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PRACTICE INSIGHTS

A habitat connectivity reality check for fish physical habitat model results and decision-making for river restoration

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Abstract

1. Fish physical habitat models are a tool for guiding restoration efforts in lotic ecosystems, but often they overestimate restoration outcomes because currently they do not incorporate habitat connectivity. This persistent issue can, in extreme cases, result in little or no improvement to fish populations after the restoration, wasting valuable conservation resources.
2. We present a case study where practitioners applied a fish habitat model for multiple life stages of gravel spawning fishes to a 52-km stretch of the Iller River but did so at a microscale implementation by setting up a model based on cross sections with a maximum of 200 m distance from each other. This approach provided an opportunity to assess the connectivity of habitats for gravel spawning fishes, that is, European Grayling (*Thymallus thymallus*) and Common Nase (*Chondrostoma nasus*), integrating probabilities to find suitable habitats for all life-history stages and seasonal movements.
3. We used the assessed habitat estimates (availability of distinct habitat types within reaches defined by the 200 m cross sections) to calculate the minimum distance a fish would need to overcome to change from one habitat type into the other as it hypothetically 'grew up' from egg to full spawning adult. This approach can be interpreted as a life cycle habitat check as it considers all habitat types that are necessary to fulfil the life cycle of gravel spawning fishes including their size, distance and flow direction-related orientation (e.g. larvae habitats only used when downstream of spawning areas).
4. Our results show that the assumption of complete connectivity would require long movement distances for vulnerable life stages to find suitable habitat. This puts the high priority on the creation of migration corridors and passability of migration barriers in question. Without consideration of habitat types for all life stages of a species and their spatial context, restoration will not be successful. Shortly said: A perfect migration corridor does not necessarily provide habitat connectivity.

5. We recommend the application of the habitat connectivity approach when predicting the effect of restoration measures and particularly setting the priority of measures for mitigation of fish migration.

KEYWORDS
connectivity, dispersal, fish habitat models, instream habitat models, river restoration

1 | INTRODUCTION

Restoration and management of rivers depend on a variety of metrics to inform decision-making, but habitat is typically the focal metric when animal populations are among the key restoration goals (Palmer et al., 2014). One advantage of using habitat suitability as a metric is that it can be considered a proxy for potential population changes regarding both, enhancements or impacts under specific circumstances (Stephens et al., 2015; Wegscheider et al., 2020). One of the most prevalent uses of habitat suitability models in rivers of North America and Europe involves assessing habitat for fish species (Parasiewicz & Dunbar, 2001). Practitioners select species for assessments because of their economic (e.g. fishery), ecological (e.g. keystone species) or sensitivity importance (e.g. indicator species). Once selected, a variety of approaches can be used to parameterize a fish habitat model given a site's hydraulic flow conditions and physical parameters of the stream bed (Conallin et al., 2010).

Historically, practitioners have modelled fish habitat in streams and rivers using a suite of physical habitat modelling software, but their use has come under more scrutiny in recent years (Kemp & Katopodis, 2017; Railsback, 2016; Reiser & Hilgert, 2018). For physical habitat models, habitat is usually described by water depth, flow velocity, substrate and cover based on results of hydrodynamic modelling for different discharges and surveyed spatial information on morphology, in most cases, subreach scale (i.e. <1 km of river) (Conallin et al., 2010; Kemp & Katopodis, 2017; Wegscheider et al., 2020). As a result, the suitability of river model elements can be derived by the use of habitat preferences defined via microhabitat assessment, literature data or/and expert knowledge. The integration of habitat suitabilities in terms of weighted sums or proportions of certain habitat suitability classes is then used as indicator for habitat availability and its change with river discharge changes (naturally or anthropogenic).

A major confusion to this approach is that changes in habitat area are often incorrectly assumed as corresponding to changes in population size, although this assumed correlation does hold empirically in some cases (Parasiewicz & Dunbar, 2001). For instance, this view on habitat rarely includes any aspects of the fish community, other abiotic variables, density-dependence or connectivity that may influence the dynamics of the selected population (Railsback, 2016). Similarly, if the home range of the selected species and life history is larger than the study area, future recruitment of the selected population depends on multiple areas that are not studied (Fausch et al., 2002). Knowledge gaps about movement between habitats and upper limits of distances to overcome act as a key barriers for assessing the potential viability of restored habitat and a recovering population (Humphries et al., 2019; Torgersen et al., 2021).

One way to potentially address this gap is to investigate the distances necessary to reach all habitats for each life-history stage (Hermoso & Filipe, 2021). This view encourages that all life stages need to be supported before any positive changes in the population occurs (Humphries et al., 2019; Torgersen et al., 2021). Such a view is also in line with the restoration measures supported by the EU water framework directive and the proposed restoration plan of our case study system (Schneider et al., 2021). In this practice insight, we used an existing physical habitat model assessment of a heavily impacted river to assess this view of connectivity. In other words, we identify the role of connectivity for gravel spawning fishes by measuring the distances between habitats to be travelled for the completion of life cycles from initial spawning habitat locations as an egg up to spawning habitat locations as adults. Assuming the absence of migration barriers (a fully passable river), our objectives were threefold: (1) assess the number of hypothetically completed life cycles under a variety of discharges (from minimum flow conditions to mean flow conditions), (2) assess the minimum distance to travel for each life stage to complete life cycles and (3) visualize the locations and sizes of life stage-specific habitats that support life cycle completion in the Iller River. The restoration implications for this best-case scenario of a fully passable river are to highlight the impact of habitat connectivity in river restoration.

2 | MATERIALS AND METHODS

The Iller River (48° 22′ 53″ N 9° 58′ 23″ E) is a tributary of the Danube River, with its headwaters forming in the Alps. The river was filled by gravel since the last ice age, but today hydropower heavily regulates the river's flow and geomorphology. The habitat assessment in a former study (Schneider et al., 2021) of the Iller River used CASiMiR Fish, a fuzzy logic physical habitat model, for the last 52 km (for 10 different river discharges, ranging from 3 up to 70 m^3/s) based on a 2D hydrodynamic numerical model and integrated results in 200 m intervals (Figure 1; Noack et al., 2013). The results from the original assessment were to inform planned restoration measures in the Iller to satisfy EU water framework directive goals (Figure 2). But, generally in habitat modelling, uncertainty exists about location and life stage prioritization particularly when it comes to restoration type and site specification.

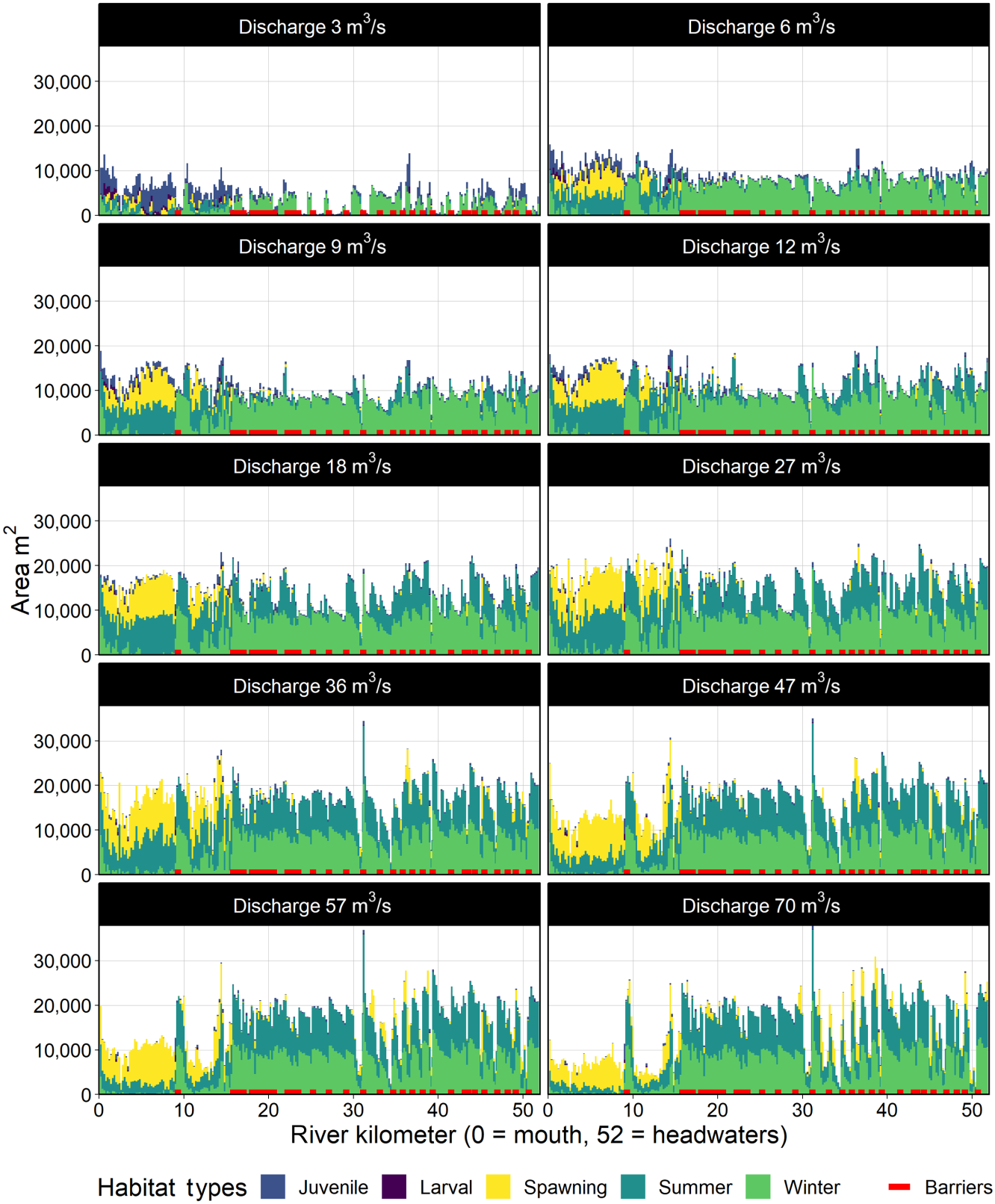

FIGURE 1 Results from original habitat assessment for the last 52 km of the Iller River before draining into the Danube River. Habitat area estimates (suitability >0.4) are from a physical fish habitat model (CASiMiR Fish) for gravel spawning fishes (stacked bars). *X*-axis indicates position along river in 200-m increments, *Y*-axis indicates area (m^2) by habitat type. Habitat is a function of discharge, so each plot shows a particular discharge (m^3/s) in the river. Existing low head dam and weir barrier locations are shown in red.

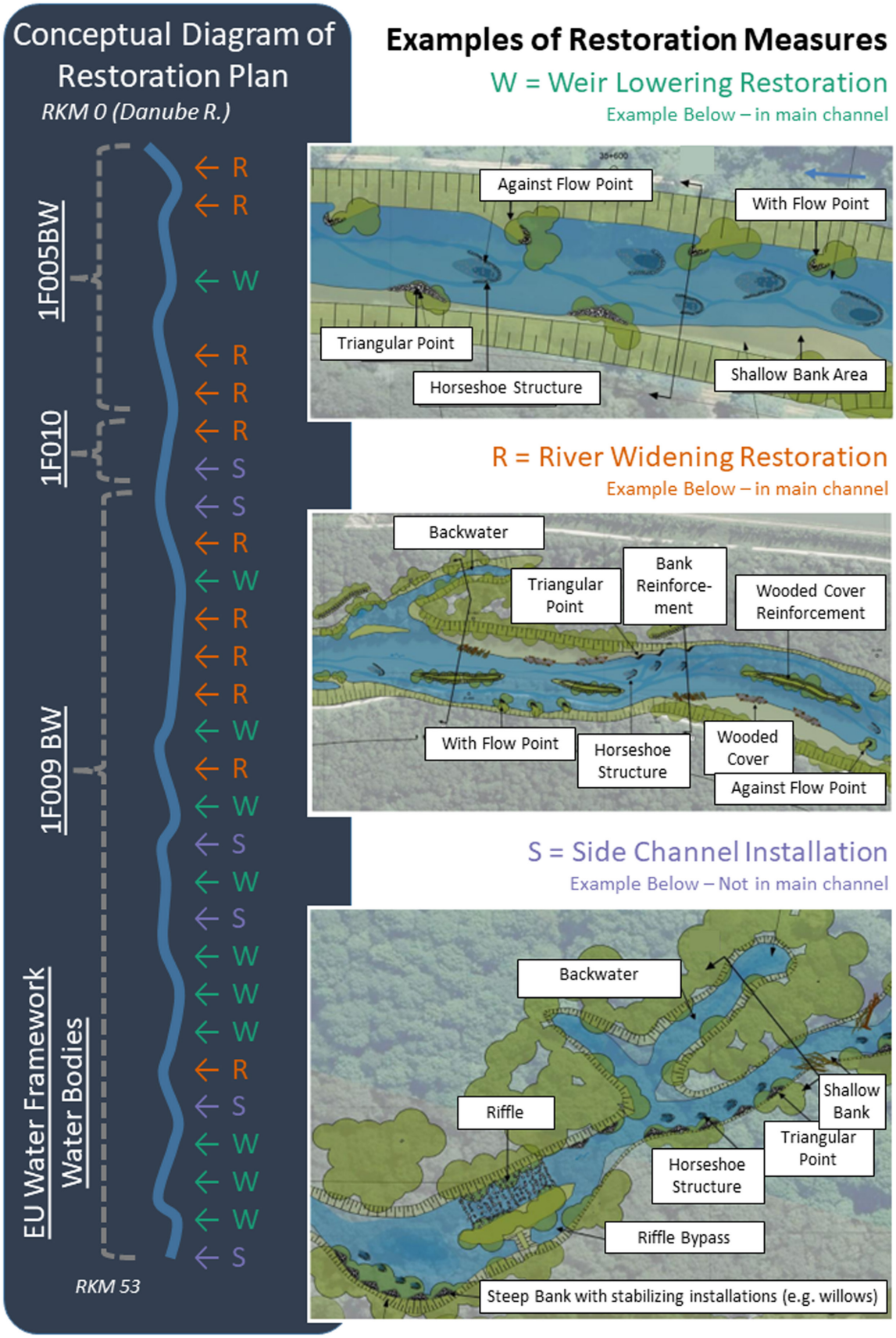

FIGURE 2 Proposed restoration plan for the Iller River showing approximate locations, EU water framework directive water body designations and examples of restoration measures. Each restoration measure (i.e. Weir Lowering [W], River Widening [R] and Side Channel Installation [S]) has an associated number of morphological features (white boxes) that are constructed during restoration.

CASiMiR uses a fish's habitat preference for water depth, flow velocity, substrate and cover as an index of habitat using a multivariate approach. The fuzzy logic aspect of CASiMiR allows users to incorporate expert opinion on fish suitability when empirical measurements are absent and strong distinction is not helpful. The original habitats assessed were: (1) larval, (2) juvenile, (3) spawning, (4) summer and (5) winter habitat for gravel spawning fishes (Figure 3). Two gravel spawning indicator species informed the habitat suitability criteria (i.e. for the Iller, Grayling *Thymallus thymallus* and Common Nase *Chondrostoma nasus*) to encompass the gravel spawning reproduction life-history strategy (Schneider et al., 2021). Further details on the case study and modelling (such as suitability index criteria) that produced the outputs used in this paper are found in the Supplementary Material or in the original publication (in German; Schneider et al., 2021).

Here, a life cycle is defined as the complete success of all movement transitions for each life stage to its corresponding habitat as a fish grows (i.e. spawning habitat to larval habitat to juvenile habitat to summer habitat to winter habitat to spawning habitat). To assess the number of hypothetically completed life cycles under a variety of discharges, we first identified suitable spawning habitat locations from the original assessment. These were defined as sites with good and very good suitability for spawning (i.e. suitability greater than 0.6). Next, we considered habitat that was characterized as fair, good and very good (calculated suitability index >0.4; less than 0.4 is considered poor habitat) for each remaining life stage. With all life stage-specific habitat locations identified, we then needed to constrain the possible movement transitions that could occur as a fish grows up. These transition requirements ultimately determine the minimum distance calculations which we use to assess connectivity. For our case study, we focused on larval/juvenile drift, adult dispersal and adult spawning migration (i.e. the life stages, where movement is an obligation to complete its life cycle for most gravel spawning fishes; Figure 3).

Once all life stage-specific habitats were identified for each discharge, we calculated the nearest downstream larval habitat from each of the initial spawning locations, then calculated downstream to juvenile habitat and then nearest locations (upstream or downstream) for summer adult habitat, winter adult habitat and spawning habitats. We recorded the area of each habitat that was used. We considered all distance measures to be one-dimensional; thus, distances were just differences in river kilometre (which is equal to the real distances given the centreline of the river). When an appropriate habitat was at the same site, we considered that as a no movement necessary situation.

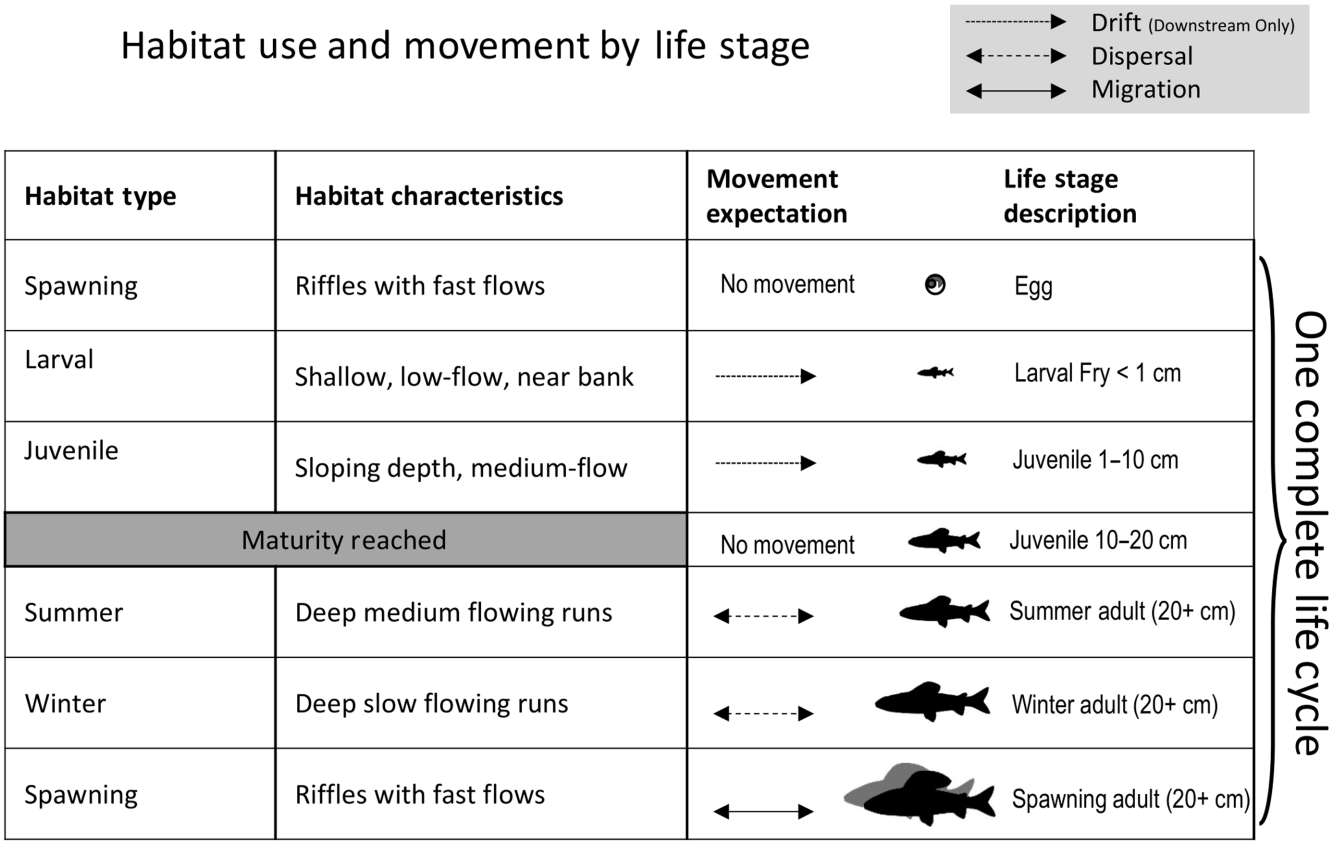

FIGURE 3 Overview of distance calculation assumptions given habitats modelled, expected habitat uses for life-history stage and type of movement for each transition between habitats. Fish images indicate expected direction of travel for each life-history stage, timeline shows general habitat occupied throughout a year for each life-history stage and the table describes the type of habitat suitable for each life-history stage. Fish larger than juveniles could move in either direction in the calculation, while juveniles and fry could only move with the flow downstream.

To make our calculations as realistic as possible, we made four assumptions for the calculation of movement distances. First, we assumed that no homing was required to fulfil spawning; thus, fish could choose a different spawning site from which the fish hatched. Second, as no major tributaries enter the explored section of the river, we assumed that any fish that could not find suitable habitat within the 52 river kilometres we deemed as an incomplete life cycle, and thus 'flushed' into the Danube River (this only applies to juvenile and smaller life-history stage since their movement is only downstream drift). Third, we assumed the design of the original habitat model assessment would be representative of most gravel spawning fishes. Fourth, we assumed that habitats are selected only by suitability criteria and incorporate no density dependence limitations. Finally, to assess importance of connectivity, we assumed that the presence of barriers had no effect on life cycle completion, so we could investigate implications of a barrier-free/perfect passability scenario. This scenario is the current conservation priority for long-term dam mitigation. Under this best-case scenario, our calculations act as the reality check to see if such a scenario would help gravel spawning fishes as intended.

3 | RESULTS

Minimum movement distance calculations revealed that a discharge of 18 m^3/s allowed for 66 completed life cycles, with no life stage being flushed from the system (Table 1). As discharges increased over 18 m^3/s, the total number of initial spawning sites increased, but flushed life-history stages also increased, resulting in a lower completion percentage. Completed life cycles seemed to reach an asymptote after 18 m^3/s, with completed life cycles ranging from 66 to 71. A total number of life cycles increase with discharge, except for discharge 57 m^3/s.

Minimum distances (averaged) for each life stage showed that larval fish required the longest movements (Figure 4). At discharge 12 m^3/s, larval fishes required the lowest distance to reach suitable habitats, whereas increasing or decreasing from 12 m^3/s on average required greater distances (km). We recorded larger variability in larval distances (in km) compared to other life stages with standard error ranges from 0.43 to 1.28. Except for larval fishes, most life stages could find suitable habitat within 2.5 km across discharges: larval (mean = 4.11 km, SD = 1.05 km), juvenile (mean = 0.04 km, SD = 0.11 km), summer (mean = 0.14 km, SD = 0.29 km), winter (mean = 0.53 km, SD = 0.51 km), spawning (mean = 0.29 km, SD = 0.62 km). We identified higher distances for winter habitats compared to other non-larval habitats. At a discharge of 3 m^3/s, we found raised distances for summer and spawning movements.

Habitats potentially used throughout the completed life cycles, when considering complete connectivity, ranged from ~1000 m^2 up to ~70,000 m^2, indicating life stage-specific limitations of habitat throughout the study area (Table 2). Discharge of 18 m^3/s had greatest total habitat area with the largest contributions coming from summer and winter habitat. Discharges greater than 47 m^3/s saw decreases in total habitat area with usually only one or two life stage habitat types (i.e. summer, winter) dominating instead of a more equal allocation across life stages. The location of most completed life cycle habitats typically occurred in the undammed lower river regions (river kilometres 0–10) for all discharges (Figure 5). Dams often surrounded remaining habitats both upstream and downstream. It was rare to find a completed life cycle habitat point beyond river kilometre 25 despite our approach allowing for full passabililty.

4 | DISCUSSION

In comparison to the original assessment of the Status Quo situation in the 52 km of the lower Iller river (Schneider et al., 2021; Figure 1), our results (Figure 5) show that locations that support the entire life cycle for gravel spawning fishes are extremely site specific, and almost exclusively located in the dam-free region (downstream of river kilometre 25) even under the assumption of complete connectivity. This suggests that even if every dam was passable because of thorough fish passage installation investments, limited amounts of habitat for all life stages would be found in dammed regions. Such an outcome could be interpreted as an ecological trap (fish move into habitat with lower fitness potential) producing potentially even

Discharge m^3/s	Total initial spawning sites	Completed life cycles	Incomplete life cycles	Completion (%)
3	12	12	NA	100%
6	25	25	NA	100%
9	36	36	NA	100%
12	51	51	NA	100%
18	66	66	NA	100%
27	70	66	4	94%
36	75	69	6	92%
47	77	71	6	92%
57	74	64	10	86%
70	77	67	10	87%

TABLE 1 List of discharges modelled in original habitat assessment with associated completed life cycles, total number of life cycles available given initial spawning conditions for the Iller River, complete life cycles, incomplete life cycles and percentage comparison.

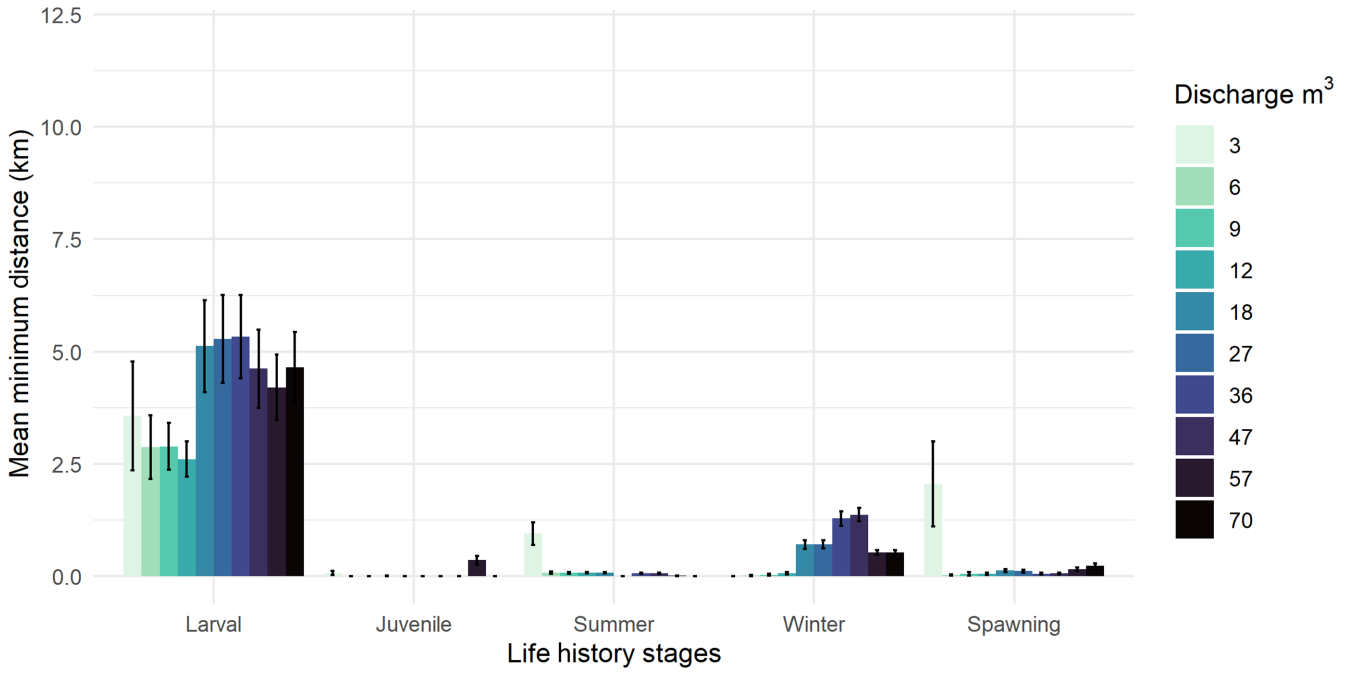

FIGURE 4 Average minimum distances (mean ± SE) by discharge for each transition from larval to spawning adult.

TABLE 2 Habitat area used by different life stages only for completed life cycles at different discharges in the Iller River. Red colour shows relative low value, blue colour shows a high value.

Habitat area (m^2) by discharge and life-history stage						
Discharge	Larval	Juvenile	Summer	Winter	Spawning	Total
3	4208	18,466	6488	9275	4529	42,966
6	4900	13,351	18,166	11,148	6086	53,651
9	5207	12,753	28,243	19,348	9194	74,746
12	6851	19,150	57,958	26,399	9325	119,682
18	4561	13,231	73,912	27,759	17,242	136,706
27	4445	9913	63,273	27,998	15,696	121,325
36	3217	9005	41,777	25,467	12,463	91,928
47	3849	8832	37,231	22,596	28,272	100,780
57	3314	9362	39,315	31,595	16,075	99,662
70	1615	7124	31,750	25,994	11,368	77,851

worse outcomes than prior to fish passage investments (Pelicice & Agostinho, 2008) due to fishes migrating into the river sections with certain habitat types being unavailable. Distances for larval fishes emerging from eggs to suitable larval habitat would likely incur high mortality or fish be flushed from the system entirely, since young-of-year habitats are missing during these downstream movement phases. We found areas of high habitat amount that allow for life cycle completion, but dams and weirs often surrounded these places. Our approach indicated, for the situation without any restoration measures but only enabling migration, an optimum discharge of 18 m^3/s that would enable the greatest amount of completed life cycles without losing fish to flushing and supported the greatest amount of total habitat area. Although discharge is not constant because of hydropower production and seasonal hydrological changes, our analysis highlights opportunities where specific flows may support gravel spawning fish recovery at critical time periods related to movement transitions and life stages.

There are limitations to our calculation that come directly from our assumptions, which may not transfer to other systems and species. First, we assume transitions are linear and are not habitat size dependent but for systems that have numerous tributaries with varying habitat patch sizes, mobile fish may elect to move laterally instead of staying in the main channel (Pracheil et al., 2009). Most of the tributaries are small which are typically considered unsuitable by the representatives of the considered gravel spawners grayling and nase. However, this assumption could be incorporated correctly if sizes and locations of the tributaries and fish movement behaviours are both known and assessed. For our study, the only major tributary-like connections are the side channels from the hydropower plants, so we assumed

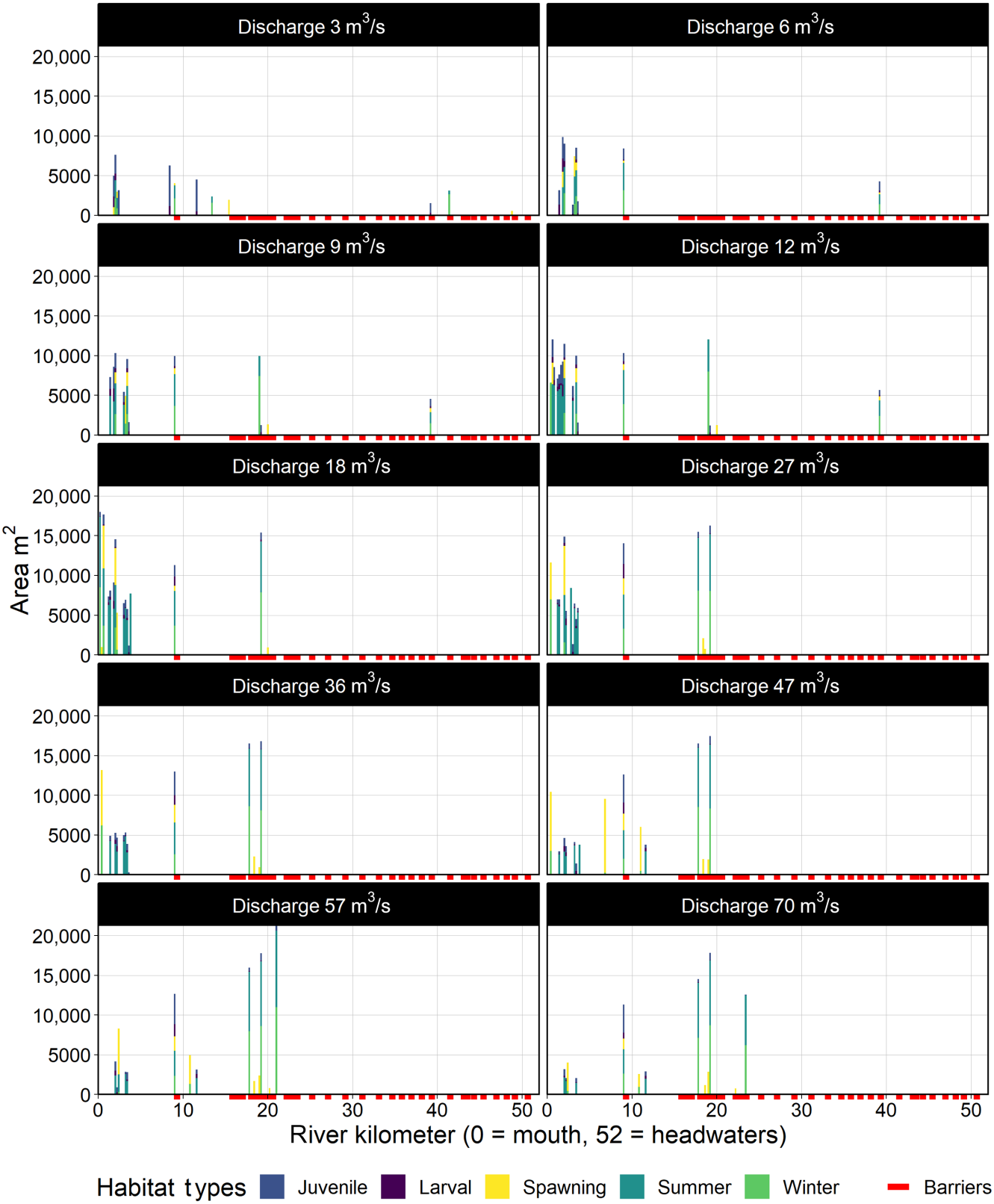

FIGURE 5 Location (river kilometre) and area (m^2) of habitats identified in the life cycle movement calculations. Existing barrier locations are shown in red but considered passable within the life cycle calculations. Most habitat areas that support all life stages typically occur in already dam-free reaches.

they would not provide suitable habitat, due to their monotonous morphology and hydropeaking. For movements within the river, a stricter criterion of movement could be incorporated such as a minimum habitat size, habitat geometry (extends to both banks vs. narrow strip centreline of river) or density dependence (e.g. no habitat can be occupied by the same life cycle transition), but more detailed information on site selection would be needed for target species. Second, we assumed that flushing out of the Iller River and into the Danube River would suggest a negative impact on young-of-year fish, but this may not be the case if this approach was used for a different species that naturally undergoes long-dispersal distances into larger rivers. Additionally, maximum movement distances were not considered here but for more immobile fish, this may be important.

Restoration of gravel spawning fishes in the Iller would likely benefit from increased larval habitat downstream of spawning sites, which is a general challenge for rheophilic fish populations in European rivers (Stoffers et al., 2022). But it is difficult to know the optimal location where restoration should occur, given that discharge is dynamic and larval fish recruitment requirements are under documented (Scheidegger & Bain, 1995). One approach would be to pinpoint the largest gaps and minimize the spacing, so there are multiple sites for larval fish to settle. Alternatively, one could consider making one large site downstream of each spawning site to improve the settling of larval fish. Regarding future restoration plans (Figure 2), our approach opens new research priorities concerning life stages that require greater connectivity opportunities. Which restoration technique and morphological features are best suited for larval fishes? How critical is the location of the chosen technique? Will a restoration technique work for all discharges and all life stages, or only certain ones? Future work will investigate the efficacy of these proposed restoration plans from a habitat connectivity view and attempt to identify which techniques and locations should be prioritized.

There are three adjustments needed before applying the calculation to the proposed restoration plan. It is not clear whether low-head dams and weirs have some effect on mortality of younger life stages in the Iller River, but impacts on post-spawning recruitment have been documented elsewhere (Humphries & Lake, 2000). In a system where such information is available, changing the calculation to accommodate the number of dams needed to pass or difficulty of passage may improve understandings of movement limitations and thus passage prioritization of restoration dollars. Second, if discharges are variable throughout the year, movements should correspond to expected discharge for that time of year (e.g. juveniles at 27 m^3/s may need to move to summer habitat at 18 m^3/s). Lastly, from a practitioner perspective, we elected to include only the habitat suitability (i.e. fair, very good and good) that would be ideal to restore into the system but suitability criteria should be decided on case-by-case basis (Radinger et al., 2016). Incorporating minimum sizes of habitat and maximum distances would also impose more realism on the approach when such data become available.

Here, we demonstrated a practical way to assess physical habitat suitability model output for fish in river systems that directly addresses connectivity as a limitation. Our approach not only showed movements that would likely impact survival of vulnerable life stages but also did so in relation to discharge and future habitat improvement planning. We contend similar calculations would provide a much needed spatial understanding for river restoration projects that depend on fish physical habitat suitability models.

AUTHOR CONTRIBUTIONS

Henry H. Hansen, Matthias Schneider and Tobias Hägele conceptualized the study, wrote the article and edited the manuscript. Henry H. Hansen and Tobias Hägele performed the analysis. Matthias Schneider and Tobias Hägele managed the data preparation.

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CONFLICT OF INTEREST STATEMENT

None.

PEER REVIEW

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1002/2688-8319.12291.

DATA AVAILABILITY STATEMENT

Repository for code and data can be found in Zenodo: https://doi.org/10.5281/zenodo.7657315 (Hansen et al., 2023).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1. Overview of Iller River (rkm 0–56) and the three side channels to support hydropower operations (green, yellow, and red lines).

Figure S2. Example of habitat suitability metrics for summer grayling habitat (type from Table S1).

Figure S3. Example of habitat assessment for summer grayling habitat for all 52 km of the Iller River at a discharge of 12 m^3/s. *X*-axis is positon in the river, *y*-axis is area of habitat (10^3 m^2), color indicates quality of habitat (gray = very poor habitat, orange = poor habitat, yellow = fair habitat, green = good habitat, blue = very good habitat).

Table S1. Overview of habitat types of two indicator species and the corresponding structure type used in the habiat assessment of the Illler River.

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