River restoration is prone to failure unless pre-optimized within a mechanistic ecological framework | Insights from a model-based case study

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Abstract
River restoration with the use of in-stream structures has been widely implemented to maintain/improve physical habitats. However, the response of aquatic biota has often been too weak to justify the high costs of restoration projects. The ecological effectiveness of river restoration has thus been much debated over claims that large-scale environmental drivers often overshadow the potential positive ecological effects of locally placed in-stream structures. In this study, we used a two-dimensional hydrodynamic-habitat model to evaluate the ecological effectiveness of habitat restoration with the use of in-stream structures in various water discharges, ranging from near-dry to environmental flows. The habitat suitability of benthic macroinvertebrates and of three cyprinid fish species was simulated for six restoration schemes and at four discharge scenarios, and was compared with a reference model, without in-stream structures. We found that the ecological response to habitat restoration varied by species and life stages, it strongly depended on the reach-scale flow conditions, it was often negative at near-environmental flows, and when positive, mostly at near-dry flows, it was too low to justify the high costs of river restoration. Flow variation was the major environmental driver that our local habitat restoration schemes attempted -but mostly failed- to fine-tune. We conclude that traditional river restoration, based on trial and error, will likely fail and should be ecologically pre-optimized before field implementation. Widespread use of in-stream structures for ecological restoration is not recommended. However, at near-dry flows, the response of all biotic elements except for macroinvertebrates, was positive. In combination with the small habitat-suitability differences observed among structure types and densities, we suggest that sparse/moderate in-stream structure placement can be used for cost-effective river restoration, but it will only be ecologically effective -thus justifying the high implementation costs- when linked to very specific purposes: (i) to conserve endangered species and (ii) to increase/improve habitat availability/suitability during dry periods, thus proactively preventing/reducing the current and future ecological impacts of climate change.

Keywords
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1. Introduction

The notion that healthy habitats support healthy biota, which, in turn, support healthy human societies, emerged after decades of uncontrolled human development that caused severe degradation in both terrestrial and aquatic ecosystems (Vörösmarty et al., 2010; Grizzetti et al., 2017). Degraded natural systems have hence been engineered to restore their hydrologic, geomorphic and ecological processes (Wohl et al., 2005), a practice that has been commonly termed ‘ecological restoration’. In rivers, restoration techniques vary from in-stream interventions, such as removal of man-made structures that inhibit natural flow, removal of barriers to fish passage, installation of natural or artificial structures to enhance aquatic habitats, to riparian or basin-wide modifications, land restoration, flow diversions, dam removal, and erosion control (RRC, 2002; Yochum, 2018). Among these methods, the placement of engineered in-stream structures that create pools, modify channel morphology and increase habitat complexity has long been applied in habitat enhancement (Stewart et al., 2009). Weirs, deflectors and cover structures made from root wads, logs, boulders and gravel are used to increase biota population density and improve ecosystem functioning (Roni et al., 2005).

Although physical habitat is enhanced by the placement of in-stream structures, the relevant response of aquatic biota has been much debated; it is not always positive, it varies by species and life stages, and when positive, it is often weak (Roni et al., 2005; Thompson et al., 2005; Stewart et al., 2009; Palmer et al., 2010; Roni, 2019). According to previous research on salmonids, 70% of studies show increased abundance around engineered in-stream structures, while approx. 7%-28% of studies suggest no response and 7%-18% show lower abundance in restored habitats (Stewart et al., 2009; Roni et al., 2015). Compared to pre-restored conditions, the positive salmonid responses around in-stream structures (increased population density/abundance) often range from 10% to 50%. Nevertheless, increased abundances of up to 167% have also been reported (Whiteway et al., 2010; Roni et al., 2015). For non-salmonid species, results range from no significant responses (Lonzarich and Quinn, 1995) to 90% increase in fish abundance/density in restored habitats (Shields et al., 1993). Varying responses have also been observed for benthic macroinvertebrates (Miller et al., 2010). According to Roni et al (2015) approx. 67% of studies suggest increased macroinvertebrate density around engineered in-stream structures, while 33% show similar or lower densities in restored habitats. Typically, the positive macroinvertebrate responses are not higher than 28% of the pre-restored conditions (Miller et al., 2010). Considering the high costs of river restoration, ranging from €2,200,000 to €31,000,000 per km² for European rivers (Ayres et al., 2014; Szalikiewicz et al., 2018), weak positive ecological responses may not be enough to characterize a restoration project as successful. Thus, ineffectiveness -or failure- in ecological restoration is a common outcome (Palmer et al., 2014; Swan and Brown, 2017).

The reasons for failure have been well documented; a multitude of environmental, ecological and anthropogenic factors interact across temporal and spatial scales, acting as filters to the effectiveness/success of ecological restoration (Mika et al., 2010; Feld et al., 2018; Liao et al., 2018). Local habitat restoration in a degraded river basin may trigger no observable ecological response. Reach-scale flow modification may also undermine the effectiveness of local habitat restoration; dam-induced flow regulation upstream of a restored river reach may reduce the positive ecological effect of locally placed in-stream structures. In addition, catchment-scale land use or the proximity to upstream and downstream populated areas are often not accounted prior to habitat restoration (Bernhardt et al., 2005). It has been argued that local habitat conditions may not be the major driver of ecological processes for fish and benthic macroinvertebrates (Brown et al. 2011, Heino et al. 2015, Karaouzas et al., 2019). Within the concept of environmental filtering, local habitat is accounted as a low-level filter for the regional pool of aquatic species (Friberg et al., 2016). It is thus considered that an optimized/restored low-level habitat filter will result in optimized local ecological processes, given that higher-level filters (e.g. reach-scale) are also optimal (Stoll et al., 2016).
All the above suggest that ecological restoration should be carefully designed and pre-optimized. Yet, many restoration projects have often been implemented within a process of trial and error (Friberg et al., 2016), without any mechanistic pre-optimization that would connect decisions to objectives (Bandrowski et al., 2015). To this end, hydrodynamic habitat models (HHMs) have been recently introduced in habitat restoration (RRC, 2017). In HHMs, a hydraulic/hydrodynamic model simulates the water depths (D) and depth-averaged flow velocities (V) at multiple discharges in a computational mesh (Papadaki et al., 2016; Papaioannou et al., 2020). The values of V and D are compared with habitat criteria of aquatic biota to estimate the habitat suitability for each simulated discharge (Gopal, 2013). Species density/abundance is thus related to habitat suitability, which is ultimately related to restoration effectiveness. Habitat restoration with the use of in-stream structures can be cost-effectively optimized prior to actual implementation by simulating different structures and patterns/densities of structure placement in various discharge scenarios, aiming to find the most effective restoration scenario, i.e. the one that yields maximum overall habitat suitability, and thus maximum species densities, for the reach under investigation (Adeva-Bustos et al., 2019).

In this paper, we are not pioneering the use of hydrodynamic habitat models for designing effective ecological restoration projects; this practice has been already incorporated into habitat restoration during the last decades (Brown and Pasternack, 2009; Schwartz et al., 2015; RRC, 2017). Rather, this study highlights that the physical, hydro-morphological and ecological processes that ecological restoration attempts to control and optimize (i) are often too complex to be addressed within the traditional trial-and-error based river restoration schemes and (ii) they should be carefully designed and pre-optimized within a mechanistic ecological framework before implementation. To reach this conclusion, we used a two-dimensional hydrodynamic habitat model and simulated the hydrological/hydraulic and habitat properties in a river reach for various habitat restoration schemes with the use of in-stream structures, at various discharge scenarios. Although case-specific, the results of the study are analyzed within a wider framework to emphasize that ecological restoration requires extensive, yet cost-effective pre-optimization before being applied to real life, to reach levels of effectiveness that will justify the high costs of restoration projects.

2. Materials and Methods
2.1. Study area and topographic data

The study area was a 443 m long reach (approx. 10,226 m²) in an intermittent Mediterranean watercourse, the Evrotas River, southern Greece (Fig. 1a, c). The current study built upon a previous model-based environmental flow assessment that was carried out in the same river reach (Theodoropoulos et al., 2019). Riverbed topography was mapped with 719 points recording longitude (X), latitude (Y) and bottom elevation (H), using a Real-Time Kinematic (RTK) GPS consisting of the Spectra Precision SP60 GNSS Receiver and the Mobile Mapper 10 GIS - GPS Receiver (Trimble Inc., USA). The topographic data (X, Y, H points) were afterwards imported into the Blue Kenue software (CHC, 2011) and an unstructured triangular computational mesh was generated by linearly interpolating channel topography across the reach. Here, we used the riverbed topography that was acquired during that previous research, and the relevant generated mesh, as a base model (reference) for designing/simulating multiple in-stream habitat restoration schemes. In total, we designed six habitat restoration schemes and modelled the habitat suitability for five biotic elements at four discharge (Q) scenarios. In total, 24 hydrodynamic simulations (4 Q scenarios x 6 habitat restoration schemes) and 120 habitat simulations were applied (24 hydrodynamic simulations x 5 biotic elements) to ultimately predict the habitat suitability at each node of the computational mesh of the study area for each habitat restoration scheme and at each discharge scenario (Fig. 2).
Fig. 1. Study area (a, b), bottom elevation (c), in-stream structures and habitat restoration scenarios (d, e) that were simulated. S1: Sparse simple structures, every 85 m, S2: Moderate simple structures, every 42.5 m, S3: Dense simple structures, every 21 m, C1: Sparse complex structures, C2: Moderate complex structures, C3: Dense complex structures.

Fig. 2. Flow diagram of the modelling process applied to evaluate the ecological effectiveness of six habitat restoration schemes at four discharge scenarios for five biotic elements. S1: Sparse simple structures, every 85 m, S2: Moderate simple structures, every 42.5 m, S3: Dense simple structures, every 21 m, C1: Sparse complex structures, C2: Moderate complex structures, C3: Dense complex structures.
2.2. Habitat restoration schemes

Two types of in-stream structures were designed (Fig. 1d, e); (i) Simple structures (S), representing wood logs: single pieces, 0.5 m in diameter and 10 m long, placed on opposite sides of the channel in a downstream direction, at an angle of 135° to the bank (Fig. 1d); (ii) complex structures (C), representing log jams: two single pieces, 0.5 m in diameter and 5 m long, and six single pieces, 0.5 m in diameter and 2.5 m long, tied together in two quadruplets (each quadruplet included a 5 m long piece combined with three 2.5 m long pieces), placed on opposite sides of the channel (two quadruplets per side) in a downstream direction, at an angle of 135° to the bank (Fig. 1e). The structure diameter and lengths were selected based on natural in-stream wood structures that have been previously recorded in the study reach (Kalogianni et al., 2020). The densest scheme included in-stream structures that were placed immediately after the end of the recirculation zone created by the previous structure. Six habitat restoration schemes were developed based on the type of structure (either simple or complex) and the density/pattern of the placed structures (Fig. 2).

1. S1: Sparse simple structures, evenly spaced at approx. every 85 m
2. S2: Moderate simple structures, evenly spaced at approx. every 42.5 m
3. S3: Dense simple structures evenly placed at approx. every 21 m
4. C1: Sparse complex structures evenly spaced at every 85 m
5. C2: Moderate complex structures, evenly spaced at approx. every 42.5 m
6. C3: Dense complex structures evenly spaced at approx. every 21 m

For each habitat restoration scheme, a different computational mesh was developed in Blue Kenue with the following properties; S1: 12,147 nodes, 23,249 elements; S2: 12,601 nodes, 24,159 elements; S3: 13,513 nodes, 25,985 elements; C1: 14,982 nodes, 29,035 elements; C2: 17,798 nodes, 34,667 elements; C3: 23,105 nodes, 45,281 elements. All meshes were refined around the structures to obtain locally detailed hydrodynamic results.

2.3. Model calibration-validation and hydrodynamic simulation

The base model, with no added in-stream structures, has been previously calibrated at \( Q = 0.008 \text{ m}^3\text{s}^{-1} \) and validated at \( Q = 0.02 \text{ m}^3\text{s}^{-1} \) and \( Q = 0.5 \text{ m}^3\text{s}^{-1} \) (Theodoropoulos et al., 2019). \( Q \) was prescribed at the upstream boundary and water surface elevation (\( Z \)) was prescribed at the downstream boundary based on a stage-discharge curve developed using hydrological information from a nearby gauging station. Calibration and validation of the model were applied by adjusting the riverbed’s roughness Manning’s \( n \) values, until an acceptable correlation (\( R^2 > 0.85 \)) between observed and simulated \( D \) and depth-averaged \( V \) values was achieved. It is considered that mesh-changes occurring from the placement of in-stream structures in already calibrated/validated base models will produce equally accurate hydrodynamic simulations (Wheaton et al., 2004; Hafs et al., 2014), as long as the computational mesh properties are based on the same topographic dataset and the same boundary conditions used in the base model. For each habitat restoration scheme, we used the TELEMAC 2D v6.2 (Galland et al., 1991) to simulate \( D \) and \( V \) in four \( Q \) scenarios, (i) environmental flow, previously determined at \( Q = 1 \text{ m}^3\text{s}^{-1} \) (Theodoropoulos et al., 2019), (ii) 0.8 \text{ m}^3\text{s}^{-1}, (iii) 0.6 \text{ m}^3\text{s}^{-1} \) and (iv) near-dry conditions (0.02 \text{ m}^3\text{s}^{-1}).

2.4. Habitat preferences and habitat suitability curves

The habitat preferences of benthic macroinvertebrates and of three endangered endemic fish species, the Evrotas chub \textit{Squalius keadicus} (Stephanidis, 1971), the Spartan minnowroach \textit{Tropidophoxinellus spartiaticus} (Schmidt-Ries, 1943) and the Evrotas minnow \textit{Pelasgus laconicus} (Kottelat and Barbieri, 2004) were used in this study to investigate differences among potential habitat restoration schemes and discharge scenarios. For the larger-bodied Evrotas chub, two size classes were recorded: small, total length (\( TL \)) < 10 cm, corresponding to juveniles and large, \( TL > 10 \text{ cm} \), corresponding to adults. Thus, four fish groups were studied; adult chubs, juvenile chubs, minnowroaches and
2.5. Habitat suitability modelling

For each of the 24 hydrodynamic simulations and for each of the five biotic elements (four fish groups + benthic macroinvertebrates), the habitat suitability (preference) was estimated at each node of the computational mesh of the study reach for three hydraulic parameters; V, D and S, respectively. The fish habitat suitability was calculated by converting the numerical values of V, D and S of the hydrodynamic model to habitat suitability preference, using the relevant habitat suitability curves. Then, a combined habitat suitability was estimated as:

\[ K = \sqrt[3]{K_V \cdot K_D \cdot K_S}, \]

where \( K_V \): velocity habitat suitability-preference, \( K_D \): depth habitat suitability-preference, \( K_S \): substrate habitat suitability-preference.

For benthic macroinvertebrates, a fuzzy rule-based Bayesian algorithm (FRB) was implemented in the HABFUZZ software (Theodoropoulos et al., 2016). The numerical values of V and D were converted to overlapping, five-class, trapezoidal-shaped membership functions (fuzzy sets). The K values were classified into five classes (0 ≤ bad ≤ 0.2; 0.2 < poor ≤ 0.4; 0.4 < moderate ≤ 0.6; 0.6 < good ≤ 0.8; 0.8 < high ≤ 1). Each numerical value of V and D was assigned to one or more fuzzy sets with a membership degree ranging from 0 to 1 (the type of substrate was treated as a crisp input and classified based on Schneider et al. (2010)). The training dataset, with a priori calculated K values, was used to develop sets of data-driven IF-THEN rules, relating the input fuzzy sets with a specific K class. The fuzzy membership degree (MD) of each input variable (V, D and S) was then considered as the probability of occurrence of the particular fuzzy set, such as ‘IF V is low with a membership degree of 1 AND D is moderate with a MD of 1 AND S is gravel with a MD of 1 THEN K is high with a MD of 0.3 and good with a MD of 0.7’. The IF-THEN rules were then combined using the Bayesian joint probability, so that (referring to the previous example) the probability of the specific microhabitat’s K being high is the joint probability that V is low AND D is moderate AND S is gravel AND K is high (1 x 1 x 1 x 0.3 = 0.3), while the probability of K being good is the joint probability that V is low AND D is moderate AND S is gravel AND K is good (1 x 1 x 1 x 0.7 = 0.7). Based on a utility function (Brookes et al., 2010), a score was assigned to each K class (bad: 0.1, good: 0.3, moderate: 0.5, good: 0.7, high: 0.9) and the habitat suitability (K) at each node of the computational mesh was ultimately predicted as:

\[ K = \sum M_{ij} S_{ij}, \]

where \( M_{ij} \) denotes the joint probability of occurrence of each K class and \( S_{ij} \) denotes the score of each K class. For the previous example, K equals to 0.7 x 0.9 + 0.3 x 0.7 = 0.84 (high).

2.6. Effectiveness of habitat restoration

To assess the effectiveness of each habitat restoration scheme for each biotic element at each Q scenario, we calculated the weighted usable area (WUA). WUA is an indicator of the available area (m²) of the study reach that can be exploited by each biotic element, by multiplying the K value of each node of the computational mesh with its relevant cell area and aggregating all values. Restoration effectiveness was then calculated based on the difference (and the percent deviation) between the WUA of the base model (without in-stream structures) and the WUA of the...
habitat restoration schemes/models. Increased WUA (positive change) indicates positive ecological response and decreased WUA (negative change) indicates negative ecological response. The model-based process described above, ultimately resulted in the assessment of the effectiveness of the six habitat restoration schemes in four flow scenarios and for five biotic elements of the Evrotas aquatic ecosystem. This point forward, habitat restoration schemes and flow scenarios are often combined as ‘habitat-restoration/discharge scheme’; for example, the C1/0.02 scheme indicates sparse complex in-stream structures modelled in the Q = 0.02 m³s⁻¹ scenario, while the base/0.6 scheme suggests Q = 0.6 m³s⁻¹ modelled without in-stream structures.

3. Results
3.1. Hydrological-hydraulic variation
The results indicate that water discharge was the primary factor that influenced the hydrodynamic simulations. The habitat restoration schemes had a lower overall effect (Fig. 3; Supplementary material Fig. S1, S2). Three generic patterns of water flow-hydraulic effects- around the in-stream structures were observed in the restored reach: (i) the in-stream structures deflected the flowing water, causing the formation of new water pools, either upstream or downstream of the structure, depending on the higher-level, reach-scale hydrodynamics; (ii) the in-stream structures modified the natural habitats by deepening and/or widening already established water pools, or by shallowing and/or narrowing the pools downstream of the structures in a distance that often surpassed several nearby structures; (iii) the in-stream structures had no effect on the water depth; the water overtopped the structures, without any visible water depth change compared to the base model; however, the flow velocity field around the structures was often substantially modified. The effect of habitat restoration was highest at the lower water discharges. As water discharge increased, most structures were overtopped by the flowing water. Ultimately, the presence of in-stream structures had an overall pool-forming, pool-deepening/widening and flow-reducing hydraulic effect compared to the base model.

Regardless of the habitat restoration scheme, near-dry water discharge (Q = 0.02 m³s⁻¹) had the lowest V and D values (Vmax = 0.79 ms⁻¹ for the C3/0.02 scheme; Dmax = 1.14 m for the S3/0.02 scheme). As discharge increased from 0.02 m³s⁻¹ to 1 m³s⁻¹, V and D also increased, reaching highest values at the base/1 (Vmax = 1.89 ms⁻¹) and the S3/1 schemes (Dmax = 1.74 m), respectively. Within the same water discharge, the presence of in-stream structures clearly influenced the local hydraulic conditions. All habitat restoration schemes maintained increased water volume in the channel, compared to the base model (Fig. 3e, f). The total additional water volume was highest in the C2/0.6 scheme (+226 m³) and lowest in the C1/0.8 scheme (+9.56 m³). Maximum percent volume change was observed in the C3/0.02 scheme (+14%) and lowest in the S1/0.8 scheme (+0.3%). All habitat restoration schemes had higher water depths compared to the base model (Dmax = 0.88 m), ranging from 1.02 m (+16%; S2/0.02 scheme) to 1.74 m (+97%; S3/1 scheme). Overall, flow velocity decreased as in-stream structures were added; in Q = 1 m³s⁻¹, Vmax decreased from 1.86 ms⁻¹ (base model) to 1.55 ms⁻¹ (−17%; C3 scheme). In Q = 0.02 m³s⁻¹, however, the base model had the lowest Vmax (0.56 ms⁻¹), while the C3 scheme had Vmax = 0.79 ms⁻¹ (41% increase).
3.2. Habitat suitability and the effectiveness of habitat restoration

The effects of river restoration on the weighted usable area were diverse, varying by water discharge and biotic element (Fig. 4, Fig. S3 to S9). Overall, the response of all biotic elements to habitat restoration was often negative, and when positive, mostly at near-dry flows, it ranged from near zero to +28.6%. Maximum positive ecological response was observed in moderate and sparse habitat restoration schemes, but the average WUA change between densities was low (approx. 10%), as was also the average change between simple and complex structures (< 10%). The highest positive WUA change was observed for the juvenile chub at the S2/0.02 restoration scheme (+28.6%). As discharge increased from $Q = 0.02 \, m^3s^{-1}$ to $Q = 0.6 \, m^3s^{-1}$, the positive effect of in-stream structures on habitat suitability decreased, and reached negative values in higher discharges ($0.8 \, m^3s^{-1}$ and $1 \, m^3s^{-1}$). The highest negative WUA change was observed for macroinvertebrates at the C3/1 restoration scheme (~23%). Except for macroinvertebrates, the WUA change in near-dry conditions ($Q = 0.02 \, m^3s^{-1}$) was positive for all biotic elements with
higher changes being observed for low- and moderate-density restoration schemes (S1, S2, C1, C2). The WUA in Q = 0.6 m$^3$s$^{-1}$ was either low (< 10%) for macroinvertebrates, minnowroaches, juvenile and adult chubs) or negative (for minnows). WUA changes for Q = 0.8 m$^3$s$^{-1}$ and 1 m$^3$s$^{-1}$ for all restoration schemes examined were negative, with the highest negative values being observed for macroinvertebrates. WUA differences among structures were not significant; the average difference was approx. 5-10%, reaching a maximum of 15% for macroinvertebrates, between the S1/0.02 and S2/0.02 schemes.

More specifically, the placement of in-stream structures had a positive effect on the WUA of adult chubs at low flows (Q = 0.02 m$^3$s$^{-1}$ and Q = 0.6 m$^3$s$^{-1}$), ranging from +4% (C3/0.06 scheme) to +16% (C2/0.02 scheme), and a negative effect at higher flows (Q = 0.8 m$^3$s$^{-1}$ and Q = 1 m$^3$s$^{-1}$), ranging from −4% (C2/0.8 scheme) to −13% (C3/1 scheme). The same trend was observed for minnowroaches; the positive, low flow effect ranged from +4% (S1/0.6) to +26% (S2/0.02), and the negative, high flow effect ranged from −2% (C3/0.8) to −9% (C1/0.8). The WUA of juvenile chubs was positively influenced in near-dry conditions, ranging from +14% (S3/0.02) to +28.6% (S1/0.02) and negatively influenced in higher discharges, ranging from −0.6% (S1/1) to −9% (C3/1). Minnows also showed a similar response; the positive, low-flow effect ranged from +8% (S2/0.02) to +16% (C2/0.02), and the negative, high flow effect ranged from −4% (C2/0.6) to −15% (C2/0.8). The WUA of macroinvertebrates was positively influenced only in Q = 0.6 m$^3$s$^{-1}$, ranging from +3.7% (S3/0.6) to +7% (C1/0.6) and negatively influenced in near-dry and higher flows, ranging from −4% (C1/0.8) to −23% (C3/1).

3.3. Habitat use of fish and macroinvertebrates around in-stream structures
Fish and benthic macroinvertebrates had varying responses to the placement of in-stream structures, depending on the particular hydraulic effect that was developed. More specifically, the same structure, in the same location, caused different hydraulic effects in every water discharge tested. Complex pool patterns were developed around complex structures, compared to simple structures, but the overall difference in the local habitat suitability for all biotic elements was low.

3.3.1. Fish response to in-stream structure placement
Fish responses around in-stream structures were typical of their life strategy strategies. In near-dry conditions (Q = 0.02 m$^3$s$^{-1}$), fish behavior was mostly influenced by water depth. Adult chubs, minnowroaches and minnows preferred deeper, slow-flowing habitats (water pools) that were often developed or widened upstream or downstream of the structure, and avoided shallow, faster flowing habitats (Fig. 5; Fig. A1). In contrast, juvenile chubs avoided lentic conditions, developed downstream of the structures; the habitat suitability of juvenile chubs was higher in shallower, and -often- faster-flowing habitats (Fig. 5, Fig. A1). As water discharge increased, the influence of flow velocity on fish response increased. Minnowroaches and minnows avoided habitats of high flow velocity when water overtopped the in-stream structures (Fig. 6, Fig. A2) and preferred low flow habitats. The habitat suitability of juvenile chubs was further reduced in deep-water pools, and increased in shallower, fast flowing habitats. In contrast, adult chubs preferred the deeper and faster flowing conditions that were developed in higher discharges.

3.3.2. Response of macroinvertebrates to in-stream structure placement
Overall, the habitat suitability of benthic macroinvertebrates around in-stream structures was low, both at near-dry and higher flow conditions, ranging from 0.1 to 0.6. Macroinvertebrates avoided the generic pool-forming, pool-deepening (Fig. 5; Fig. A1) and flow-reducing hydraulic effects (Fig. 6; Fig. A2) that were caused by the structures. Macroinvertebrate habitat suitability increased only in the rarely occurring cases when the presence of a structure reduced the water depth of an already established pool, causing water to flow downstream, or reduced both the water depth and the flow velocity in otherwise fast-flowing, deep habitats.
Fig. 4. Weighted usable area differences (WUAd) and percent WUA change between the base models (WUAb) in the six habitat restoration schemes (WUAr) at the four discharge scenarios simulated. WUAd = WUAb - WUAr for each biotic element at each discharge.
Fig. 5. Habitat use of fish and macroinvertebrates around in-stream structures at near-dry conditions (0.02 m$^3$s$^{-1}$). The image shows the habitat suitability for the various biotic elements in the S2/0.02 habitat restoration scheme (moderate single structures). Structure effect: deepening of already established water pools.
Fig. 6. Habitat use of fish and macroinvertebrates (BMIs) around in-stream structures at high flow conditions (1 m$^3$s$^{-1}$). The image shows the habitat suitability for the various biotic elements in the S2/1 habitat restoration scheme (moderate single structures). Structure effect: flowing water overtops the right structure; water is deflected in the left structure, thus changing the flow velocity field compared to the base (no structure) model.
4. Discussion

4.1. River restoration based on trial and error is prone to failure ...

The results of the study agree with previous research on river restoration; the simulated ecological response to the placement of in-stream structures varied by species and life stages, in agreement with Friberg et al. (2016). It strongly depended on the reach-scale flow conditions, as previously reported by Brown et al. (2011) and Heino et al. (2015). It was often negative (at Q = 0.6 m\(^3\)s\(^{-1}\), 0.8 m\(^3\)s\(^{-1}\) and 1 m\(^3\)s\(^{-1}\)) (Stewart et al., 2009), and when positive (mostly at near-dry flows), it was not large enough (average 10%; maximum 28.6%) to justify the high costs of river restoration (Szálkiewicz et al., 2018). We further found that flow variation may be a major driver/filter of the response of biota to habitat restoration, and thus of restoration effectiveness. The reach-scale flow variation did not only reduce the magnitude of positive ecological effects from locally placed in-stream structures; the same restoration scheme triggered contrasting ecological responses in different water discharges that typically ranged from approx. 15% - positive- habitat enhancement (adult chub, S2 scheme, near-dry flows) to 8% -negative- habitat degradation (adult chub, S2 scheme, environmental flows). The results ultimately suggest that river restoration based on trial and error will likely fail. The probability of reaching levels of effectiveness that will justify the costs of ecological restoration within a trial-and-error based process is very low, considering the numerous combinations of types, sizes, diameters, angles and patterns of in-stream structure placement. All restoration schemes applied in this study caused various ecological responses, both positive and negative, depending on the biotic element and on the reach-scale flow conditions, partially justifying the long debate among researchers on the ecological effectiveness of river restoration (Roni et al., 2005; Thompson et al., 2005; Stewart et al., 2009); the odds of success are not in favor of traditional, trial-and-error based river restoration projects.

4.2. ... Unless pre-optimized within a mechanistic ecological framework

Mechanistic frameworks quantify expectations and connect management actions to measurable objectives-endpoints (Bandrowski et al., 2015). In mechanistic ecological frameworks, the endpoints are often measurable proxies of the response of biota to hydrogeomorphic drivers (Cabral et al., 2017). In this study, we applied-demonstrated a mechanistic, model-based, ecological framework that considered the various habitat restoration schemes as management actions and used the (micro) habitat suitability as a measurable proxy for ecological effectiveness. In agreement with previous model-based studies (Lange et al., 2015) we showed that within this and similar frameworks that actually convert the traditional, field-based, trial-and-error restoration process, to a computer-simulated trial-and-error process, the ecological effectiveness of multiple river restoration schemes can be cost-effectively evaluated. The optimal restoration scheme simulated can be afterwards implemented, thus increasing the probability of success of river restoration. Within this concept, however, the results further suggest that model-based pre-optimization of river restoration may require considerable time and effort to evaluate the multitude of possible restoration schemes.

4.3. Ecological response varied by species and life stages

When the reach-scale hydrodynamics facilitated the pool-forming, pool-deepening/widening and flow-reducing hydraulic effect around the in-stream structures, the response of fish was typical of their life stage. This effect was highest at near-dry flows and thus, all fish groups had a positive ecological response at Q = 0.02 m\(^3\)s\(^{-1}\) that reached up to 28.6%. This is in agreement with previous in-situ results from the same river (Kalogianni et al., 2020) that highlighted the importance of in-stream wood structures for fish at periods of water stress, in which the water pools developed around them act as drought refugia facilitating fish survival. Adult chubs, minnowroaches and minnows had similar preferences for deeper, slow-flowing habitats, but we found contrasting responses between juvenile and adult chubs; the habitat suitability of juvenile chubs was -on average- lower around the in-stream structures and
higher between structures. This difference in habitat preference conforms to a previously evidenced ontogenetic shift in the use of pool habitats, attributed to dietary partitioning that ultimately results in reduced intra-species competition (Kalogianni et al., 2020), as also suggested for other chub species (Quist and Guy, 2001). Overall, the placement of in-stream structures at near-dry flows favored all fish groups that may had had varying habitat preferences, but, compared to the base model, they found optimized habitats either around -adult chubs, minnowroaches and minnows- or between the structures -juvenile chubs-. At near-environmental flows, however, the already optimized hydraulic conditions were negatively fine-tuned by the in-stream structures (possibly due to increased overtopping), which either caused extremely deepened water pools or extremely increased flow velocities. Thomas et al. (2013) have previously shown that local physical habitat diversity may increase by the placement of in-stream structures. However, if not properly designed and maintained, it may cause stream habitat fragmentation that ultimately leads to decreased population abundance/density and diversity and thus, decreased ecological response. The same negative response was also observed for macroinvertebrates, which further supports this hypothesis of negative fine-tuning (deoptimizing). In contrast to fish, however, but typical of lotic-adapted benthic communities, restoration was optimal for macroinvertebrates only at Q = 0.6 m^3 s^{-1}. Unlike lentic, lowland river reaches, in which marginal, silt-dominated water pools may host rich-diverse macroinvertebrate communities (Principe and Corigliano, 2006), in lotic mid-reaches, increased macroinvertebrate abundance, richness and diversity have been recorded in riffles (areas with shallow water depths and moderate flow velocities) compared to pools (characterized by high water depths and low flow velocities) (Brown and Brussock, 1991; Nelson and Liebermann, 2002; Wang et al., 2012). Thus, the optimal combination of shallow, moderately flowing habitats was obviously found for macroinvertebrates at intermediate flows, in contrast to the almost stagnant waters of the near-dry flows and the negatively fine-tuned waters of near-environmental flows.

4.4. Ecological response strongly depended on reach-scale flow conditions

Our results also indicate that the effectiveness of ecological restoration strongly depends on higher-level (reach-scale) drivers, acting as filters that critically regulate the local response of biota to the placement of in-stream structures. Overall, we found that within suboptimal conditions of high-level drivers/filters (the reach-scale water discharge), the influence of lower-level filters on the distribution of aquatic biota may increase. In contrast, optimal conditions of high-level filters may reduce the positive response of biota to local, in-stream habitat restoration, and can further trigger negative responses. In near-dry flows (suboptimal high-level filter), the percent habitat suitability change of all biotic elements (except for benthic macroinvertebrates) for all restoration schemes was positive, reaching up to +28.6% (juvenile chub, S1 scheme). When, however, environmental flow was provided (optimal high-level filter), the relevant habitat suitability change was negative, ranging from −0.006% (adult chub, S1 scheme) to −23% (macroinvertebrates, C3 scheme). Previous studies have also shown that the distribution of aquatic biota is critically driven by high-level filters, with local habitat conditions exerting a lower-level, fine-tuning effect (Karaouzas et al., 2019). In our case, the reach-scale water discharge was the high-level filter that the locally placed in-stream structures attempted to fine-tune. As it was shown, man-made fine tuning (ecological restoration with the use of in-stream structures) may not only reduce the positive response of aquatic biota (Stoll et al., 2016); there is a high probability that negative responses will be triggered.

4.5. Ecological response did not justify the costs of river restoration - climate change implications

Overall, we observed a negative response of biota to the placement of in-stream structures. The positive ecological response was approx. 10%, while the maximum positive ecological response was 28.6%, observed for juvenile chub only at near-dry flows. Thus, our results support the conclusions of Stewart et al. (2009) -also discussed in Palmer et al. (2010)- that ‘widespread use of in-stream structures for river restoration is not supported’. Considering though,
that, at near-dry flows, the response of all biotic elements (except for macroinvertebrates) was positive, in combination with the low habitat-suitability differences among structure types and densities, we suggest that sparse/moderate in-stream structures can be used for cost-effective habitat restoration, but restoration would only be effective - thus justifying the high costs required - when linked to very specific purposes: (a) to enhance the resistance/resilience of endangered species and (b) to increase/improve habitat availability/suitability during dry periods, thus proactively preventing/reducing the current and future ecological impacts of climate change on - often endangered - local biota (Palmer et al., 2009). This can be implemented either in perennial rivers affected by climate-change or human-induced flow reduction/stabilization, or, more widely, in intermittent rivers, which account for more than 50% of the global river length, they dominate arid, semi-arid and Mediterranean climates and are expected to increase due to climate change (Datry et al., 2014). We found that, for this specific case, the placement of in-stream structures had an overall positive effect; small (4% - 28.6%) but probably significant enough to ensure the survival of the local biota in deepened or newly-formed water pools around the in-stream structures until flow resumption. In the presence of endangered species, although the overall effect of habitat restoration on the fish/macroinvertebrate communities may be only slightly positive (approx. 10%) or even slightly negative (10% - 20%), river restoration and its high implementation costs would be justified, if it ultimately benefits these endangered species and prevents their extinction, again within a species-specific mechanistic pre-optimization.

5. Conclusions
Our study showed that success in river restoration with the use of in-stream structures critically depends on high-level drivers; in our case, the reach-scale water discharge. The placement of in-stream structures has only a local, fine-tuning effect. The response of biota to the placement of in-stream structures varied by species and life stages, it was positive at near-dry flows and negative at near-environmental flows; this leads us to species-specific restoration but the placement of in-stream structures cannot be species-specific. There is a multitude of types, sizes, diameters and patterns of potential in-stream structure placement that minimize any chance of success for the traditional trial-and-error based restoration projects. Even our model-based study practically failed to find an optimal one-size-fits-all restoration scheme (for all discharges and biotic elements). All the above suggest that (i) the widespread use of in-stream structures for river restoration should be avoided; (ii) successful river restoration requires extensive pre-optimization within a mechanistic ecological framework prior to field implementation; (iii) restoration can be effective and its high costs would be justified when benefiting endangered species and increasing/improving habitat availability/suitability during dry periods, thus proactively preventing/reducing the current and future ecological impacts of climate change.

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References


Appendix

Fig. A1. Habitat use (suitability) of fish and macroinvertebrates at near-dry flow conditions (0.02 m$^3$s$^{-1}$) without in-stream structures (compared to Fig. 5).
Fig. A2. Habitat use (suitability) of fish and macroinvertebrates at environmental flow conditions (1 m$^3$s$^{-1}$) without in-stream structures (compared to Fig. 6).