gasterosteidae	0.10		0.33					8.99
Gasterosteus aculeatus	0.10		0.33					8.99
Gobiidae	60.07	50.69	37.92	37.39	5.88		7.33	
Babka gymnotrachelus	8.57	4.03	4.15					
Neogobius melanostomus	51.51	42.79	4.48	30.84	5.88			
Ponticola kessleri		3.88	29.29	6.55			7.33	
Percidae	1.33	5.36	17.54	2.01	17.64	23.75	18.83	19.05
Gymnocephalus cernua	0.02							
Gymnocephalus schraetser	0.02							
Perca fluviatilis	0.15	0.87	3.37		5.78	2.28	2.75	14.29
Sander lucioperca	0.83	4.24	11.07	1.79	6.09	11.66	16.08	4.76
Sander volgensis	0.10		1.06					
Zingel streber		0.12	0.33			3.36		
Zingel zingel	0.20	0.13	1.72	0.22	5.78	6.45		
Salmonidae	0.20	0.30	0.48					
Coregonus sp.	0.20	0.30	0.48					

Note. *n* = 14,555 caught larvae; species designation is based on mtDNA verified information of 671 individuals.

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

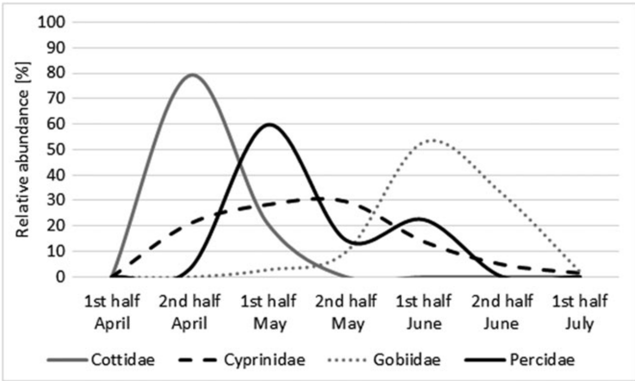

FIGURE 4 Seasonal pattern in relative abundance for the most abundant families in 2014

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 litho/phytophilic 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 (Borcherding 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.

ACKNOWLEDGEMENTS

The authors would like to thank E. Lautsch for his help in data analysis and C. Dorninger for technical assistance. E. Thaler improved the English. The study was financed by Verbund Hydro Power GmbH.

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How to cite this article: Meulenbroek P, Drexler S, Huemer D, et al. 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. *River Res Applic*. 2018;34:854–862. https://doi.org/10.1002/rra.3303

[A 2] - Meulenbroek et al. (2018b)

Meulenbroek P., Drexler, S., Nagel, C., Geistler, M. & Waidbacher, H., 2018b: The importance of a constructed near-nature-like Danube fish by-pass as a lifecycle fish habitat for spawning, nurseries, growing and feeding: a long-term view with remarks on management. *Marine and Freshwater Research* 69, 1857-1869.

SPECIAL ISSUE

CSIRO PUBLISHING

Marine and Freshwater Research, 2018, **69**, 1857–1869
https://doi.org/10.1071/MF18121

The importance of a constructed near-nature-like Danube fish by-pass as a lifecycle fish habitat for spawning, nurseries, growing and feeding: a long-term view with remarks on management

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Abstract. Major sections of today's rivers are man made and do not provide the essential requirements for riverine fish. A nature-like fish by-pass system in Vienna-Freudenau was assessed for its function as a fish habitat. The study was conducted continuously over 3 years; 15 years after construction of the by-pass. The chosen nature-like construction of the by-pass system functions like natural tributaries. More than 17 000 fish and 43 species, including several protected and endangered species, in all life stages, including eggs, larvae, juveniles and adults, were captured. Furthermore, the indicator species of the free-flowing Danube, nase (*Chondrostoma nasus*) and barbel (*Barbus barbus*), migrated into the fish by-pass and successfully spawned before returning. Therefore, our results suggest that by-pass systems can function as an important habitat for the conservation of native fish fauna. The heterogenic habitat configuration provides conditions for all ecological guilds and, consequently, increases biodiversity. Finally, approved management tools are discussed. We suggest that fish by-pass channels may be suitable at other sites in the Danube catchment.

Additional keywords: *Barbus barbus*, by-pass management, *Chondrostoma nasus*, cyprinids, large river.

Received 26 March 2018, accepted 2 August 2018, published online 17 October 2018

Introduction

Hydromorphological alterations for navigation, flood protection, hydroelectric power generation, as well as the disconnection of tributaries, have resulted in riverine habitat degradation and fragmentation, especially in large rivers such as the Danube (Schiemer 2000; Morley and Karr 2002; Dudgeon *et al.* 2006). These habitat modifications affect the integrity and diversity of freshwater biota (Karr *et al.* 1985; Allan and Flecker 1993; Richter *et al.* 1996). Lack of functional spawning grounds, nursery habitats and reduced connectivity are now considered to be limiting factors for riverine fish populations (Keckeis and Schiemer 2002; Jungwirth *et al.* 2003; Pander and Geist 2010; Jungwirth *et al.* 2014).

According to the key objective of the European Water Framework Directive (WFD), all waterbodies in the EU need to achieve good ecological status. This is defined in Annex V of the Water Framework Proposal as a slight departure from the biological community (fish, benthic invertebrates and aquatic flora) that would be expected in conditions of minimal anthropogenic impact (European Parliament and the Council of the European Union 2000). For WFD implementation, among others, the Austrian legal framework (NGP, Gewässerbewirtschaftungsplan 2009) focuses on the provision of a longitudinal migration for aquatic organisms by installing fish by-passes. Investigations showed that a free passage alone does not improve the ecological status of a river satisfactorily in many cases (Schmutz 2012; Reyjol *et al.* 2014; Harreiter *et al.* 2015). To improve connectivity, near-natural fish by-passes provide passage for a wider range of species, age classes and sizes and are, therefore, preferred over hard technical fish by-passes (Jungwirth *et al.* 1998; Calles and Greenberg 2007; Tummers *et al.* 2016).

There are many river restoration projects (e.g. the creation of gravel banks, riparian bays and channel systems or lateral connections of waterbodies) that attempt to create and restore important key habitats for the different life stages of endangered species such as spawning grounds, and larval and juvenile habitats to strengthen fish populations (Schiemer and Waidbacher 1992; Barlaup *et al.* 2008; Pulg *et al.* 2013; Geist and Hawkins 2016; Pander and Geist 2016; Zauner *et al.* 2016; Meulenbroek *et al.* 2018; Waidbacher *et al.* 2018). Near-natural by-pass solutions can provide both, namely, possibility of migration as well as the provision of the abovementioned key habitats. There are limited studies, mostly focusing on salmonids at by-passes in smaller rivers, showing this multifunctional role for different species (Eberstaller *et al.* 1998; Parasiewicz *et al.* 1998; Calles and Greenberg 2007; Gustafsson *et al.* 2013; Pander *et al.* 2013; Tamario *et al.* 2018). However, to the best of our knowledge, the present study is the first on a large river such as the Danube (mean annual discharge 1910 $m^3\ s^{-1}$, Niederösterreich 2018) that considers all life stages of fish deriving from a broad range of species. Besides improved connectivity, shown by Eberstaller *et al.* (2001) in 2000, there have been first indications of possible additional benefits, such as spawning activities during this time.

The objective of the present study is to assess the near-natural by-pass system in Freudenau-Vienna as a habitat. We hypothesised that the fish by-pass would provide habitat for spawning, nurseries, growth and feeding. Furthermore, following the principles of ecological guilds (Balon 1990; Schiemer and Waidbacher 1992), the heterogenic configuration should provide conditions for different species compositions. Therefore, we sampled fish larvae, juveniles, and adult fish and analysed species occurrences and spatial and temporal differences of assemblage structure.

Materials and methods

Study sites

The Hydropower plant (HPP) Vienna-Freudenau is the newest HPP in the Danube (mean discharge 1910 $m^3\ s^{-1}$) and was built in 1998. A fish migration by-pass system was incorporated with two major components, namely, a near-natural by-pass channel and a near-natural pool pass (Fig. 1). The fish by-pass starts 500 m downstream of the HPP, with a delta system in the tailwater that has calm, shallow waters over some 200 m with two permanent wetted channels. The subsequent semi-natural by-pass channel has an average slope of 0.7% and is situated in a 7-m-wide riverbed with and an average current speed of ~0.6 $m\ s^{-1}$. The first 160-m length is straight (hereafter called the straightened section), followed by a 300-m-long meandering section (hereafter meandering section) and a 140-m-long branched section.

One of the branches is blocked by a beaver dam and has calm to stagnant water for ~50 m (hereafter stagnant sidearm). The remaining section of 170 m up to the weir is straight again. The total length of this free-flowing section is ~1000 m. The channel bottom was constructed with a 1-m-thick layer of gravel and sand; subjacent is a 0.4-m-thick silt layer that seals the fish by-pass. Some rifle-pool sequences are developed and very dense riparian vegetation has been well established, consisting mainly of willows and alders.

The uppermost part of the system is a pool pass of 19 pools (20–40 m in length and 3–16 m in width), with a minimum of 70 m^2 per pool, a water-level difference of 11 cm from pool to pool, and a total length of 420 m (hereafter pool pass). It is characterised by a pool depth of 1.5 m, different flow conditions (from reverse flow to velocities up to 1 $m\ s^{-1}$), high abundances of reeds and macrophytes. There are big boulders (30–50 cm) at the ramps between the pools and different substrate patterns, ranging from gravel to very fine sediments with high quantities of xylal. Sediments ranged from megalithal to pelal (Önorm-6232 1995; Fig. 2). The straightened and meandering sections were rather similar, showing a high percentage (~80%) of lithal (mega, macro, meso, microlithal) fractions. In contrast, the pool pass and the stagnant sidearm exhibited higher percentages (~65%) of finer fractions (Akal, Psammal and Pelal). At the fishing points, water depth, river width and flow velocities were measured (Fig. 3). Mean flow velocity was calculated following Kreps (1975). For a detailed description of the by-pass, see Eberstaller *et al.* (1998). The discharge of the by-pass is not constant but changes depending on the discharge of the Danube and the season, ranging from 1.5 $m^3\ s^{-1}$ in winter to a maximum of 3.6 $m^3\ s^{-1}$ during higher discharges in the main river (Table 1).

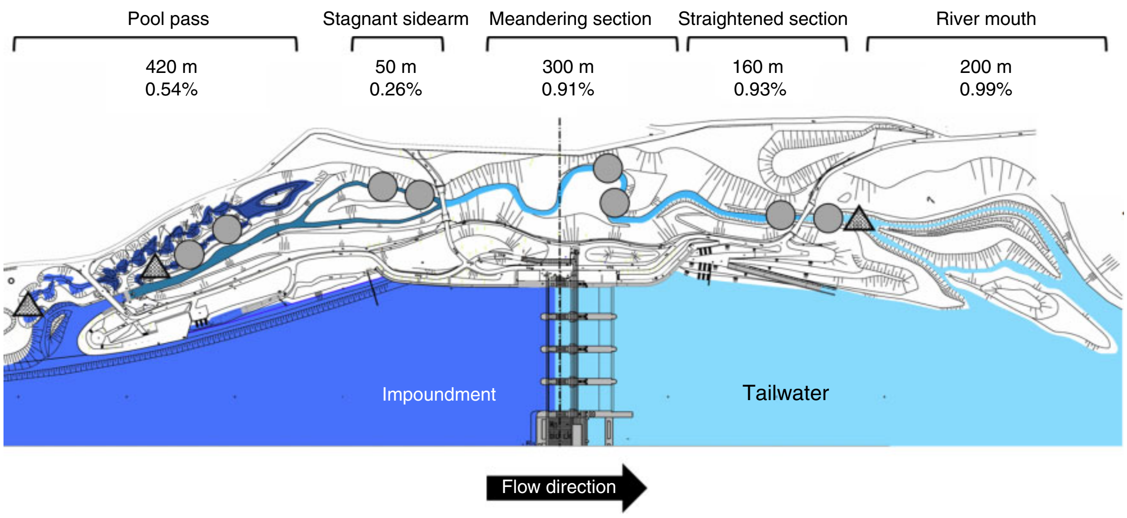

Fig. 1. Fish by-pass system Freudenau. Triangles indicate fish larvae sampling points, circles indicate electrofishing points; length of the sections (m) and slope (%) are given beneath each section name (adapted after Eberstaller *et al.* 2001).

Field sampling, identification and data analyses

The main sampling campaign comprised point abundance sampling by electrofishing (EF) of juvenile and adult fish (Copp and Peňáz 1988) from January 2014 to December 2015. For EF, the backpack-generator ELT60-IIH (Hans Grassl GmbH, Schönau am Königssee, Germany) was used, according to the code of practice and national standard in Austria (Haunschmid *et al.* 2010). The generator operates with direct current at 1.3 kW and 500 V. The same two points (~20 m^2) in each section (straightened section, meandering section, pool pass and stagnant sidearm) were fished approximately every 2 weeks, with a total of 225 sampling events. A constant fishing effort was applied for each sampling event and the catch per unit effort (CPUE) was used for further analyses on the basis of these data. Additional fishing was undertaken at selected habitats in 2013 and 2016 (22 sampling events). Fish larvae were sampled from April to September 2015 with the same drift nets as described by Meulenbroek *et al.* (2018), in 27 sampling events at the following three different locations: one at the beginning of the pool pass, one at the end of the pool pass and one at the end of the straightened section (triangles in Fig. 1). Fish larvae samples were taken approximately once per week, always during the night with an exposure time of 12 h (CPUE). All juvenile and adult specimens were identified to species level by using morphological characters (Wiesner and Zauner 1999), counted, and their total length was measured. Early life stages of fish were identified to family level and further processed as described in Meulenbroek *et al.* (2018). A subsample of 560 individuals was analysed with mt-DNA barcoding to species level (Hebert *et al.* 2003). The selection criteria for the individuals to be barcoded were the abundance within each family found in a sampling site for each calendar week and the potential number of species. The latter represents the proportions of potential species for each family (Cyprinidae: 32 species; Gobiidae and Cottidae: 5 species; Percidae: 9 species; compare with Meulenbroek *et al.* 2018). The calculated number of individuals for barcoding was then randomly selected by the randomise tool in Excel (2016). The primers FishCo1-F and FishCo1-R (Baldwin *et al.* 2009) were used, and for some individuals we also used the cytochrome *b* primers KAI_F and KAI_R (Kotlík *et al.* 2008).

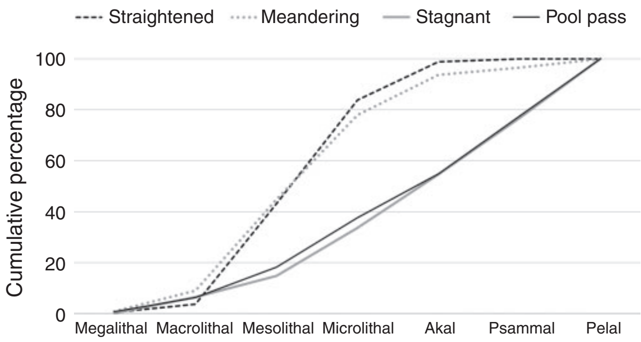

Fig. 2. Choriotop distribution (according to Önorm-6232) at four different sections of the by-pass where fish sampling was performed.

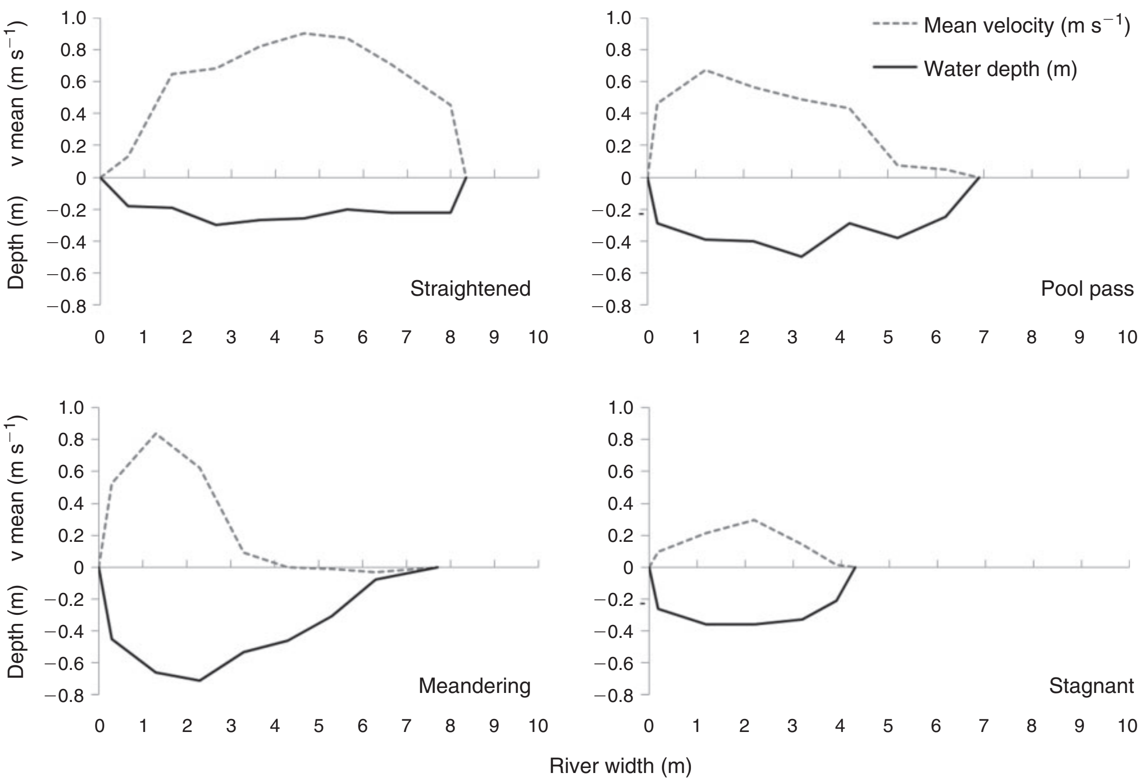

Fig. 3. Water depth, river width (m) and mean flow velocity (v mean, m s^{-1}; after Kreps 1975) for each of the sampled sections (straightened section, meandering section, stagnant sidearm and pool pass).

Table 1. Work regulation of the minimum values for the variable discharge in the fish by-pass system depending on the discharge of the Danube and the season (adapted after Renner 2012)

Season	Discharge of the Danube ($m^3 s^{-1}$)	Weir flow ($L s^{-1}$)	Pool pass ($L s^{-1}$)	$\sum$By-pass stream ($L s^{-1}$)
Winter	<3000	600	900	1500
(Dec.–Feb.)	>3000	3100	500	3600
Spawning season	<2000	900	900	1800
(Mar.–May)	>2000	3100	500	3600
Summer	<3000	900	900	1800
(Jun.–Nov.)	>3000	3100	500	3600

The affiliation to guilds followed Schiemer and Waidbacher (1992), as well as Zauner and Eberstaller (1999), and was expanded for *Neogobius melanostumus*, *Ponticola kessleri*, *Babka gymnotrachelus* and *Lepomis gibbosus* (compare with Table 2; Kottelat and Freyhof 2007). Kruskal–Wallis test was performed using SPSS (IBM SPSS Statistics for Windows, ver. 24.0, IBM Corp., Armonk, NY, USA), followed by a Dunn–Bonferroni *post hoc* test. Significance was accepted at $P < 0.05$. Frequency-of-use graphs (FUG) were calculated as normalised probability density functions ranging from 0 to 1 (Raleigh *et al.* 1984; Melcher and Schmutz 2010):

$$FUG_i = \int_i \div \int_{[max]} \quad (1)$$

where $\int_i$ is the class frequency and $\int_{[max]}$ is the maximum class frequency.

To visualise spatial differences, 95% confidence intervals (Sachs 2004), histograms, line plots and a Venn diagram were compiled. Non-metric multidimensional scaling (NMS; Kruskal 1964) was applied to the ecological guild data (densities were $\ln(x+1)$ transformed, for juveniles and adults separately). Indicator species analysis (ISA; Dufrêne and Legendre 1997) identified fish species and life stages that serve as indicators for different habitats and seasons. Only species with an indicator value (IV) of >25 and $P < 0.05$ (Monte Carlo permutation test) were considered. NMS and ISA were performed with PC-ORD (ver. 5.33, MjM Software, Gleneden Beach, OR, USA). Length–frequency diagrams were used to illustrate population structure, showing the relationships between length classes and relative frequency.

Results

During the entire study period, 17 200 fish were caught, comprising 6800 adults, 3900 juveniles and 6500 larvae. In total, 43 species from 12 families were detected with spatial and seasonal variations.

Habitat function

Most of the Danube fish species used the system at all life stages every year (compare with Table 2). There is an apparent increase in numbers of species from downstream (17) to upstream (29; Fig. 4). The straightened section is characterised by a relatively low number of species (17) and has the highest proportion of rheophilic species (58% of juveniles, 69% of adults), such as the nase (*Chondrostoma nasus*) and the barbel (*Barbus barbus*). The subsequent meandering section provides habitats for at least 27 species, with an increased proportion of eurytopic specimens (49% of juveniles, 54% of adults). In the meandering section, we caught all species that occurred in the straightened section in similar quantities, plus additionally 10 further species. Stagnophilic species such as European bitterling (*Rhodeus amarus*), three-spined stickleback (*Gasterosteus aculeatus*), rudd (*Scardinius erythrophthalmus*) or tench (*Tinca tinca*) were almost exclusively caught in the pool pass (5% of juveniles, 8% of adults) and in the stagnant sidearm (22% of juveniles, 35% of adults). The latter exhibits the highest proportion of this guild. Furthermore, hundreds of juvenile cyprinid fish used the dam cavities for overwintering.

The pool pass was dominated by eurytopic species (86% of juveniles, 77% of adults). There were highly significant differences in the distribution of adult and juvenile fish for the different flow guilds among sections in the by-pass (Kruskal–Wallis; $P < 0.05$). The *post hoc* test showed the following significant differences (Dunn–Bonferroni test, $P < 0.05$): fish communities differed between the straightened section and stagnant sidearm for all guilds; the straightened section and the pool pass differed for all guilds except for rheophilic B; the meandering section and the stagnant sidearm differed for all guilds except for rheophilic A, whereas only the stagnophilic showed significant differences between the meandering section and the pool pass; when comparing the stagnant sidearm and the pool-pass, only rheophilic B and eurytopic guilds differed.

The results of the NMS analysis (Fig. 5), presented as joint plot (cut-off value $r^2 = 0.3$), showed a relationship between riverbed slope and ecological traits of juvenile and adult fish species. On the basis of the NMS scatterplot, samples from sections with a higher slope were noticeably separated from the remaining samples. Samples from the straightened and meandering section were close to each other on the NMS scatterplot, exhibiting a rather similar faunal composition. In contrast, samples from the pool pass and stagnant sidearm were predominantly on the right side of the dashed line. Fifteen species were caught in all sections, whereas four species occurred only in the stagnant sidearm, one only in the straightened section, three only in the Meandering section, and three only in the Pool pass (Fig. 6). Overlaps indicated the number of species caught in more than one section (e.g. 22 species were caught in both the stagnant sidearm and the pool pass).

The indicator species analyses (Table 3) showed some fish species that serve as indicators for the different sections of the

Table 2. Presence or absence of fish species at adult, juvenile, larval and egg stage for the entire study period (2013–2016)
EN, endangered; VU, vulnerable; NT, near threatened, according to Wolfram and Mikschi (2007). The affiliation to ecological guilds (habitat and reproduction) follows Schiemer and Waidbacher (1992), as well as Zauner and Eberstaller (1999) and was slightly expanded for *Neogobius melanostumus*, *Ponticola kessleri*, *Babka gymnotrachelus* and *Lepomis gibbosus* (compare with Kottelat and Freyhof 2007). These categories are denoted by: A, Schiemer and Waidbacher (1992); B, Zauner and Eberstaller (1999). eury, euryotopic; limn, limnophilic; rheo, rheophlic; pel, pelagophil; phyt, phytopil; lith, lithophil; psam, psammophil; ostrac, ostracophil; speleo, speleophil

Family	Species	Guild		Life stage			
		Habitat	Reproduction	Adult	Juvenile	Larvae	Eggs
Anguillidae	*Anguilla anguilla*	eury.	pel.	x			
Centrarchidae	*Lepomis gibbosus*	limn.	phyt.	x			
Cobitidae	*Cobitis taenia*[A], VU	rheo. B	phyt.	x			
Cottidae	*Cottus gobio*[A], NT	rheo. A	lith.	x	x		
Cyprinidae	*Abramis brama*	rheo. B	phyt./lith.		x		
	Alburnoides bipunctatus	rheo. A	lith.	x	x		
	Alburnus alburnus	eury.	phyt./lith.	x	x	x	
	Aspius aspius[A], EN	rheo. B	lith.		x	x	x
	Ballerus sapa EN	rheo. B	lith.	x	x	x	
	Barbus barbus NT	rheo. A	lith.	x	x	x	x
	Blicca bjoerkna	eury.	phyt./lith.	x	x		
	Carassius gibelio	eury.	phyt.	x			
	Chondrostoma nasus NT	rheo. A	lith.	x	x	x	x
	Cyprinus carpio EN	eury.	phyt.	x			
	Gobio gobio	rheo. A	psam.	x			
	Leuciscus idus EN	rheo. B	lith.	x	x	x	x
	Leuciscus leuciscus NT	rheo. A	phyt./lith.	x	x	x	
	Pelecus cultratus[A], NT	eury.	pel.	x			
	Rhodeus amarus[A], VU	limn.	ostrac.	x	x	x	
	Romanogobio vladykovi[A]	rheo. A	lith.	x		x	
	Rutilus pigus[A], EN	rheo. A	lith.		x	x	
	Rutilus rutilus	eury.	phyt./lith.	x	x	x	
	Scardinius erythrophthalmus	limn.	phyt.	x			
	Squalius cephalus	eury.	lith.	x	x	x	x
	Tinca tinca VU	limn.	phyt.		x		
	Vimba vimba VU	rheo. B	lith.		x		
Gasterosteidae	*Gasterosteus aculeatus*	limn.	phyt.	x	x		
Gobiidae	*Babka gymnotrachelus*	limn.	speleo.	x		x	
	Neogobius melanostomus	eury.	speleo.	x	x	x	x
	Ponticola kessleri	eury.	speleo.	x	x	x	x
	Proterorhinus marmoratus EN	eury.	speleo.	x	x	x	x
Lotidae	*Lota lota* VU	eury.	lith./pel.	x			
Nemacheilidae	*Barbatula barbatula*	rheo. A	psam.		x		
Percidae	*Perca fluviatilis*	eury.	phyt./lith.	x	x	x	
	Sander lucioperca NT	eury.	phyt.	x	x	x	
	Sander volgensis EN	rheo. B	phyt./lith.			x	
	Zingel zingel[A], VU	rheo. A	lith.	x		x	
	Gymnocephalus cernuus	eury.	phyt./lith.			x	
Salmonidae	*Hucho hucho*[A], EN	rheo. A	lith.		x		
	Oncorhynchus mykiss	rheo. A	lith.	x			
	Salmo trutta NT	rheo. A	lith.	x	x		
	Thymallus thymallus VU	rheo. A	lith.		x		
Siluridae	*Silurus glanis* VU	eury.	phyt.		x	x	x

[A]Listed in Annex II of the Flora–Fauna–Habitat Directive (Richtlinie-92/43/EWG 1992).

by-pass. For the pool pass, those were *Neogobius melanostomus*, *Alburnus alburnus*, adult individuals of *Squalius cephalus* and *Gasterosteus aculeatus*, and juvenile *Chondrostoma nasus*. The best indication was given by *Neogobius melanostomus* (IV: juvenile = 55.2; adult = 50.2). For the straightened section, only adult *Cottus gobio* was listed. For the meandering section, no species met the chosen indicator species criteria (IV > 25, Monte Carlo permutation test: $P < 0.05$). For the stagnant sidearm, the best indicator species were *Rhodeus amarus* (IV: juvenile = 55.7; adults = 63.9), followed by juvenile *Squalius cephalus* and adult *Proterorhinus marmoratus.* Eleven species were detected throughout the whole year in the system (chub (*Squalius cephalus*), trout (*Salmo trutta*), bullhead (*Cottus gobio*), bleak (*Alburnus alburnus*), roach (*Rutilus rutilus*),

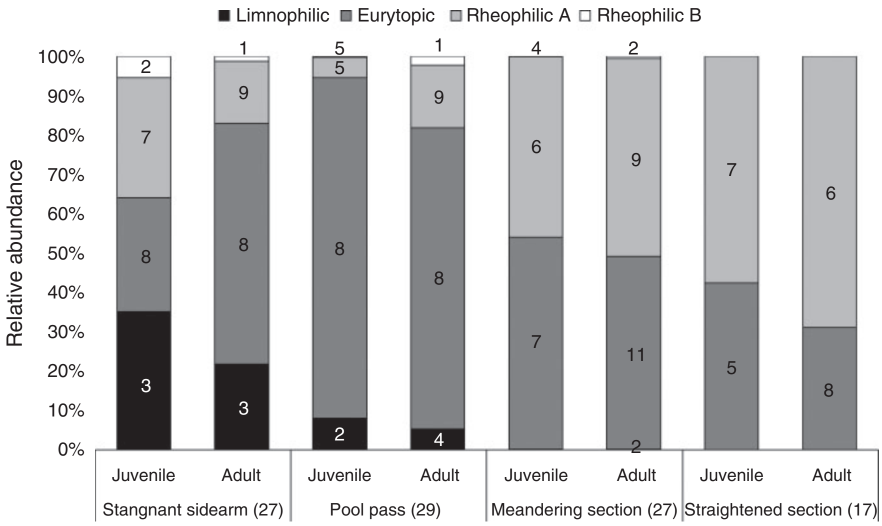

Fig. 4. Relative abundances of flow guilds and number of species for the given sections. Bars indicate relative abundance of flow guilds for juvenile and adult of all caught fish; numbers within each category show the number of species per guild; numbers in parentheses indicate total number of species per section.

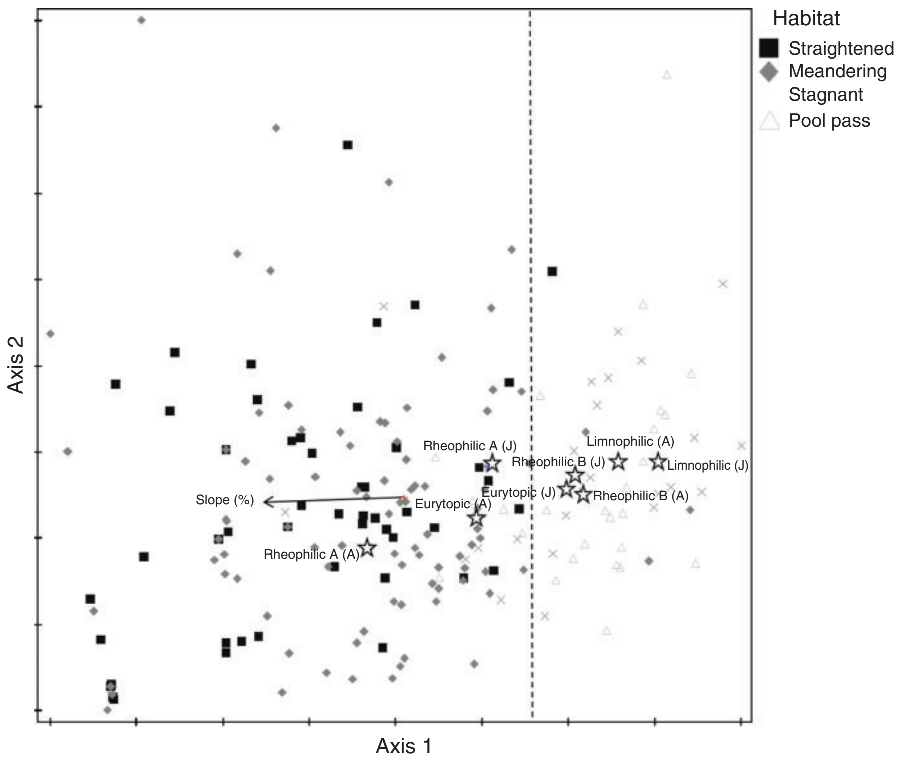

Fig. 5. Joint plot of the non-metric multidimensional scaling analysis for fish samples of the by-pass system Freudenau ($n = 193$ fishing events); vector (joint plot cut-off value $r^2 = 0.3$) represents the slope (in %), stress: 10.87 for the three-dimensional solution (number of iterations = 500). Stars indicate scores for each ecological guild (juveniles and adults are separated).

spirlin (*Alburnoides bipunctatus*), round goby (*Neogobius melanostomus*), barbel, bitterling, three-spined stickleback, and nase). Some species, such as grayling (*Thymallus thymallus*), gudgeon (*Gobio gobio*), Danube salmon (*Hucho hucho*), carp (*Cyprinus carpio*), stone loache (*Barbatula barbatula*) and sichel (*Pelecus cultratus*), were detected only once or very rarely in catches. However, there were also seasonal differences in the occurrence of species. In general, the lowest abundances

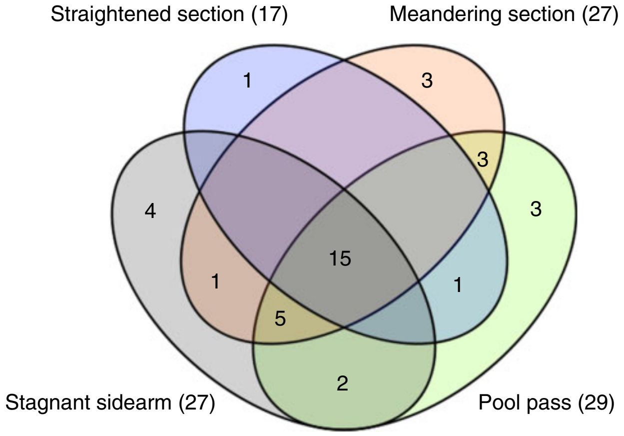

Fig. 6. Venn diagram summarising the relations between the different sections and the number of fish species (early life stages of fish were excluded). Each circle represents one section; overlaps indicate number of species caught in more than one section.

Table 3. Monte Carlo permutation test of significance of observed maximum indicator value (IV) for each species (IV > 25 and *P* < 0.05) for the different habitats within the by-pass system and seasons, based on 1254 randomisations and 4999 permutations (compare Dufrêne and Legendre 1997)

Species	Life stage	Habitat	IV	Mean	s.d.	*P*-value
Cottus gobio	Adult	Straightened	30.6	14.8	3.13	0.0006
Rhodeus amarus	Adult	Stagnant	63.9	8.0	2.93	0.0002
Rhodeus amarus	Juvenile	Stagnant	55.7	6.4	2.90	0.0002
Squalius cephalus	Juvenile	Stagnant	40.4	14.4	3.42	0.0002
Proterorhinus marmoratus	Adult	Stagnant	27.8	5.8	2.50	0.0002
Neogobius melanostomus	Juvenile	Pool pass	55.2	9.6	3.21	0.0002
Neogobius melanostomus	Adult	Pool pass	50.2	17.6	3.88	0.0002
Chondrostoma nasus	Juvenile	Pool pass	35.1	15.5	4.13	0.0014
Squalius cephalus	Adult	Pool pass	33.4	22.9	3.10	0.0058
Alburnus alburnus	Adult	Pool pass	33.3	18.9	5.68	0.0200
Alburnus alburnus	Juvenile	Pool pass	32.4	10.5	4.11	0.0004
Gasterosteus aculeatus	Adult	Pool pass	31.6	8.0	3.12	0.0002
Chondrostoma nasus	Adult	Spring	46.2	16.5	3.44	0.0002
Barbus barbus	Adult	Summer	30.0	16.2	3.10	0.0012
Squalius cephalus	Adult	Summer	32.7	22.7	2.97	0.0064
Neogobius melanostomus	Adult	Autumn	25.1	17.4	3.67	0.0392
Chondrostoma nasus	Juvenile	Autumn	32.0	15.2	3.89	0.0024
Cottus gobio	Adult	Winter	32.6	14.6	2.97	0.0006
Alburnus alburnus	Adult	Winter	37.9	18.7	5.26	0.0026

were found for most species during winter (November–February), except for bleak, Danube whitefin gudgeon (*Romanogobio vladykovi*) and dace (*Leuciscus leuciscus*), which inhabited the system numerously in this period. This seasonal pattern is clearly illustrated in Fig. 7, which illustrates the frequency of species occurring in the by-pass for adult

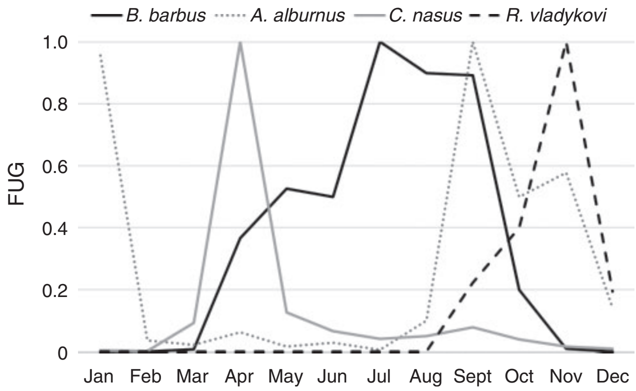

Fig. 7. Seasonal frequency-of-use graphs for 2014 and 2015 (frequency-of-use-graph) of the by-pass for adult individuals of *Barbus barbus* (mean standard deviation: σ = 0.07), *Chondrostoma nasus* (σ = 0.02), *Alburnus alburnus* (σ = 0.09) and *Romanogobio vladykovi* (σ = 0.12).

individuals of *Barbus barbus* (most abundant from May to September), *Alburnus alburnus* (most abundant from September to January), *Chondrostoma nasus* (maximum in April) and *Romanogobio vladykovi* (most abundant from October to December). On the basis of these data, the only significant ($P \leq 0.05$) indicator species identified as colonising the by-pass system in spring was the adult stages of *Chondrostoma nasus*. In summer, the adult stages of *Barbus barbus* and *Squalius cephalus* were identified as indicator species. Adult *Neogobius melanostomus* and juvenile *Chondrostoma nasus* were indicator species in autumn, and adult *Cottus gobio* and *Alburnus alburnus* were indicator species in winter (Table 3).

There were noticeable differences for all caught nase for the four investigated sections (Fig. 8), specifically the following:

(1) length classes from 200 to 350 mm were highly underrepresented;
(2) juveniles were found in all four sections, with higher abundance in the stagnant sidearm and especially the pool pass; and
(3) larger individuals (>350 mm) were almost exclusively found in the meandering and straightened sections.

Spawning and fish larval drift

Nase showed a distinct seasonal pattern. In both years, the adult individuals migrated in high numbers into the fish by-pass at the beginning of April and remained there for ~4 weeks. The nase, together with chub, which were most frequent in May, and barbel in July, were the most frequently found species. Spawning activities were observed multiple times, especially in riffle sections, for these species (Fig. 3). A single pool and one riffle section were fished carefully quantitatively during a single spawning event, showing massive spawning runs of nase. In the pool, which had a surface area of 30 m^2, 44 adult individuals were caught with a mean weight of 1.5 kg. A further 10 individuals were caught in the adjacent 20-m^2 riffle section. Estimates of fish biomass calculated from these data equated to 22 t of fish per hectare in the pool and 7 t of fish per hectare in the riffle section. We collected a total of 6557 fish larvae,

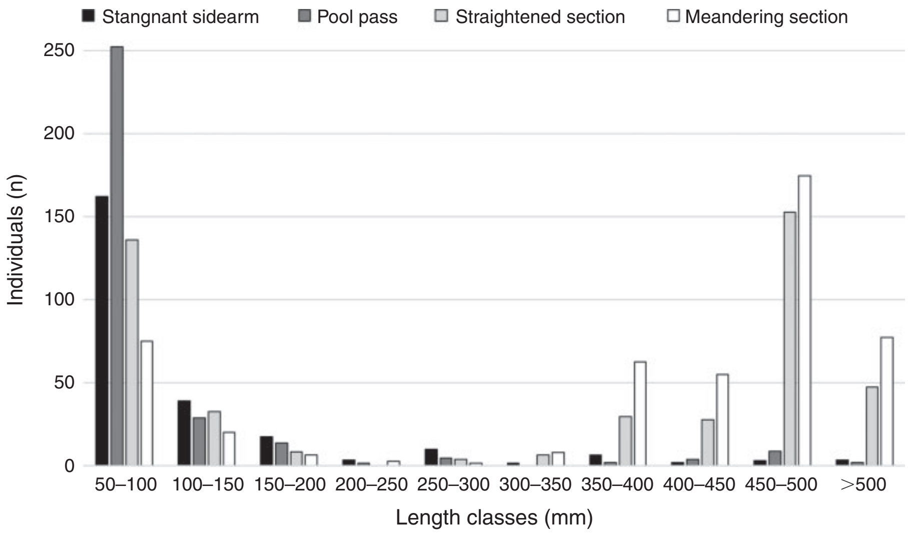

Fig. 8. Length–frequency of nase (*Chondrostoma nasus*) for four different sections of the fish by-pass system.

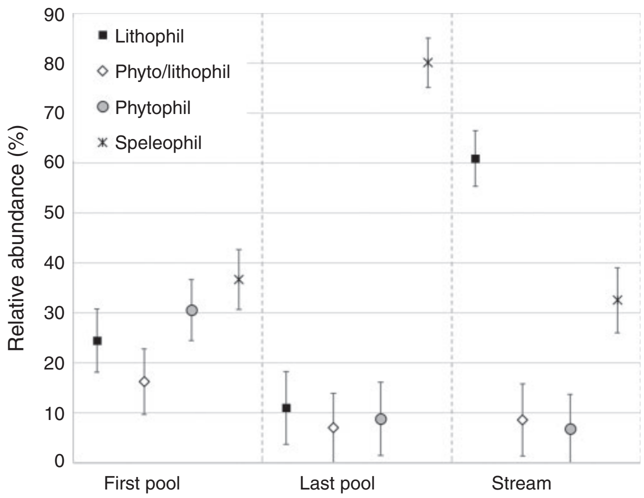

Fig. 9. Confidence intervals (95%; Sachs 2004) on relative abundance of all caught fish larvae appointed to their spawning guild for each of the drift net sampling points (compare with Fig. 1); ostracophilics were excluded.

representing 22 species, from three sampling points. The following results presented a clear picture of the spatial distribution and spawning-guild composition:

(1) in the first pool, a mixed set of fish larvae drifted into the system ($n = 2465$);
(2) the sampling point downstream at the end of the pool pass ($n = 2734$) was dominated by speleophilic (75–85%) and equal shares of lithophilic and phytophilic (1–16%) species; and
(3) in contrast, in the stream section ($n = 1358$), most of the larvae caught consisted of lithophilic species (55–66%), followed by speleophilic species (26–39%; Fig. 9).

These pronounced differences were also reflected in family and species compositions at the three sampling sites (Table 4). In the uppermost pool of the pool pass, the majority of the caught fish larvae were from European catfish (*Silurus glanis*: 37%), followed by invasive Gobiidae, namely the round goby (*Neogobius melanostomus*: 20%) and bighead goby (*Ponticola*

Table 4. Relative distribution (%) of all caught fish larvae species and families separated for all sampling sites
n, 560 barcoded larvae of 6571 caught larvae

	First pool	Last pool	Stream
Cyprinidae	24.5	9.3	68.1
Alburnus alburnus	1.2	0.4	1.2
Aspius aspius[A]	1.3	0.7	5.6
Ballerus sapa	0.1		
Barbus barbus[A]	14.3	3.2	25
Chondrostoma nasus[A]	3.3	2.1	16.9
Leuciscus idus[A]	0.4	0.2	0.6
Leuciscus leuciscus	0.2	0.2	
Rhodeus amarus		1.4	0.4
Romanogobio vladykovi		0.3	
Rutilus rutilus	2.4	0.5	1.3
Rutilus virgo		0.1	
Squalius cephalus[A]	1.3	0.1	17
Gobiidae	34.1	83.5	24.7
Babka gymnotrachelus	2.4		
Ponticola kessleri[A]	10.9	21	8.5
Neogobius melanostomus[A]	20.8	62.5	15
Proterorhinus marmoratus[A]			1.2
Percidae	4.1	3.4	7.1
Gymnocephalus cernuus	2.4	0.1	
Perca fluviatilis	0.1	1.5	0.6
Sander lucioperca	1.3	1.6	2
Zingel zingel	0.3	0.2	4.6
Siluridae	37.4	3.8	
Silurus glanis[A]	37.4	3.8	

[A]Additional, drifting eggs were genetically confirmed.

kessleri: 11%). In addition, barbel formed a relatively high percentage (14%) of the fish larvae caught. The remaining 12 species were found in lower frequencies. The species information from the last pool and the stream presented a contrasting picture: whereas the stream was dominated by cyprinids (68%), the pool pass clearly showed high proportions of Gobiidae (84%). Of the 22 species of fish larvae collected, nine were also detected by mt-DNA analysis of drifting eggs (Table 4).

Discussion

Our observations and the occurrence of the majority of the Danube fish species from different life stages validates our hypothesis that the fish by-pass provides habitat for spawning, nurseries, growing and feeding for a wide range of species. In total, 43 species deriving from 12 families were detected. These included eight species classified as endangered, eight species classified as vulnerable and a further seven species classified as near threatened for Austria (Wolfram and Mikschi 2007). On a European scale, nine species are listed in Annex II of the Flora–Fauna–Habitat Directive (Richtlinie-92/43/EWG 1992) and, consequently, locations where these species occur must be managed in accordance with the ecological needs of the species. Furthermore, the occurrence of various life stages of protected species such as *Aspius aspius*, *Barbus barbus*, *Chondrostoma nasus*, *Leuciscus idus*, *Proterorhinus marmoratus*, *Rhodeus amarus*, *Ballerus sapa* or *Rutilus pigus* highlighted the importance of such fish by-passes for their conservation. In total, the 43 verified species represent three-quarters of all species that were sampled in all habitat assemblages of the Viennese Danube waterbodies in 2013–2016 (Waidbacher *et al.* 2016). Most of the missing species are rare in the area, such as *Acipenser ruthenus*, *Misgurnus fossilis*, *Romanogobio kesslerii* or *Ballerus ballerus.* It remains unclear why other species, such as *Gymnocephalus schraetser*, *Esox lucius* or *Zingel streber* do not inhabit the fish pass, and why the abundance of top predators seems to be low.

Whether the sampled juvenile and adult fish originate from downstream or also from upstream sections remains uncertain because no traps were used. In a monitoring study conducted by Eberstaller *et al.* (2001) in 2000, the downstream migration was evaluated as negligible, mainly consisting of a few juvenile individuals of *Alburnus alburnus* and *Blicca bjoerkna*. These authors also found that mainly ‘indifferent’ fish species, especially the bleak, white bream, European roach, vimba and zobel, traverse the entire by-pass system into the impoundment. Only a few individuals of stagnophilic species were detected; however, they are also rare in the tailwater of the power plant. During the spawning season in spring, nase and barbel migrate into the bypass channel in high abundance. Whereas barbel frequently ascends into the impoundment via the pool pass, comparatively few nase traverse the entire system. These authors concluded that the Freudenau bypass channel can be classified as broadly functional (Eberstaller *et al.* 2001).

Habitat function for fish species, young-of-the-year classes and adults

The taxonomic composition and distribution of the fish fauna varied among the different sections and seasons, and it is likely that this was related to the high variability of the habitat conditions (such as, for example, water depth, flow velocities and substrate). This is in line with one of the key elements of ecology, namely, that habitat heterogeneity increases biodiversity (Ricklefs and Schluter 1993). Additionally, large organic debris is often added from the well-stocked riparian zone, which also has a positive effect on the richness of biota (Crook and Robertson 1999; Dossi *et al.* 2018). Noteworthy is the stagnant sidearm, which is clogged by a beaver dam, with its calm-water conditions that rarely exist in by-passes. This section supplements the range of available habitats and this is reflected in the proven fish community, which shows a high proportion of stagnophilic species. The increase in species number from the straightened section to the meandering section can be explained by the complex hydrodynamics of convex and concave riverbanks in short succession that produce the sequence of shallow, calm-flowing habitats and deep fast-running sections. This fast-changing sequence produces a variety of essential habitat types in immediately adjacent spots. (Gorman and Karr 1978; Garcia *et al.* 2012).

The pool pass differs substantially in its habitat specifications, by providing deeper areas with low flow velocity, large boulders at the ramps between the pools, and a well-established riparian vegetation with high proportions of reed and different substrate patterns, ranging from gravel to very fine sediments with a high component of xylal. It shows an abundance of the invasive round goby (*Neogobius melanostomus*), which prefers the above-mentioned large boulders or riprap structures (Ahnelt *et al.* 1998; Borcherding *et al.* 2013; Brandner *et al.* 2015; Meulenbroek *et al.* 2018). The reed belt provides shelters and habitats for small species and masses of young-of-the-year fish from all guilds.

It remains unclear whether the apparently under-represented length classes (200–350 mm) of *Chondrostoma nasus* were caused by either

(1) the low attractiveness of the by-pass system for these length classes, or
(2) the limited abundance of these length classes in the tailwater of the main river channel.

Evidence in support of the second point comes from the monitoring of the by-pass entrance conducted by Eberstaller *et al.* (2001) who reported that nase in the 200–350-mm length classes were migrating into the system in the Year 2000, and from our survey of the Danube from 2013 to 2015, in which these length classes were under-represented in the main channel (Waidbacher *et al.* 2016).

Little is known about a self-sustaining *Salmo trutta* population within the river Danube, but this species is considered rare (Schiemer and Spindler 1989). It is worth mentioning that some of the caught individuals are most likely to derive from stocking activities, indicated by body pigmentation and deformations of gills and fins (Arndt *et al.* 2001; Aparicio *et al.* 2005), and some from autochthonous populations. In total, we caught 48 *Salmo trutta* individuals throughout the years and seasons, ranging from 100 mm to 350 mm in total length. Most of the adults were caught in late autumn, which corresponds to their spawning season, whereas the presence of some smaller individuals in summer indicated that reproduction had occurred in the system.

The peaks of *Chondrostoma nasus* and *Barbus barbus* are linked to their spawning seasons, whereas those of

Romanogobio vladykovi and *Alburnus alburnus* indicate their use of the system as a winter habitat. The latter was also confirmed in the indicator-species analyses. The provision and accessibility of winter habitats are essential for fish communities, especially in highly degraded river systems (e.g. Schlosser 1995; Cunjak 1996).

Spawning function and fish larvae drift

The observed migration of the indicator species of the free-flowing Danube, nase and barbel, and their multiple spawning acts within the fish by-pass are comparable to those described in natural streams and tributaries of the Danube (Keckeis 2001; Ovidio and Philippart 2008; Melcher and Schmutz 2010) and highlight the quality of the fish by-pass system as a functional spawning habitat.

In total, the 22 genetically verified species of fish larvae represent nearly half of all species sampled in the by-pass. This does not necessarily mean that the others do not reproduce there, because they might either spawn at other sites or avoid drifting (Reichard and Jurajda 2007). Artificially built systems often provide functional spawning grounds (Pander and Geist 2016; Meulenbroek *et al.* 2018), which can be assessed by the occurrence of early life stages of fish (Pavlov 1994). The differences in composition and abundance of larval species among the three sampling points are particularly pronounced and indicate a locally separated reproduction of different fish species.

Most of the catfish larvae (*Silurus glanis*) in the first pool were caught on a single day together with catfish eggs. This indicates that spawning took place in the area upstream of the first net. Other species found in the first net drifted in a balanced distribution and were derived from somewhere in the Danube upstream. Not all drifting larvae were collected in the first net; some of the species by-passed the first net and were found in the second net in the last pool of the pool pass. The large differences between the two sampling points demonstrated the contribution of the stretch between as a reproduction area. As mentioned above, the high proportion of speleophilic species (in particular Gobiidae) at the second sampling point originates from the rock habitats found in ramps and ripraps within the pool pass. The repeated capture of *Rhodeus amarus* larvae indicated the occurrence of mussels, which are a prerequisite for the reproduction of this ostracophilic species (Mills and Reynolds 2003).

The third and most downstream larval sampling point in the stream section was clearly dominated by lithophilic cyprinids, primarily by nase, barbel and chub. This showed that the observed spawning acts resulted in successful reproduction. In comparison to a larval-drift investigation undertaken several kilometres upstream (Meulenbroek *et al.* 2018), additional species of drifting larvae (*Silurus glanis*, *Proterorhinus marmoratus*, *Ballerus sapa* and *Romanogobio vladykovi*) were detected only in the described fish by-pass. Further investigations are needed to provide a clear explanation for this. However, the distribution of the caught larvae in the stream section of the by-pass is comparable to that of gravel bars in the remaining free-flowing Danube and its tributaries. The distribution of larvae caught in the pool pass is more similar to that of riprap sections in the main channel (Lechner *et al.* 2010, 2014; Melcher and Schmutz 2010; Ramler *et al.* 2016; Meulenbroek *et al.* 2018).

Management aspects

Even though close-to-nature types of fish passes are easier to maintain (Food and Agriculture Organization of the United Nations and the Deutscher Verband für Wasserwirtschaft und Kulturbau e.V. 2002), these artificial systems need continuous management to function sustainably. Besides maintenance of all technical facilities, ecological maintenance needs to be implemented. Currently, the plant operator needs to ensure a free passage of fish by an official notification. This comprises mainly the yearly removal of beaver dams and log or driftwood jams (Renner 2012).

In general, higher discharge provides better passage, but it needs to be in accordance with the morphology of the fish pass (Food and Agriculture Organization of the United Nations and the Deutscher Verband für Wasserwirtschaft und Kulturbau e.V. 2002). The critical swimming capacity (Plaut 2001) of different species and life stages needs to be taken into account to facilitate a complete passage through the by-pass. Furthermore, the stability of the spawning habitats must be guaranteed for nearly 4 weeks for successful spawning to occur (Hauer *et al.* 2007). In 2016, a high discharge occurred for a long time shortly after migrating nase arrived, resulting in zero catches and the loss of a whole generation of young-of-the-year fish (P. Meulenbroek and H. Waidbacher, unpubl. data). Hydrological disturbances or dynamic floods are still recommended as they can 'clean up' the interstitial of the sediments, which enhances the habitat not only for fish and egg development but also for other organisms such as macroinvertebrates (Dudgeon *et al.* 2006; Dole-Olivier 2011) or biofilms (Boulton 2007). Implementing this 'cleaning up' of the sediments before the migration season, which is not linked to a particular date but more to water temperature, discharge and other parameters (Northcote 1984), is recommended.

Another fact that should be considered is the deepening of the by-pass riverbed. After 17 years of operation, the whole system deepened by an average of 24 cm, resulting in a loss of more than 3000 m^3 of gravel (Hagel and Westermayr 2016). Compensation is required to ensure system stability and to fill up the developed washouts, which can impede some species from swimming upstream and we recommend implementing this at 10-yearly intervals. Gravel addition could also create or improve suitable spawning grounds (Pulg *et al.* 2013). This demonstrates the absolute need for continuous management actions to secure the positive ecological values for fish and other riverine faunal elements.

Conclusions

Most species from the Austrian Danube were observed using a man-made by-pass and some have accepted the surroundings as habitats for different life stages. The diversity of species and sizes of the colonised fish, as well as the evident reproduction of some, correspond to a situation in a natural sidearm or tributary (Haunschmid *et al.* 2006). Therefore, the fish by-pass may serve as a key habitat for the conservation of a variety of endangered species. Furthermore, we have shown that the heterogenic configuration provides conditions for different ecological guilds and, consequently, increases biodiversity. The spatial extent of by-passes is limited in comparison to the degradation and disconnection of former habitats, and the habitat quality of these artificial systems may be lower than that of natural habitats. Nevertheless, near-nature fish by-passes have high potential as a remediating or mitigating measure (Quigley and Harper 2006; Tamario *et al.* 2018) and this was clearly visible in the present study. Future studies should focus on the influence of near-nature fish by-passes on the population size, population dynamics, and the production of offspring of the protected and endangered fish species in the context of the lost habitats and fish populations in the river system. However, such artificial systems need to be managed continuously to function sustainably.

Almost 60% of all Austrian waterbodies are affected by interruption of river continuity, whereby, in larger rivers ($>$100 km^2 catchment), 26% derives from hydropower plants. More than 70% of these facilities are not passable at present (Gewässerbewirtschaftungsplan 2015). Until now, the focus for the implementation of fish by-passes has mostly been to enable migration corridors. Accepting the Danube as an originally braided river with highly diverse habitats (Hohensinner *et al.* 2013), a systematic approach to the creation and connection of habitats is necessary to improve the ecological situation of such a system under pressure and to achieve the requirements formulated in the EU–WFD. Especially in highly modified waterbodies, the provision of functioning spawning and juvenile habitats are two of the most essential tasks to strengthen the remaining fish stocks (Keckeis and Schiemer 2002; Pander and Geist 2010; Jungwirth *et al.* 2014; Waidbacher *et al.* 2018). In planning river modifications, interruptions, or by-passes, the ecological functioning of these key habitats must be incorporated.

Conflicts of interest

The authors declare that they have no conflicts of interest.

Acknowledgements

The authors thank C. Dorninger for technical assistance and P. Rauch, D. Stadler, W. Westermayr and T. Hagl who assisted with field work. H. Meulenbroek improved the English. S. Krumböck and V. Waidbacher are thanked for laboratory assistance. The study was partly financed and enabled by Verbund Hydro Power GmbH; special thanks go to Roswitha Renner and Mr Ringel.

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Handling Editor: Lee Baumgartner

[A 3] - Waidbacher et al. (2018)

Waidbacher H., Drexler, S.-S. & Meulenbroek, P., 2018: Danube Under Pressure: Hydropower Rules the Fish, in: Schmutz, S., Sendzimir, J. (Eds.), Riverine Ecosystem Management. Springer, Cham, pp. 473-489

Chapter 24
Danube Under Pressure: Hydropower Rules the Fish

Herwig Waidbacher, Silke-Silvia Drexler, and Paul Meulenbroek

24.1 Introduction

Major studies, conducted recently at some Danube hydropower impoundments and along the river itself, have pinpointed certain challenging ecological situations for certain faunal associations (Schiemer 2000; Jungwirth 1984; Waidbacher 1989; Herzig 1987; Bretschko1992). One of the important groups affected are riverine fish assemblages. Fish communities are good indicators of habitat structure as well as of the ecological integrity of river systems due to their complex habitat requirements at different stages of their life cycles (Schmutz et al. 2014; Schiemer 2000; Schmutz and Jungwirth 1999). The construction of impoundments changes river systems ecologically by disrupting the connection between the river and the lateral backwaters, by changing the shoreline, and by stabilizing previously dynamic water levels as well as other impacts (Schiemer and Waidbacher 1992).

Impoundments confront fish with new situations that present a challenging difference with the sets of parameters they have adapted to in unmodified river habitats. Due to reduced flow, increased depth, low water temperatures, short retention times, silty to muddy sediments resulting from increased sedimentation, and higher benthic biomass in the sediment depositions, these impoundments conform more to the habitat needs of lacustrine fish species. However, the relatively low average annual temperature of the river, the lack of shoreline structures, and low plankton density inhibit better development of such "backwater" fish associations. The original dominant riverine fish species can mainly be found only in free-flowing sections, except for a few individuals in the uppermost part of the impoundments (Waidbacher 1989).

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S. Schmutz, J. Sendzimir (eds.), *Riverine Ecosystem Management*, Aquatic Ecology Series 8, https://doi.org/10.1007/978-3-319-73250-3_24

In light of these results, strategies have been developed to counteract and minimize negative impacts caused by the construction of new hydropower dams. A more ecologically sustainable solution has been implemented during the construction of a low head dam (8.6 m height) for the impoundment at “Freudenau” in Vienna in 1998. A special attempt has been made here to maintain the ecological integrity of the river system by introducing a large number of mitigating measures. These include creating large gravel areas, improving the lateral integration between the river and the backwaters, and increasing the diversity of the inshore riverbed structures to improve the quality of spawning substrates and nurseries for fish (Waidbacher et al. 1996).

The results of the latest monitoring 2013–2015 are presented here and can be seen as a first indication of the response of the fish association to the innovative large-scale measures of “Freudenau” impoundment.

24.2 Historic Development of the Austrian Danube and Its Faunal Elements

The upper part of river Danube extends from the river’s source in Germany to the Austrian/Slovakian border and is topographically well defined by its high slope (0.43‰ in Austria) and high bedload transport. Large tributaries from the Alps considerably increase river discharge, which reached a mean value of approx. 2000 m^3/s eastward from Vienna prior to river engineering (Liepolt 1967). The pristine morphological condition of the river alternated between canyons with narrow riparian zones to braided reaches with large alluvial areas, especially in the plains of Eastern Austria. A variety of river arms offered a rich diversity of ecological structures with gradients of flow velocity, substrate, and riparian vegetation. This provided ideal conditions for a typical Austrian Danube fish community (Hohensinner et al. 2005).

During the last 100 years, these ecological conditions have been considerably changed by river regulation and damming (Hohensinner et al. 2004). The main regulation started in the second half of the nineteenth century and resulted in substantial changes due to straightening and enforcement of most of the river’s flow into one channel and an abandonment of side arms. This had major effects on:

(a) The ecological conditions of the river habitats (e.g., increase of flow velocity, bedload erosion, and deepening of the riverbed)
(b) The interactive dynamics between river and riparian zone
(c) The relative proportion of alluvial habitat types

The construction of large run-of-the-river hydropower plants started in the 1920s with the ultimate goal of forming a continuous chain of impoundments along the German/Austrian Danube section (Rathkolb et al. 2012). These developments resulted in severe ecological degradation due to an almost complete disconnection between river and lateral backwaters, mostly monotonous shoreline constructions and a stabilized water level over long distances. The characteristic limnological features of these impoundments are:

(a) Short retention times
(b) Low water temperatures
(c) Sedimentation of fine particles in the central impoundment
(d) Reduction of littoral gravel banks to the uppermost sections of the impoundments
(e) Low plankton density
(f) Higher densities of benthic invertebrates in the fine sediment deposits

24.3 Basic Scheme of Impacts of Danube Hydropower Impoundments on Native Fish Associations

Fish communities are good indicators of ecological integrity of river systems because of their complex habitat requirements that shift in the course of their life cycles. The changes in population structures and abundances induced by damming can be elucidated by comparing the fish fauna in free-flowing sections with that of impounded areas. The first such investigations were done in river Danube as part of an interdisciplinary study of the impoundment of "Altenwörth" (50 km upstream of Vienna) in the mid-1980s (Hary and Nachtnebel 1989; Waidbacher 1989; Schiemer and Waidbacher 1992). The fauna in the free-flowing river is characterized by a dominance of rheophilic species (i.e., their life cycle is bound to rapid-flowing water conditions). Species such as barbel (*Barbus barbus*) and nase (*Chondrostoma nasus*) occur in high abundances in the free-flowing section of the "Wachau," followed by a distinct predominance of eurytopic species [e.g., roach (*Rutilus rutilus*) and bleak (*Alburnus alburnus*)] in the impounded section. Data are based on electro-boat fishing along the shoreline (system Coffelt, attracting efficiency approximately 6 m width and 2.5 m depth) and additionally long-line fishing at the river bottom. The difference in the species composition between the uppermost part of the impounded river, with high flow velocity and coarse-grained sediments, and the central part of the impoundment, with reduced flow, fine substrates, and monotonous shoreline structures, is relatively low (Table 24.1). However, the population density of the characteristic riverine species, nase and barbel, declines noticeably in the main impoundment (Fig. 24.1).

Table 24.1 Number of adult and juvenile species in the different sections of the impoundment in the main channel of the Danube at "Altenwörth" and "Freudenau"

	Altenwörth		Freudenau	
	Adult	Juvenile	Adult	Juvenile
Free-flowing	32	21	24	21
Head of impoundment	35	18	23	17
Central impoundment	36	18	21	12

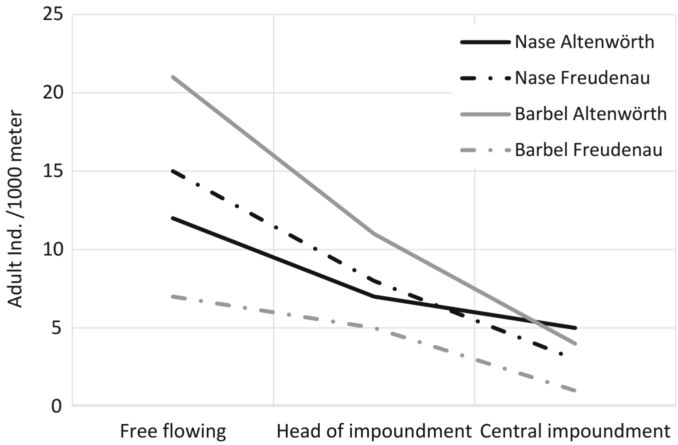

Fig. 24.1 Example for the distribution of two originally dominant fish species in the monotonous constructed Danube impoundment of "Altenwörth," 50 km westward of Vienna, and the latest constructed impoundment of "Freudenau"; adult nase and barbel individuals per 1000 m electro-fishing in the riparian zones (own data, late spring/summer situation)

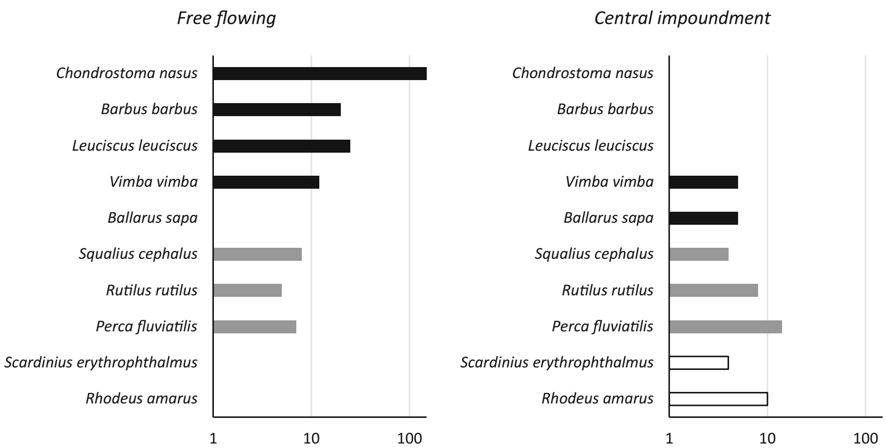

Fig. 24.2 Mean numerical composition of juvenile fish in three shore seine catches; free-flowing area is located in "Wachau"; central impoundment in the impoundment of "Altenwörth"; black, rheophilic; gray, eurytopic; white, limnophilic species (own data)

An analysis of the size structure of the characteristic riverine species shows that in the vicinity of the dam, only old age classes are represented, supported by abundant food supplies in the rich benthic deposits (Waidbacher 1989). Surveys of fish juveniles, as seen in Fig. 24.2, show that the overall density is low, and riverine species are rarely represented or are completely missing in the main impoundment zone. Flow velocity and the nature of littoral substrates (mainly riprap) are not adequate to function as spawning sites and rearing areas for riverine species.

24.4 Implementation of Mitigation Measures in the Latest Constructed Hydropower Dam and Impoundment of Vienna/Freudenau

Based on the results of research at the "Altenwörth" impoundment in the mid-1980s, strategies have been developed to improve the ecological conditions of affected areas. Ecological improvements were designed to counteract and reduce negative impacts caused by the hydropower dams over periods long enough to make such improvements sustainable.

As an example, the objectives for habitat improvements for characteristic Danube fish populations contain the creation of:

(a) Dynamic gravel banks
(b) Dynamic sand habitats
(c) Shelters in times of flood events
(d) Possibility for upstream migration
(e) Lateral connections of water bodies
(f) Riparian bays and channel systems

Various "ecologically sustainable" solutions have been implemented during the construction of the low head dam for the impoundment at "Freudenau" in Vienna. In this case, for the first time, a whole suite of mitigating measures has been introduced to maintain the ecological integrity of the Danube and especially to support the development of self-reproducing fish communities. Figure 24.3 gives a rough overview of the location of implemented measures in four sections, which are described in more detail below.

Section 1

Along riparian floodplains, the connection of lateral water bodies to the main river channel favors the migration of fish, especially lacustrine backwater fish species, and offers rearing and feeding areas (Fig. 24.4). Migration into riparian side arms is extremely important for different life stages of some endangered fish species, such as white-eye bream (*Ballerus sapa*) and zope (*Ballerus ballerus*).

Section 2

The original, dominant, rheophilic fish fauna is represented in Danube impoundments by adult individuals only. To mitigate these effects, gravel bank spawning grounds have been constructed in extended areas in the uppermost part of the "Freudenau" impoundment to support the reproduction of original faunal elements of the river (Fig. 24.5). This was done by the construction of an underwater riprap, which prevents the gravel bar from major erosion into the main channel.

Section 3

An extensive riparian channel and bay system in the central impoundment serves mainly as a spawning ground and rearing area for eurytopic species and as a feeding area for all fish associations. During flood events these zones act as refuges (Fig. 24.6).

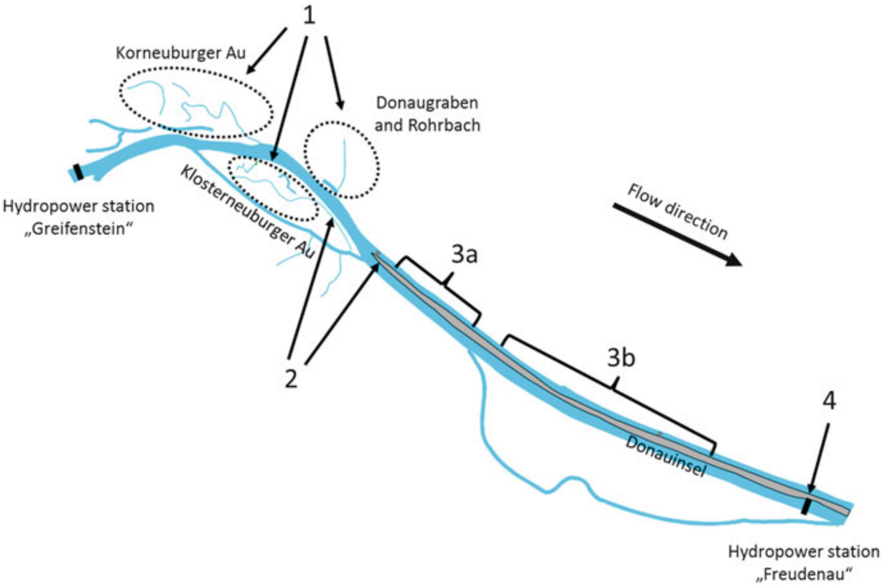

Fig. 24.3 Location of different ecologically sustainable solutions in four sections of the impoundment "Freudenau" (1. lateral connections; 2. gravel banks with riprap stabilization; 3. riparian channel and bay systems; 4. fish migration bypass)

Fig. 24.4 Lateral connection of Korneuburger Au with the main channel of the Danube via a fish bypass system (courtesy of Verbund AG)

Fig. 24.5 Extended underwater gravel bank inshore structure under construction; red arrows indicate "double riprap"; blue line indicates the water level nowadays after construction (Section 2)

Fig. 24.6 Constructed riparian channel and bay system in the central impoundment (Section 3)

Section 4
Fish migration in a bypass channel system supports genetic exchange (Fig. 24.7).

Fig. 24.7 Bypass channel system for fish migration at the power station “Freudenau” (Section 4) (courtesy of Verbund AG)

24.5 Ecological Response and Sustainability of the Constructed Habitat Improvements at "Freudenau"

A second round of research was conducted to monitor constructed habitat improvements some 18 years after construction. Without the influence of constructed measures, the fish assemblages in the main channel of Freudenau responded in the same pattern as already seen in "Altenwörth," namely:

- Decrease or lack of juvenile fish in the central impoundment
- Low number of species in the riparian part of the impounded area
- Low abundance of riverine assemblages in the central part of the impoundment

Considering the ecological improvements indicated by research some 18 years after construction, a clear positive sign for fish assemblages becomes visible:

In Section 1, a better connection has been constructed between the channel and the riparian floodplain waters of "Klosterneuburger Au" (right bank of the Danube). A pool pass allows fish migration at two different water levels of the backwater (summer and winter) and has been accepted by 29 fish species in the direction to the backwater and by 38 species in the direction to the main river channel. In addition to the movement pattern expected in times of spawning activities, the results (fish trap in the pool pass) from 2006 show a remarkably fast response of riverine fish, which were washed into the backwater system during a flood event, in finding again the migration pass for leaving the backwaters in the direction of the main Danube channel. Eighty-five percent of the composition of the sampled migrating rheophilic fish, which showed locomotion after the flood event, belongs to the species assemblage of nase, ide (*Leuciscus idus*), vimba (*Vimba vimba*), asp (*Leuciscus aspius*), and schrätzer (*Gymnocephalus schraetser*)—a classic river fish assemblage (Fig. 24.8).

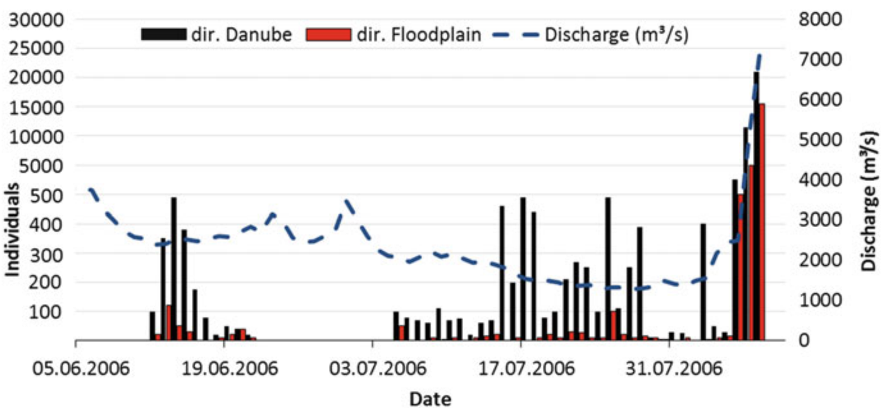

Fig. 24.8 Left axis: Number of migrating individuals into the floodplain system (dir. Floodplain) and vice versa in the direction of the main channel of the Danube (dir. Danube). Right axis: Discharge of the Danube (adapted after Schinninger 2008)

Expected peaks in fish migration are visible in the period of late spring, pinpointing migration activities for spawning and after reproduction (Schinninger 2008).

Investigation via a pool pass system of migration activities to the "Korneuburger Au"—situated on the left bank of the Danube—has shown similar results (Jungwirth and Schmutz 1988). In total, 32 species migrated in both directions. Bleak, roach, white bream, bream (*Abramis brama*), barbel, nase, and zope were the most frequently observed species in this study.

Where connection to the main channel is limited, i.e., lack of a pool pass or other migration facilities, fish communities in backwaters can show a high specialization and often are inhabited by rare species. Some species, such as the weatherfish (*Misgurnus fossilis*) recorded in this study, occur exclusively in disconnected floodplain waters. The design concept implemented for ecological improvement at "Freudenau" supports such species by leaving small floodplain habitats disconnected in years without natural flood events (e.g., "Rohrbach" habitat).

In Section 2, a large amount of gravel material was excavated from the riverbed and newly located in the riparian area to construct gravel bank spawning grounds. Extended shallow areas of several hectares have been artificially established and secured against abrasion by a massive underwater riprap structure (Fig. 24.5). Despite several flood events (up to a 200-year-flood event) over 18 years, no massive changes in the constructions are visible, and the gravel banks are still functioning as spawning grounds. Figure 24.9 shows results from 2013 where larval stages of fish

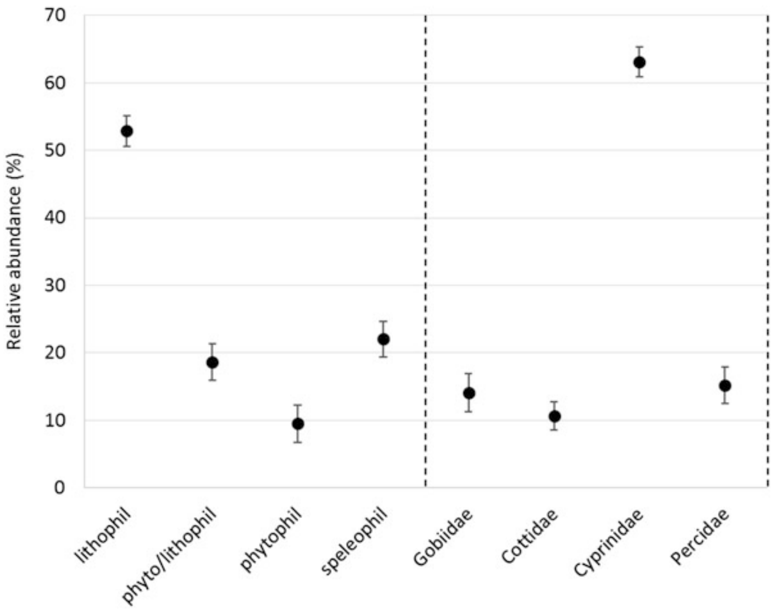

Fig. 24.9 Mean and confidence limits of relative abundance of drifted fish larvae for spawning guilds and families at an artificially built gravel bank, $n = 171$ (adapted after Meulenbroek et al. 2017a)

have been sampled downstream of a large artificial gravel bank situated at the upper most part of the "Viennese Donauinsel." The fish larvae have been identified via barcoding and displayed high shares of lithophilic riverine cyprinids in their abundances (Meulenbroek et al. 2017a). Although spawning activities of adult individuals could not be observed in turbid waters, the drifting of fish larvae in the presumed time period provides indications of successful reproduction activities at the artificially constructed gravel bank.

Section 3 is divided in two parts where one part (3a) is self-cleaning from fine sediments along the shoreline after flood events, while the other one (3b) is not.

In Section 3a, flow velocity is high enough at mean discharge (1 m/s) to wash out fine sediments, which are deposited during flood events in the riparian structures. Inside of the constructed riparian arms, a riverine fish assemblage has developed and persists even after 18 years (Table 24.2).

In Section 3b, the fine sediment deposition along the shoreline is not cleared at mean discharge. The constructed riparian bays are hotspots of biodiversity in the depauperated, i.e., species impoverished, central impoundment of "Freudenau." Their quick colonization by fish and benthic invertebrates just after their construction was documented by Chovanec et al. (2002) and Straif et al. (2003). The importance of such measures was highlighted in 2013–2015, by the high diversity, e.g., total 38 fish species, and high abundances of juvenile riverine species found in these areas (Fig. 24.10).

Recent findings of early life stage abundances suggest several colonization patterns for such riparian habitats. The most unlikely pattern is colonization only from the main channel via unidirectional drift. But there are three different drift patterns visible as described by Meulenbroek et al. (2017a):

(1) Larvae drift into the side arm over longer time periods with different densities and the use of the habitats as nursery grounds.
(2) There are spawning activities at different densities within these side systems.
(3) There is additional drifting of larvae in the direction of the main channel.

These factors identify the multiple functions of these habitats in providing suitable nursery and spawning grounds for an essential variety of Danube fish species.

Furthermore, the high abundance of juveniles in these riparian flat habitats with high sedimentation is additionally sustained by low predating pressure from fish-eating birds. Such water bodies are too shallow for cormorants or goosanders to hunt for prey, and it is most likely that a few herons, stepping, picking, and taking fish,

Table 24.2 Comparison of the number of species within the most upstream riparian side arm for each habitat guild between years 1999/2000 and 2014/2015

	1999/2000	2014/2015
Eurytopic	8	8
Limnophilic	1	1
Rheophilic A	5	4
Rheophilic B	2	3
Total	16	16

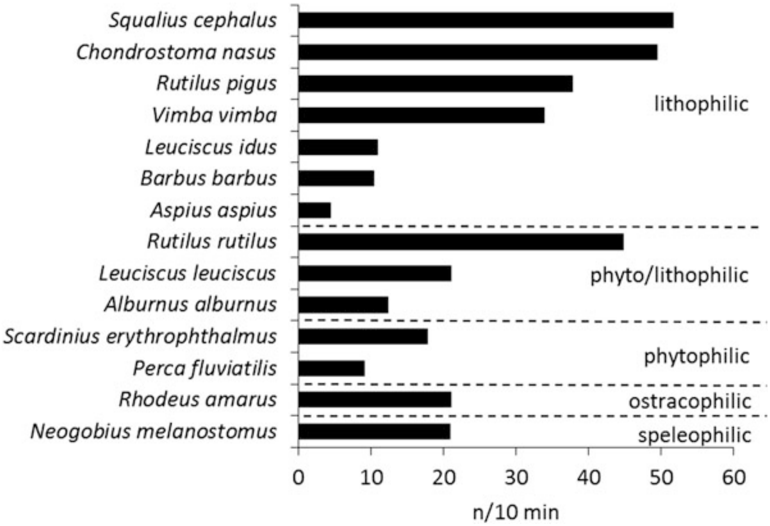

Fig. 24.10 Mean density (per 10-min electrofishing) of the 14 most abundant fish species for different reproductive guilds of one of the riparian side arms in 2014 (Section 3)

can be surely sustained by the system. The repeated validation over 18 years indicates that these mitigation measures are sustainable, even though some vegetation and sediment management needs to be established in the near future.

Results of the latest surveys, 18 years after construction, show that the fish assemblage in the impoundment of "Freudenau" follows the same pattern as in other Austrian Danube impoundments if the riparian mitigation measures are not taken under consideration (compare Figs. 24.2 and 24.11).

However, the mitigation measures show satisfactory improvements in the habitat conditions and support the functions of lost habitats essential for riverine fish. Fish association of juveniles found in a riparian side arm in the central impoundment in 2015 shows that nase and barbel as well as rudd (*Scardinius erythrophthalmus*) and bitterling (*Rhodeus amarus*) are part of the young-of-the-year assemblage and ready for building up new adult stocks.

Additionally, a new development became visible. It's the first time in major scientific Danube investigations that alien species are visible in extraordinarily high densities. Beside the racer goby (*Babka gymnotrachelus*) and the bighead goby (*Ponticola kessleri*), the round goby (*Neogobius melanostomus*) dominates the bottom fish fauna at least in the impounded area. The bottom of main channel and the bottom of side arms, especially close to ripraps, are completely "infected" with enormous ecological effects on food webs and the native fauna caused by competition (Ahnelt et al. 1998; Wiesner 2005; Ebm 2016).

In Section 4, a fish migration bypass system has been constructed with three major components that robustly complement each other in a sustainable way. It starts with a bay system in the tail water (Fig. 24.7) with calm, shallow waters over some 200 m.

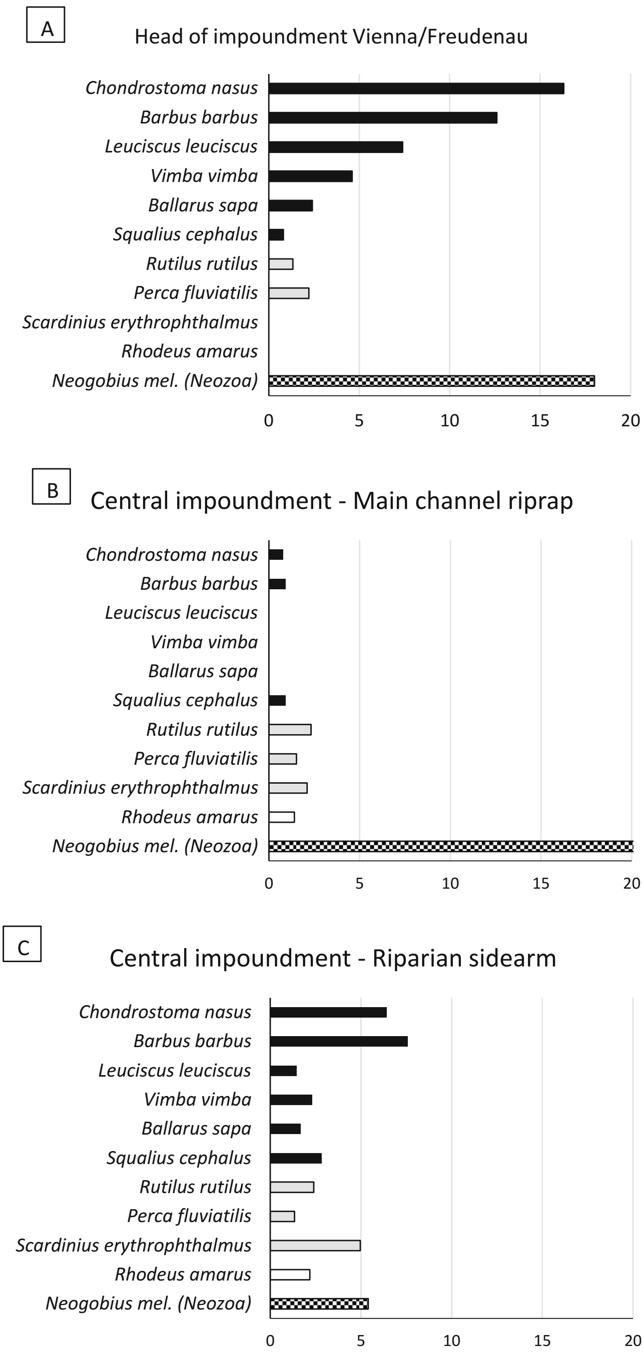

Fig. 24.11 Species composition of juvenile fish in the impoundment of "Freudenau"; black are rheophilic, gray are eurytopic, and white are limnophilic species; $n =$ individuals/10-min electrofishing

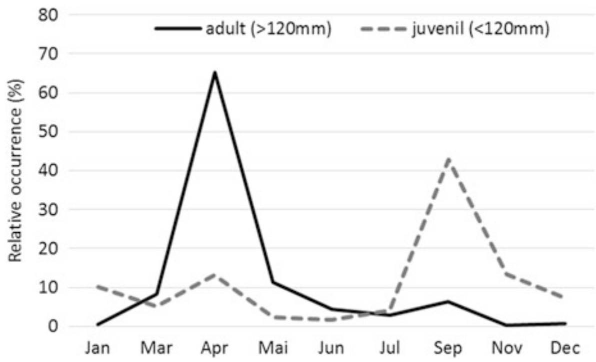

Fig. 24.12 Relative occurrence of juvenile and adult nase within the fish bypass system of "Freudenau" (adapted after Meulenbroek et al. 2017b)

The subsequent, seminatural bypass channel with a mean discharge of 1.6 m^3/s and an average slope of 0.7% is situated in a riverbed of 7 m width and a corresponding average current speed of 0.6 m/s. The discharge is not constant but follows the mean discharge of the Danube, reaching a maximum of 3.6 m^3/s. The length of this free-flowing section is approximately 900 m. The uppermost part of the system is built as a pool pass of 19 pools with a minimum of 70 m^2 per pool and a water level difference of 11 cm from pool to pool.

Beside the systems function as migratory facility, shown in 2000 by Eberstaller and Pinka (2001), the bypass system also provides a spawning ground for all the guilds of Danube fish and therefore makes an important contribution to the maintenance of several endangered species. In a monitoring survey, conducted throughout 2013 and 2014, seasonal changes in abundances, species diversity, and spawning events were observed. A total of 41 species colonize the bypass with temporary and spatial fluctuations. In early spring, the indicator species of the free-flowing Danube, nase and barbel, migrated into the fish pass in very high quantities. After spawning in April and May, most of the adults left the system. Shortly afterward a massive drift of early life stages of riverine fish species was observed, followed a few months later by thousands of juvenile fish (Fig. 24.12) (Meulenbroek et al. 2017b).

Present studies at the bypass system of "Freudenau" show that, in contrast to a pure technical construction, the seminatural bypass system provides a migration function and performs like a Danube tributary. However, geodetic research showed a deepening of the riverbed caused by continuous erosion due to lack of gravel input from upstream. This demonstrates the absolute need of management actions from time to time (after 15–20 years) to secure the positive ecological values for fish and other riverine faunal elements (Meulenbroek et al. 2017b).

24.6 Conclusion

In the Austrian stretch of river Danube (approx. 350 km), ten hydropower stations/impoundments have been implemented within the last 70 years. All of them massively affect the fish fauna. The most threatened fish are those of the rheophilic guild, which was dominant during pristine conditions. Straightening the river channel at larger scales started in the 1850s. Their further development favored lacustrine as well as eurytopic species at the same time that it decreased abundances and occurrences of riverine species by shortening free-flowing habitats and cutting off side arms.

Impoundments deny rheophilic fish a number of structures found in free-flowing river stretches: suitable gravel spawning grounds, small- and large-scale inshore structures for nursery and juvenile development, and shelters in times of flood events and winter situation as well as proper food security. As a consequence, fish ecological research shows an extreme decrease of riverine adults in the central impoundments, and successful reproduction is only possible in small, restricted areas of running waters with gravel habitats in the tail water of the dams.

However, in impoundments stronger development of eurytopic and lacustrine fish species is hampered by comparatively low water temperatures, low plankton density needed as starter feed for their larvae, a lack of macrophytes as spawning habitats, and a lack of structured refuge and nursery habitats.

Based on these abiotic and biotic conditions, a Danube impoundment does not serve the development of a proper life cycle for riverine fish or for lacustrine communities. Eurytopic species are most likely to accept suboptimal conditions, and therefore in most impoundments a very limited number of eurytopic species dominate the fish fauna.

Planning and constructing of the latest Danube hydropower plant at "Freudenau" (operation started 1998) considered a variety of ecological measures to improve the biotic integrity of the affected river section. Large-scale habitat constructions—based on the lessons learned at other impoundments—include double-riprap secured gravel banks, creation of massive inshore riverbed structures, a bypass system for fish migration, and creation/connection/integration to riparian backwaters and side arms. Results from the fish assemblages as seen in Fig. 24.11 pinpoint the positive ecological development of the central impounded area only when riparian side arms and structures are situated.

Because of "aging" of the constructed riparian elements, succession happens in the riparian vegetation as well as in the habitat morphology, and hence continuous human management and maintenance are vital to sustain the habitat's functioning. Given the scale that humans use the river's flow to satisfy such needs as electricity, in response habitat management has to secure the functioning of ecological improvements to guarantee future fish stocks for next generations. Hydropower rules the fish!

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Acknowledgements

Zunächst möchte ich mich bei allen Co-Autoren bedanken, die mitgeholfen haben, diese wissenschaftlichen Arbeiten zu publizieren!

Ein großer Dank gilt meinem Betreuer Herwig Waidbacher! Du bist sowohl menschlich, als auch fachlich ein echtes Vorbild. Deine Vorlesungen während meines Bachelorstudium, waren der Hauptgrund mich weiter in diese Richtung zu vertiefen. Direkt nach dem Abschluss des Masterstudiums mit dir gemeinsam zu arbeiten und die vielen gemeinsamen Stunden im Freiland werden mir immer in Erinnerung bleiben! Deine ganzheitliche Betrachtungsweise und kreative Herangehensweise an Problemstellungen haben mich nachhaltig geprägt. Auch dein Engagement und die Freude an der Arbeit sind ganz einfach ansteckend. Danke auch für dein Vertrauen und die vielen Möglichkeiten die du mir eröffnet hast – viele haben nicht nur meine fachliche, sondern auch meine persönliche Entwicklung stark beeinflusst.

Besonderer Dank ergeht an meine Kollegen und Freunde vom IHG. Zum einen für den fachlichen Input in unzähligen Diskussionen, vor allem aber auch für all die gemeinsamen Stunden der „Ablenkung" in den letzten fünf Jahren.

Danke an die vielen engagierten und motivierten Diplomanden! Ohne euch wäre die Datenaufnahme für diese Dissertation nie in dieser Form möglich gewesen.

Danke dir, Michael Geisler für die vielen Stunden Diskussion über die Donau – und sind wir uns mal ehrlich, in einer Mittagspause an einem intensiven Befischungstag, mit deiner Gourmetjause in der einen, dem Radler in der andren Hand, auf einer Schottenbank im Sonnenschein sitzend, diskutiert sich's einfach am besten.

Danke an Erwin Lautsch. Dein Rat in statistischen Belangen und die Gespräche mit dir waren immer sehr bereichernd und oft unterhaltsam.

Christian Dorninger und Martin Seebacher, ohne eure Unterstützung, sei es am Computer, mit dem Schweißgerät oder durch den regelmäßigen Griff in die SchokoLade, wäre vieles nicht mögliche gewesen.

Danke auch an Susanne Krumböck und Christian Stauffer vom Institut für Forstentomologie, Forstpathologie und Forstschutz. Wir (meine Fischlarven und ich) haben uns bei euch (und euren Borkenkäfern) immer willkommen gefühlt. Ihr habt mir nicht nur die Welt der genetischen Methoden nähergebracht, sondern mich auch sehr aktiv bei allen meinen Aufgaben und Anfragen unterstützt.

Die vorliegenden Publikationen sind im Rahmen des Projekts Freudenau ("Donau-Stauraum Freudenau" Ökosystem-Response 15 Jahre nach Einstau) entstanden. Danke an die Verbund Hydro Power GmbH für die Finanzierung und Unterstützung. Vor allem Roswitha Renner und Herr Ringel haben vieles erst möglich gemacht.

Ein großer Dank gilt natürlich auch meinen Eltern, dich mich nicht nur während der Dissertation, sondern immer in jeder Hinsicht unterstützt haben.

Abschließend möchte ich Dir danken, Nina. Deine Unterstützung, Liebe und Geduld in den letzten Jahren waren die Grundvorrausetzung um diese Arbeit fertigzustellen. Deine motivierende und positive Art hat mich immer wieder bestärkt weiter zu machen.