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RESEARCH ARTICLE

Habitat quality and biological community responses to innovative hydropower plant installations at transverse in-stream structures

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Abstract

1. Ecological assessments of the effects of hydropower plants (HPPs) are often limited to aspects of entrainment, mortality, injuries, and passage of fish, whereas the effects on riverine habitats and biological communities in proximity to these structures are hardly documented.
2. In this study, aquatic communities comprising fish, macroinvertebrates, macrophytes and periphyton as well as physical and hydromorphological parameters were investigated in upstream and downstream river sections at five transverse structures at different seasons before and after the installation of an innovative HPP.
3. At all study sites, significant differences in the aquatic community composition between the assessed upstream and downstream sections were found after HPP construction, indicating distinct serial discontinuity.
4. Raising the damming target at the sites Großweil and Au deteriorated the habitat conditions in the upstream area close to the weir and presumably influenced in particular the macroinvertebrate community, where a significant decrease in the density of rheophilic mayfly, stonefly and caddisfly larvae was observed after HPP construction.
5. *Synthesis and applications*: The installation of different types of innovative HPPs has not improved the habitat conditions for rheophilic species, contrary to the promises raised by the developers of these concepts. Conversely, retrofitting existing weirs accompanied by further damming even significantly increased the effects of serial discontinuity and deteriorated the habitat conditions for rheophilic species in upstream sections. As evident from the findings of this study, habitat and biological community effects resulting from serial discontinuity should become better integrated into ecological assessments of HPP developments.

KEYWORDS
aquatic biodiversity, damming, fish, macroinvertebrates, periphyton, river continuum, serial discontinuity, sustainable hydropower

1 | INTRODUCTION

Unrestricted serial continuity allowing river dynamic processes, matter fluxes and longitudinal connectivity is essential for healthy river systems (Vannote et al., 1980), yet is often interrupted by man-made transverse structures such as weirs, dams or hydropower plants (HPPs; Belletti et al., 2020; Malmqvist & Rundle, 2002). Transverse in-stream structures lead to river fragmentation, flow regulation and aquatic habitat degradation, which are major causes of biodiversity decline in stream ecosystems (Dudgeon et al., 2006; Dynesius & Nilsson, 1994). To mitigate these negative ecological impacts on stream ecosystems and restore free-flowing river stretches, governmental and non-governmental organisations have made efforts to remove unused transverse structures, particularly in the USA and Europe (O'Connor et al., 2015; Schiermeir, 2018). In contrast, increasing energy demand and energy decarbonisation are leading to a worldwide advancing expansion of hydropower (Sachs et al., 2019; Zarfl et al., 2015), which is accompanied by the construction of new instream barriers or the conversion of existing ones.

There are currently policy-driven efforts to build new HPPs at transverse structures that were primarily intended to prevent riverbed deepening or to contribute to flood protection and have not yet been used for energy generation. Proponents of hydropower argue that the construction of new HPPs at existing barriers not only increases the share of renewable energies, but that the simultaneous construction of fish bypasses for upstream (U) and downstream (D) migration at these sites also improves longitudinal connectivity and could thus help fulfil the Water Framework Directive's goals regarding river continuity restoration (European Parliament, 2000). Furthermore, developers of so-called 'innovative' hydropower technologies (e.g. very low-head [VLH], Archimedes screw or shaft HPPs) claim that the installation of these facilities will also improve matter fluxes such as deadwood or sediment transport and thus habitat conditions in the immediate U and D sections of the existing transverse structures compared to the former state (cf. Figure 1). Opponents argue that installing HPPs in existing weirs degrades important habitats, especially for current-preferring gravel-spawning fish, as further damming is required and the main discharge flows through the turbine, resulting in little or no overflow of the weir, and that fish are killed during turbine passage (Geist, 2021).

Ecological assessments of the effects of innovative HPPs are often limited to aspects of entrainment, mortality, injuries and passage of fish, whereas the effects on habitats and biological communities in proximity to these structures are hardly documented (Birnie-Gauvin et al., 2017) yet urgently needed (Herbert & Gelwick, 2003; Taylor et al., 2001). Meanwhile, it is well-known that fish can also be injured or killed during turbine passage at innovative HPPs, which are often termed 'fish-friendly' (e.g. Knott et al., 2023a; Mueller et al., 2022; Pauwels et al., 2020). However, it remains largely unknown whether the installation of these innovative technologies into existing transverse structures also leads to measurable changes in abiotic habitat characteristics and the aquatic community composition (ACC) in the immediate U and D river sections.

The main objective of this study was to determine whether habitat characteristics and ACC at existing transverse structures change after the installation of different types of HPPs. For this purpose, we investigated the adjacent U and D river sections at five transverse structures both before and after the installation of an innovative HPP at different seasons using a systematic sampling design developed to assess serial discontinuity by dams and weirs in river systems (Mueller et al., 2011). Physical and hydromorphological parameters determining aquatic habitat quality, and the ACC comprising fish, macroinvertebrates, macrophytes and periphyton were investigated.

Specifically, we hypothesised that (i) due to the interruption of the river continuum by different types of transverse structures, both abiotic parameters and ACC differ significantly between U and D sections at existing weirs, that (ii) the installation of the HPPs does not change the effects of serial discontinuity and that (iii) the HPP construction, contrary to the assumptions of the developers, does not lead to an improvement of habitat conditions for riverine species.

2 | MATERIALS AND METHODS

Permissions for field work such as motor boat usage were given by the rural district offices Oberallgäu (permit number 31-641/12-05/14-Gro), Roth (44-myr 6415 TUM.Roth), Schwandorf (610-646.406), München (6.2-7732/Le, 4.4.2-7732/Le) and Garmisch-Partenkirchen (32-6416/1, 32-8502.2). Permission for electrofishing was provided by the rural district office Freising (31-1351-7562) and the fisheries rights owners. This study did not require ethical approval.

2.1 | Study sites

The study was carried out at five different rivers in Bavaria, Germany (Figure 2, Table 1). At each site, different types of transverse structures without hydropower use were present before the investigations started. From 2014 to 2020, so-called innovative HPPs were built at these transverse structures. At the study sites Au and Großweil, the existing weirs were replaced by new weirs during the construction of the HPPs, whereas at the study sites Heckerwehr, Eixendorf and Baierbrunn, no changes were made to the existing weirs and the top water level (Table 1). More details on the study sites can be found in Knott et al. (2019, 2020, 2021, 2023a, 2023b).

2.2 | Experimental design

To investigate the disruption of the river continuum by the existing weirs and potential changes due to the installation of the HPPs or the reconstruction of the weirs, the sections in the immediate U and

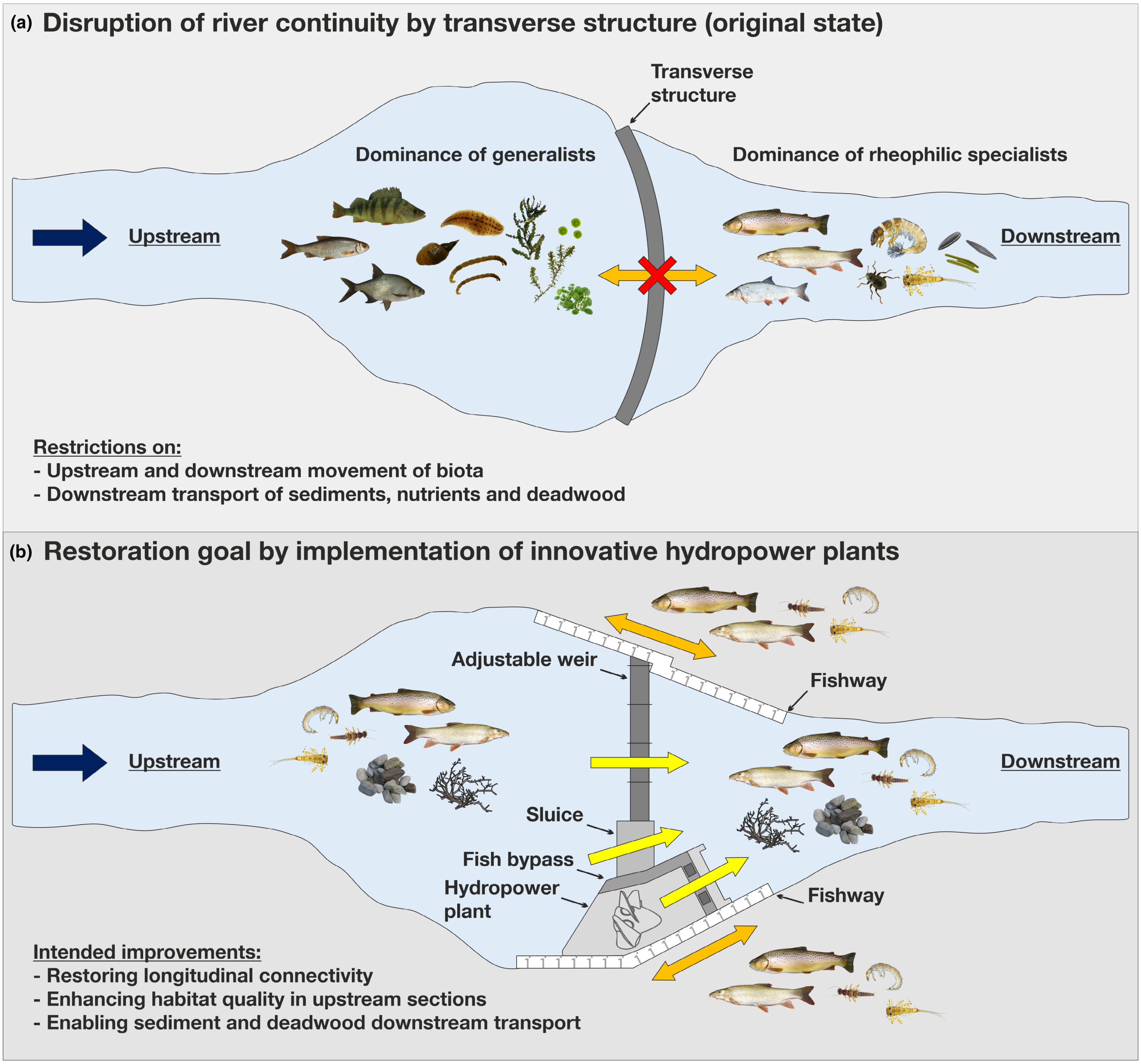

FIGURE 1 Schematic of the effects of the river continuum interruption by transverse structures on the aquatic community in adjacent upstream and downstream river sections (a) as well as intended restoration goal by reconstructing transverse structures and implementing innovative hydropower plants (b). Dark blue arrows indicate the flow direction. Orange and yellow arrows indicate upstream and downstream pathways.

D stretches of the transverse structures were investigated by a systematic sampling design following Mueller et al. (2011). This included 15–20 sampling transects with 30 m length each in U and D, depending on the river size (Table 1, Figure 2).

The taxonomic groups of fish, macroinvertebrates, macrophytes and periphyton were investigated as biotic parameters, as these groups represent the most important trophic levels in rivers and show different reactions to weir-induced habitat changes (Anderson et al., 2015; Mbaka & Wanjiru Mwaniki, 2015; Mueller & Geist, 2016). Physical and hydromorphological parameters were assessed to characterise habitat quality and to establish links to ACC. For example, increased fine sediment deposition, caused by a current velocity reduction due to damming, can clog the gravel gap system of the riverbed, impairing the exchange between open and interstitial water (Geist & Auerswald, 2007). This can lead to the degradation or loss of key habitats (e.g. for spawning, egg, larval, and juvenile development) of the aquatic community (Duerregger et al., 2018; Sternecker et al., 2014). The investigations were carried out seasonally in spring/early summer and late summer/autumn before and after the HPP construction (except at the site Au, where only one pre-sampling before HPP construction and one post-sampling were possible; Table 1).

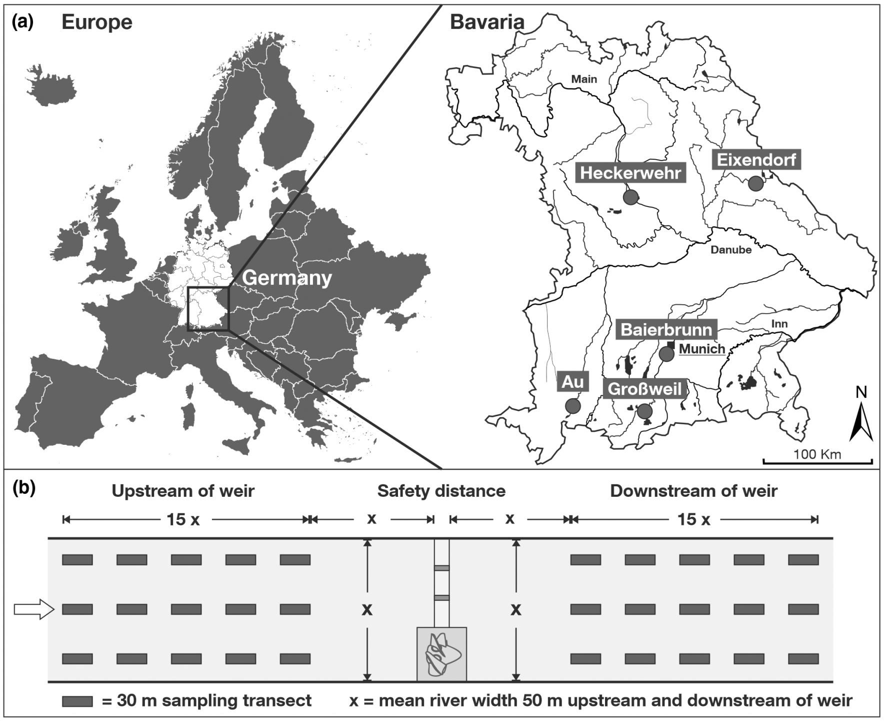

FIGURE 2 Location of the study sites in Bavaria, Germany (a) and schematic study design to assess biotic and abiotic parameters upstream and downstream of the transverse structures adapted from Mueller et al. (2011) (b). The arrow in (b) indicates the flow direction.

2.2.1 | Physical and hydromorphological parameters

In each transect, the physical properties of the open water and the interstitial zone were measured. Dissolved oxygen (mg/L), water temperature (°C), electric conductivity (µS/cm; based on 25°C), pH-value, and redox potential (mV) were measured using hand-held multimeter probes (Multi 3430, pH 3110; WTW, Weilheim, Germany). Interstitial water was taken from 10 cm substratum depth using a perforated metal tip with attached silicone tubing and a 100 mL plastic syringe (cf. Pander et al., 2015). In each transect, the current velocity (m/s) 10 cm above river bottom and 10 cm below the water surface as well as the water depth (cm) were measured (MFpro, OTT Hydromet, Kempten, Germany). To determine the grain size distribution of the riverbed, substratum samples were taken from the top layer using a box sampler or a sediment corer. In the laboratory, substratum samples were fractionated by wet sieving (mesh sizes 0.85, 2.0, 6.3 and 20 mm; Retsch GmbH, Haan, Germany). After drying, the samples were weighed, and the percentage of each fraction was calculated.

2.2.2 | Fish sampling

Each 30 m transect was sampled from a boat or wading in shallow water using a mobile electrofishing device (11 kW, EFKO GmbH, Leutkirch, Germany) according to DIN EN 14011 (2003). Captured fish were measured (total length ± 0.5 cm) and determined to species level. After examination, all fish were carefully released. At the Eixendorf reservoir, additionally three multi-mesh gill nets (DIN EN 14757, 2005; 30 m long with mesh sizes from 5 mm to 55 mm) each were placed in U and D sections, as these are very effective in surveying fish populations in stagnant, deeper waters (Jurvelius et al., 2011) and supplement the fish species inventory recorded by electrofishing.

2.2.3 | Macroinvertebrates sampling

Macroinvertebrates were collected in each transect applying Surber-sampling (Surber, 1930). The cube-shaped sampling device was positioned five times per transect (total area: 0.48 m^2) against the current, and the substratum was dug up to a depth of 10 cm for 2 min using a garden fork. Loosened macroinvertebrates drifted into a collecting container via a net (mesh size 500 µm) and were preserved with 50% ethanol. All samples were determined to the finest taxonomic resolution possible in the laboratory using binoculars and microscopes (cf. Mueller et al., 2011).

2.2.4 | Macrophytes sampling

In each 30 m transect, all occurring macrophytes were determined to species level, and the percent cover of each taxon was estimated. Since macrophytes were only sporadically detected at the sites Au, Heckerwehr, Baierbrunn and Großweil, macrophytes were solely included in the statistical analyses for the site Eixendorf.

2.2.5 | Periphyton sampling

In each transect, five replicate periphyton samples were scrapped off stones or deadwood using a knife and a flexible template (total

TABLE 1 Study site characteristics and study period of the five assessed hydropower sites.

	Au	Heckerwehr	Eixendorf	Baierbrunn	Großweil
River characteristics					
River name	Iller	Roth	Schwarzach	Isar	Loisach
Drainage system	Danube	Rhine	Danube	Danube	Danube
Riverbed slope (‰)	1.8	4.7	2.3	1.9	3.2
Mean river width [m]	73	16	107	60	33
Mean annual DC [m^3/s]	46.6	3.2	4.3	63.8	22.8
HPP characteristics					
Year of HPP construction	2014/15	2015/16	2016/17	2016/17	2019/2020
HPP/turbine type	VLH turbine	Archimedes screw turbine	Movable hydropower plant	VLH turbine	Shaft hydropower plant
Number of turbines	2	1	1	1	2
Max. turbine DC [m^3/s]	27.0	5.0	4.5	14.5	11.0
Nominal installed capacity per turbine [kW]	450	80	190	450	210
Max. head drop [m]	2.3	2.3	5.0	4.0	2.5
Weir type before HPP construction	Broad-crested weir (no sluice gate)	Sluice gate	Broad-crested weir with bottom sluice	Sluice gate	Rock ramp
Weir type after HPP construction	Inflatable weir with gravel sluice	Sluice gate	Broad-crested weir with bottom sluice	Sluice gate	Tilting weir
Changes in top water level after HPP construction [m]	+ 0.8 (at mean annual DC)	No changes	No changes	No changes	+ 0.4 (at mean annual DC)
Estimated length impounded upstream river section [m]	Before: 1400 After: 1850	700	2600	2650	Before: 950 After: 1100
Study period					
Pre-construction assessment	September/October 2014	July/August 2014 March/April 2015	May 2015 August 2015	April 2015 August 2015	October 2014 July 2015
Post-construction assessment	August/September 2016	April 2016 July 2016	May 2017 August 2017	April 2018 August 2018	October 2020 June 2021

Note: Note that at Heckerwehr, in contrast to the post-construction assessment, the spring sampling before HPP construction (March/April 2015) took place after the summer sampling (July/August 2014), but still the same seasons are compared (spring 2015 vs. spring 2016, summer 2014 vs. summer 2016).

Abbreviations: DC, discharge; HPP, hydropower plant; Max., maximum; VLH, very low-head.

TABLE 2 Global *R* values from the analysis of similarities (ANOSIM) pairwise comparisons of the recorded physical and hydromorphological parameters (= Abiotics; cf. chapter 2.2.1, Table S1 in Supporting Information) and the aquatic community composition comprising fish, macroinvertebrates, macrophytes and periphyton (= Biota) for the investigated upstream and downstream sections at the five study sites before and after hydropower plant (HPP) construction.

ANOSIM		Before HPP construction	After HPP construction
Pairwise tests		Upstream–downstream	Upstream–downstream
Au	Abiotics	0.01	0.01
	Biota	0.07*	0.07*
Heckerwehr	Abiotics	0.56***	0.21***
	Biota	0.27***	0.15***
Eixendorf	Abiotics	0.18***	0.03*
	Biota	0.21***	0.26***
Baierbrunn	Abiotics	0.21***	0.17***
	Biota	0.14***	0.16***
Großweil	Abiotics	<0.01	0.09**
	Biota	<0.01	0.11***

Note: Asterisks indicate significant differences in the pairwise comparisons: *$p < 0.05$; **$p < 0.01$; ***$p < 0.001$.

area 20 cm^2) and preserved with 20 mL of acidified Lugol's iodine solution according to Mueller et al. (2011). In the laboratory, algae were settled for at least 24 h according to the sedimentation method of Utermöhl (1931). Cell numbers in 25 squares of 100 µm^2 were counted, and all algae were determined to the finest taxonomic resolution possible using an inverted microscope at 400× magnification (DIN EN 15204, 2006).

2.3 | Statistical analyses

Since the exchange between open and interstitial water is an important variable for biological communities (Geist & Auerswald, 2007), the difference between values from open water samples and interstitial water (Δ) was calculated for each sampling transect for the abiotic parameters dissolved oxygen, water temperature, electric conductivity, pH-value and redox potential. Differences in single abiotic parameters between U and D before and after HPP construction were analysed using non-parametric Kruskal-Wallis test and Bonferroni-corrected post-hoc pairwise Mann–Whitney *U* test for non-normally distributed data or one-way analysis of variance (ANOVA) and post-hoc Tukey HSD test for normally distributed data with the statistics software R (version 4.2.2; R Core Team, 2022).

A multivariate approach was applied to compare the set of recorded abiotic parameters and the ACC between U and D of the respective study sites before and after HPP construction. To level out potential effects from individual samplings, a conservative approach comparing all abiotic and biotic data before and after HPP construction combining the seasonal samplings at each site was used. For the multivariate analyses, all abiotic parameters were normalised to account for different scales (Clarke & Gorley, 2015). Since the aquatic community was also recorded at different scales (e.g. fish: total abundance, periphyton: individuals/mm^2), biotic data were normalised according to Mueller et al. (2014) to ensure that each taxonomic group is equally weighted without losing quantitative information in the subsequent analyses. Differences in abiotic parameters and the ACC between U and D before and after HPP construction were analysed using one-way analysis of similarities (ANOSIM) based on Euclidean distances for abiotic parameters and Bray-Curtis similarities for biota (Bray & Curtis, 1957).

To visualise differences between U and D before and after HPP construction, principal component analyses (PCA) were applied for abiotic parameters and metric multidimensional scaling of bootstrap averages for the aquatic community. To find the most frequent and constantly occurring species in U and D sections and the species-specific contribution to between-group dissimilarity (U vs. D), one-way similarity percentage analyses (SIMPER; Clarke et al., 2014) were carried out. All multivariate analyses were performed with the statistic software PRIMER v7 (PRIMER-e, Massey University, Auckland, NZ). For all statistical analyses, significance levels were set to $p \leq 0.05$.

3 | RESULTS

3.1 | Physical and hydromorphological parameters

According to the multivariate ANOSIM, the measured abiotic parameters at Heckerwehr, Eixendorf and Baierbrunn differed significantly between U and D sections both before and after HPP construction (Table 2). At Au, no statistically significant differences were found between U and D sections across all measured abiotic parameters, both before and after HPP construction. Similarly, no statistically significant differences between U and D sections were detected in Großweil before HPP construction. However, after HPP construction at this site, significant differences were evident between U and D sections across all measured abiotic parameters (Table 2).

The results of the PCA for the study site Au showed that there was a gradient between the samplings before and after HPP construction, particularly for electric conductivity, the difference between values from open water samples and interstitial water (Δ) for dissolved oxygen and the grain size fraction 6.3–20 mm (Figure 3). Dissolved oxygen Δ was significantly lower after HPP construction in 2016 than before HPP construction in 2014 both in U and D sections (post-hoc Mann–Whitney *U* test: U2014 vs. U2016: $p < 0.001$, D2014 vs. D2016: $p < 0.05$), indicating an improvement in interstitial habitat quality. The proportion of gravel >6.3 mm has converged between U and D after HPP construction (Table S1 in Supporting Information).

At Heckerwehr, there was a clear gradient between U and D, especially regarding grain size distribution and current velocity (Figure 3), which did not change significantly after HPP construction. The geometric mean particle diameter and the current velocity were significantly larger in D than in U sections both before and after HPP construction (Tables S1 and S2).

The reservoir character of the investigated U and D stretches at Eixendorf was also reflected in the recorded abiotic parameters. The dominant riverbed substratum in U and D sections was fine sediment <0.85 mm with a lower proportion of fine sediment in D compared to U (Table S1). Lower levels of fine sediment <0.85 mm were found in U and D sections after HPP construction in 2017 than before construction in 2015, although this difference was not statistically significant (post-hoc Mann–Whitney *U* test: U2015 vs. U2017: $p = 0.16$, D2015 vs. D2017: $p = 0.23$). Current velocities at the water surface (a.m.: 0.02–0.05 m/s) and at the river bottom (0.01–0.04 m/s) were generally low. Dissolved oxygen Δ (9.3–10.7 mg/L) was higher compared to the other study sites and did not differ significantly between U and D both before and after HPP construction (Tables S1 and S2).

At Baierbrunn, the investigated U and D transects differed mainly in terms of water depth, current velocity, dissolved oxygen Δ, electric conductivity and substratum composition (Figure 3, Tables S1, and S2). Water depth and dissolved oxygen Δ were significantly greater in U than in D sections both before and after HPP construction, whereas the current velocity was significantly lower in U than in D before and after HPP construction, indicating the effects of damming and reduced exchange between open and interstitial water (Tables S1 and S2).

No differences in water depths and current velocities between U and D were found at Großweil before HPP construction. After HPP construction in 2020/21, the water depth in U increased by an average of 47% compared to the values before HPP construction in 2014/2015 (post-hoc Mann–Whitney *U* test: U2014/15 vs. U2020/21: $p < 0.01$) and the current velocity decreased by an average of 41% at the surface ($p < 0.001$) and 48% above the river bottom ($p < 0.001$; Table S1). In contrast to U sections, no statistically significant changes in water depth and current velocities were found in D sections after HPP construction. Dissolved oxygen Δ was also nearly the same in U and D sections before the HPP was built. After HPP construction, there was a statistically significant increase in dissolved oxygen Δ in U (post-hoc Mann–Whitney *U* test: U2014/15 vs. U2020/21: $p < 0.01$), whereas no significant changes were found in D ($p = 1.0$; Table S1).

3.2 | Aquatic community composition

The assessment of the ACC at the five study sites revealed a total of 632 taxa attributed to fishes (37 taxa, 59,820 individuals), macroinvertebrates (338 taxa, 114,546 individuals), macrophytes (13 taxa) and periphyton (244 taxa) (Table 3).

At the study sites Au, Heckerwehr, Eixendorf and Baierbrunn, differences in the ACC between U and D of the existing weirs were already significant before the installation of the HPPs (Table 2, Figure 4). Only at Großweil, analogous to the measured abiotic parameters, no statistically significant difference in ACC between U and D of the formerly existing rock ramp was detectable (Table 2, Figure 4). After HPP construction, significant differences in ACC between U and D were found at all study sites (Table 2, Figure 4).

Rheophilic fish species, such as the bottom-oriented bullhead (*Cottus gobio* L.), which is protected under the European Habitats Directive (European Commission, 1992) and less mobile than other fish species due to its absent swim bladder, were either not detected in U transects close to the weir (Au) or their share in the recorded fish community was lower after HPP construction than before (Baierbrunn: 2015: 66%, 2018: 14%; Großweil: 2014/15: 41%, 2020/21: 27%). Generalist fish species such as roach were caught considerably more frequently in U than in D, especially at Heckerwehr and Eixendorf, both before and after HPP construction. The share of roach in the recorded fish community changed only marginally after HPP construction at both sites (Heckerwehr: 2014/15: 88% U, 42% D, 2016: 83% U, 45% D; Eixendorf: 2015: 12% U, 5% D, 2017: 13% U, 5% D).

A significant decrease in the density of rheophilic mayfly, stonefly and caddisfly larvae was observed in the macroinvertebrates community at Au (2014: a.m. = 135 Ind/m^2, 2016: a.m. = 36 Ind/m^2; Wilcoxon test: $W = 12$; $p < 0.05$) and Großweil (2014/15: a.m. = 241 Ind/m^2, 2020/21: a.m. = 69 Ind/m^2; Wilcoxon test: $W = 35$; $p < 0.05$) in U sections close to the weir after HPP construction. In contrast, the density of rheophilic mayfly, stonefly, and caddisfly larvae did not change significantly in U sections close to the weir at Heckerwehr, Eixendorf and Baierbrunn after HPP construction.

At Au, among the species contributing >5% to the dissimilarity between U and D according to SIMPER, the differences in normalised average abundance between U and D were smaller after HPP construction, particularly for *Thymallus thymallus* L., *Cottus gobio* L., Ephemeroptera and Cyanophyceae. For Clitellata, larger differences in normalised average abundance between U and D were found after HPP construction than before (Figure 5).

At Heckerwehr, differences in normalised average abundance between U and D for *Rutilus rutilus* L., *Neogobius melanostomus* Pallas, Bacillariophyceae and Cyanophyceae decreased after HPP construction. In contrast, larger differences in normalised average abundance between U and D were recorded for Clitellata and Diptera after HPP construction (Figure 5).

In Eixendorf, after HPP construction, the differences in normalised average abundance between U and D were smaller for *Rhodeus amarus* Bloch, *Perca fluviatilis* L. and *Elodea nuttallii* Planch.

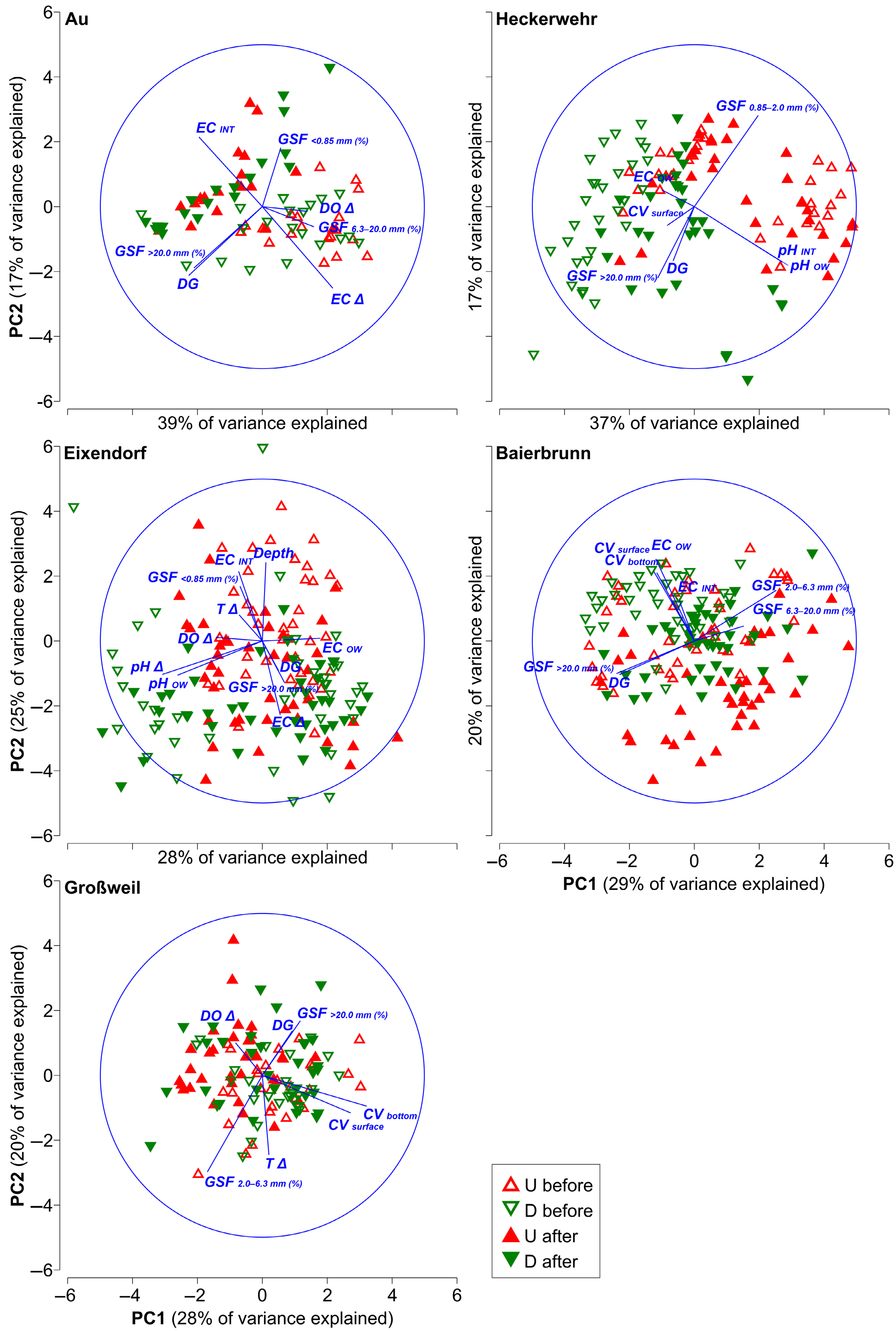
Au
Heckerwehr
Eixendorf
Baierbrunn
Großweil
PC2 (17% of variance explained)
39% of variance explained
17% of variance explained
37% of variance explained
PC2 (25% of variance explained)
28% of variance explained
20% of variance explained
PC1 (29% of variance explained)
PC2 (20% of variance explained)
PC1 (28% of variance explained)
EC INT
GSF <0.85 mm (%)
DO Δ
GSF 6.3–20.0 mm (%)
GSF >20.0 mm (%)
DG
EC Δ
GSF 0.85–2.0 mm (%)
EC OW
CV surface
pH INT
pH OW
Depth
T Δ
pH Δ
CV bottom
GSF 2.0–6.3 mm (%)
CV bottom
U before
D before
U after
D after

FIGURE 3 Principal component analysis (PCA) ordinations based on Euclidean distances of the recorded normalised abiotic parameters for upstream (U) and downstream (D) sections before and after hydropower plant construction at the five study sites. Vectors with a Pearson's correlation >0.3 are shown, representing direction and relative strength of linear increase of normalised variables in the 2-day plane (the circle represents 100% correlation). CV bottom, current velocity 10 cm above river bottom; CV surface, current velocity 10 cm below water surface; Depth, water depth; DG, geometric mean particle diameter; DO, dissolved oxygen; EC, electric conductivity; EH, redox potential; GSF, grain size fraction of the riverbed; T, water temperature; Δ, difference between values from open water samples and interstitial water.

TABLE 3 Number of fish, macroinvertebrate, macrophyte and periphyton taxa recorded at the five study sites during the samplings before and after the construction of the hydropower plants in the immediate upstream and downstream sections (maximum distance to weir = 1000 m). For fish and macroinvertebrates the total numbers of recorded individuals are shown, for macrophytes the mean percent cover per transect and for periphyton the mean density of individuals per mm^2; n, number of replicates.

		Au (*n* = 80)	Heckerwehr (*n* = 120)	Eixendorf (*n* = 160)	Baierbrunn (*n* = 160)	Großweil (*n* = 120)
Fish	Taxa	14	23	26	20	14
	Individuals	486	6875	38,325	13,356	1807
Macroinvertebrates	Taxa	92	116	149	193	138
	Individuals	8541	12,184	12,062	57,526	24,233
Macrophytes	Taxa	3	2	7	0	2
	Cover (%)	<1	<1	4	0	<1
Periphyton	Taxa	67	148	148	122	72
	Density [ind/mm^2]	253	285	648	631	1052

In the case of Clitellata, Diptera and Cyanophyceae, greater differences in normalised average abundance between U and D were found after HPP construction compared to before (Figure 5).

At Baierbrunn, only Diptera showed less difference in normalised average abundance between U and D after HPP construction. In contrast, *Alburnoides bipunctatus* Bloch, *Barbus barbus* L. and Bacillariophyceae showed greater differences in normalised average abundance between U and D after HPP construction than before (Figure 5).

At Großweil, particularly for *Thymallus thymallus* L., Diptera and Cyanophyceae, smaller differences in normalised average abundance between U and D were observed after HPP construction. For *Oncorhynchus mykiss* Walbaum, *Alburnoides bipunctatus* Bloch, *Lota lota* L., Ephemeroptera and Plecoptera, greater differences in normalised average abundance between U and D were found after HPP construction (Figure 5).

4 | DISCUSSION

The results of this study indicate that retrofitting existing transverse structures by installing innovative HPPs cannot reduce adverse effects on the river continuum and subsequently on habitat quality and ACC in adjacent U and D sections of the assessed rivers. This finding contradicts the expectations raised by the developers and stakeholders who implemented these new HPP concepts. In our study, the installation of different types of innovative HPPs, fish bypasses, and weir modifications has not improved the habitat conditions in adjacent river sections, particularly for rheophilic species that are high on the conservation agenda in freshwater ecosystems. Conversely, in addition to the recently well-documented injury and mortality risk for fish during turbine passage (cf. Mueller et al., 2022), the modifications also led to considerable deterioration of habitat conditions for the aquatic community.

Strong differences in the ACC between U and D of the existing transverse structures already existed before HPP construction. This is due to the fact that damming and associated effects on habitat quality (reduced current velocity, increased sedimentation, interruption of sediment transport, increased water depths in U sections; cf. Mueller et al., 2011; Ward & Stanford, 1983) as well as bank and riverbed reinforcements have already been effective since the installation of the transverse structures.

The installation of innovative HPPs led to only minor further changes in habitat quality at most sites in relation to the major changes that had already been caused by the installation of the transverse structures leading to river fragmentation, flow regulation and aquatic habitat degradation (Dudgeon et al., 2006; Taylor et al., 2001). One exception was the Großweil site: At this site, the construction of a tilting weir and the higher damming target by about 40 cm caused a deterioration of habitat conditions in U sections compared to the situation before HPP construction. This also led to significant differences in the ACC between U and D sections after HPP construction and was particularly evident in the macroinvertebrate community. After HPP construction, a significant decrease in the density of rheophilic mayfly, stonefly and caddisfly larvae, which react sensitively to environmental changes (Feld & Hering, 2007; Greenwood et al., 2012), was observed in U sections close to the weir.

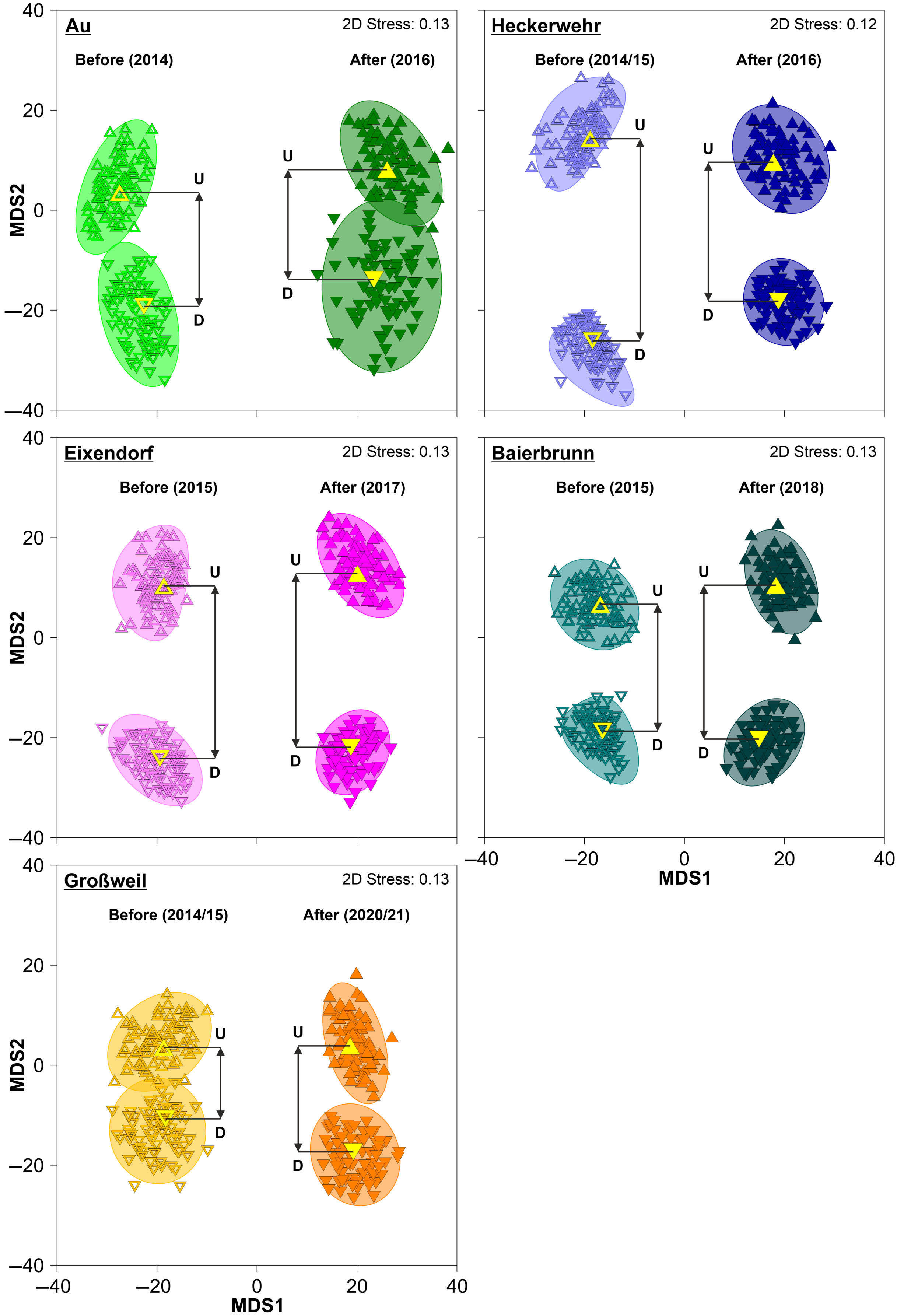
Au
2D Stress: 0.13
Before (2014)
After (2016)
Heckerwehr
2D Stress: 0.12
Before (2014/15)
After (2016)
Eixendorf
2D Stress: 0.13
Before (2015)
After (2017)
Baierbrunn
2D Stress: 0.13
Before (2015)
After (2018)
Großweil
2D Stress: 0.13
Before (2014/15)
After (2020/21)
U
D
MDS1
MDS2
40
20
0
−20
−40

FIGURE 4 Metric multidimensional scaling (MDS) of bootstrap averages of the aquatic community composition comprising fish, macroinvertebrates, macrophytes (solely for Eixendorf) and periphyton at the sampled upstream (U) and downstream (D) sections at the five study sites before and after hydropower plant construction. Bootstrap averages are based on pairwise Bray-Curtis similarities between each sampled transect calculated from normalised species abundance data. Yellow symbols represent the group means, differently coloured symbols the mean values from the sample replicates. Coloured areas indicate the 95% region estimates fitted to the bootstrap averages. The distance between the groups corresponds to the similarity of the community composition (small distance = high similarity).

At Au, the typical differences of increased water depth and reduced current velocity in U compared to D of the weir were not found, neither before nor after HPP construction. This is most likely due to the fact that in D the backwater area of the next HPP begins after only a short distance (distance to the next downstream weir approximately 800 m). Thus, comparatively low current velocities and high water depths were also measured in the sampled D stretches that were close to the next downstream HPP (Table S1). The convergence in substratum composition between U and D sections after HPP construction indicates improved sediment transport through the inflatable weir with gravel sluice, allowing coarse bed load to be transported across the entire watercourse cross-section at increased discharge. The improvement of oxygen supply into the interstitial zone in U and D sections after HPP construction is probably a result of the enhanced sediment transport via the new weir.

At Heckerwehr, fewer differences in the ACC between U and D were found after HPP construction than before, whereas the differences in abiotic parameters between U and D changed only marginally after HPP construction. However, the convergence in ACC cannot be considered an improvement for rheophilic species. Rather, it is based on the fact that particularly generalists, such as roach, Clitellata and non-biting midge larvae, which can quickly recolonise habitats (Armitage et al., 1995), were more evenly distributed between U and D after HPP construction and that fewer rheophilic species were found in D sections than before HPP construction.

At the Eixendorf reservoir cascade, due to the severely impaired sediment and flow dynamics, a high proportion of fine sediment was generally found in the investigated U and D sections, which leads to clogging of the interstitial zone and impairs the exchange with open water (Geist & Auerswald, 2007). This did not change considerably after the construction of the innovative HPP. The slight decrease in fine sediment content in U and D sections after HPP construction was probably caused by the lowering of the reservoir during the construction phase and the creation of an engineered gravel spawning ground in the tailwater (cf. Knott et al., 2021). During the construction phase, the river Schwarzach flowed in its natural riverbed, whereby deposited fine sediment was presumably partially transported downstream. Despite the considerable water level lowering of the Eixendorf reservoir during the construction phase, the impact of HPP construction on ACC was small. The prevailing differences in ACC between U and D have only marginally changed due to HPP construction.

Likewise, at Baierbrunn, no significant ecological improvements were observed in the investigated U and D sections after HPP construction compared to before HPP construction. Since at Baierbrunn, as at Eixendorf and Heckerwehr, no modifications were made to the existing weir that would allow for a more dynamic river discharge with enhanced sediment or deadwood transport, no long-term ecological improvements are to be expected at these sites.

We are aware that natural annual climatic and discharge-related fluctuations can have a pronounced influence on the ACC and abiotic parameters (e.g. Bai et al., 2020; Zhou et al., 2019). In addition, the effects of the HPP construction phase may also have overlapped effects in the immediate U and D sections. However, the relative comparison of the differences between U and D sections before and after HPP construction revealed no significant ecological improvements for rheophilic species at any of the study sites during the study period. Since fish are very mobile and macroinvertebrates and periphyton taxa can also react quickly to environmental changes due to short generation times (Barbour et al., 1999), we assume we have covered the main short-term ecological changes with our study design. However, it is possible that long-term changes in species and size composition, especially in macroinvertebrates and fish species with long generation times, may only become apparent after a few years and could not be detected during the study period. A detailed seasonal analysis over several years, which was outside the scope of this study, could further provide valuable information on seasonal changes in abiotic habitat characteristics and the ACC.

5 | CONCLUSIONS

The installation of innovative HPPs in existing weirs did not lead to significant ecological improvements in the investigated U and D sections at any of the study sites. Conversely, the reconstruction of a rock ramp into a solid tilting weir and the resulting damming by about 40 cm at Großweil even significantly increased the effects of serial discontinuity and deteriorated the habitat conditions for rheophilic species in U sections. From an ecological point of view, it must be urgently advised against retrofitting transverse structures such as rock ramps into solid weirs and increasing the damming target to avoid further ecological damage. Retrofitting solid weirs into inflatable weirs with gravel sluice may improve habitat conditions. However, to exceed small-scale effects, other existing limitations, such as other HPPs in U and D river sections, should be considered. Nevertheless, transverse structures should be removed, and impaired river sections should be restored wherever possible to counteract the ongoing decline of aquatic biodiversity. Furthermore, it must be considered that even innovative HPPs can cause severe injuries and mortality to fish during passage. Therefore, it will still be necessary to carefully trade-off pros and cons when approving such projects in the future, as the generation of renewable energy with

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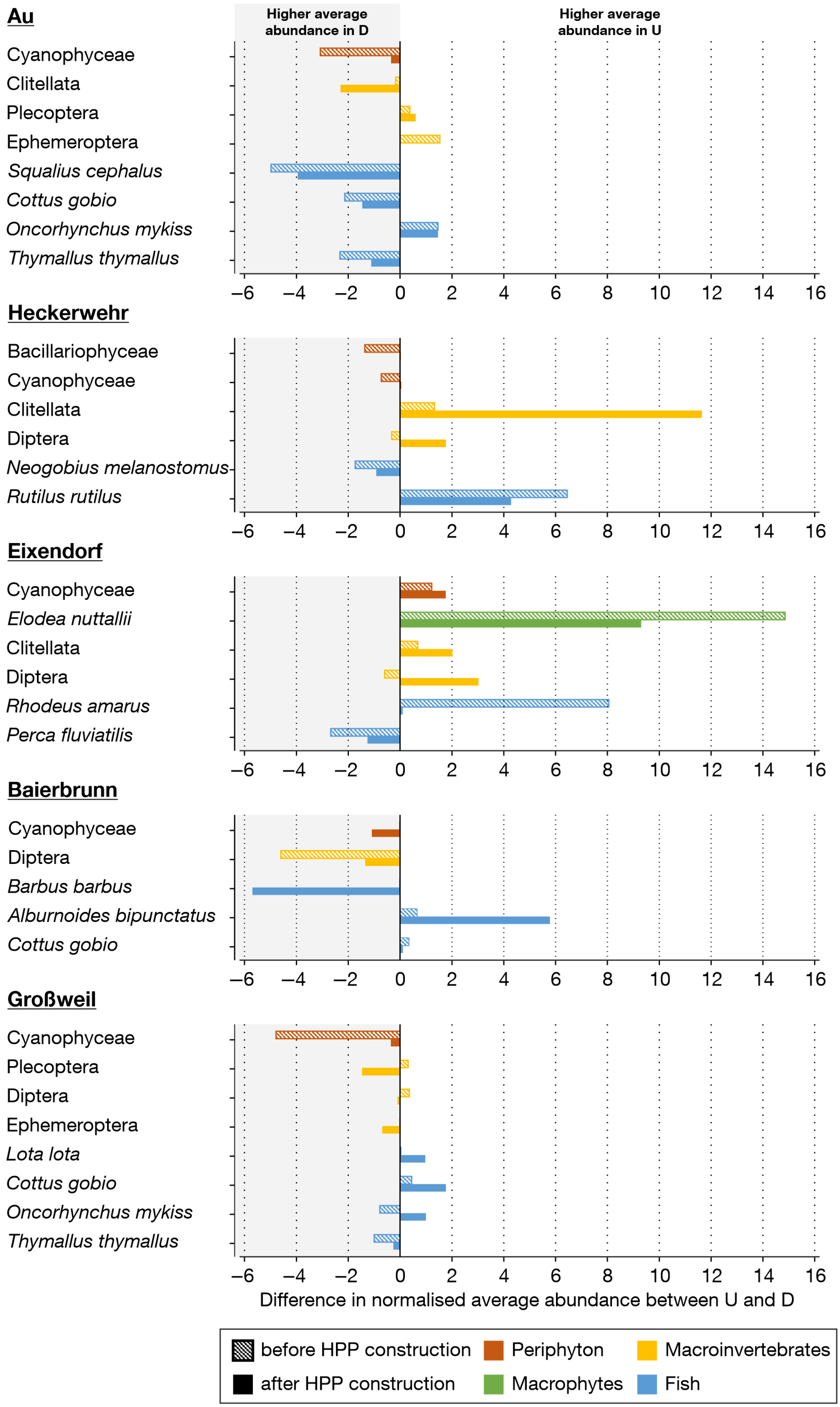

FIGURE 5 Differences in normalised average abundance of the assessed aquatic community between upstream (U) and downstream (D) sections before and after hydropower plant construction at the five study sites. Only taxa with a contribution to between-group dissimilarity (U vs. D) larger than 5% according to similarity percentage analyses (SIMPER; Clarke et al., 2014) are presented. Macroinvertebrate taxa were grouped into the orders Ephemeroptera, Diptera, Plecoptera, and the class Clitellata, periphyton taxa into the classes Cyanophyceae and Bacillariophyceae. The size of the bars indicates the delta in normalised average abundance for the respective taxa between U and D.

innovative HPPs studied herein always entails considerable ecological disadvantages at the same time.

AUTHOR CONTRIBUTIONS

Josef Knott, Melanie Mueller, Joachim Pander and Juergen Geist conceived this study and designed the methodology; Josef Knott, Melanie Mueller and Joachim Pander collected the data; Josef Knott analysed the data and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare no competing interests.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.x69p8czrh (Knott et al., 2024).

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REFERENCES

Anderson, D., Moggridge, H., Warren, P., & Shucksmith, J. (2015). The impacts of 'run-of-river' hydropower on the physical and ecological condition of rivers. *Water and Environment Journal*, *29*(2), 268–276. https://doi.org/10.1111/wej.12101

Armitage, P. D., Cranston, P. S., & Pinder, L. C. V. (1995). *The chironomidae: Biology and ecology of non-biting midges*. Springer Science & Business Media. https://doi.org/10.1007/978-94-011-0715-0

Bai, G., Zhang, Y., Yan, P., Yan, W., Kong, L., Wang, L., Chuan, W., Zisen, L., Biyun, L., Jianmin, M., Jincheng, Z., Jin, L., Jing, B., Shibin, X., Qiaohong, Z., Dong, X., Feng, H., & Wu, Z. (2020). Spatial and seasonal variation of water parameters, sediment properties, and submerged macrophytes after ecological restoration in a long-term (6 year) study in Hangzhou west lake in China: Submerged macrophyte distribution influenced by environmental variables. *Water Research*, *186*, 116379. https://doi.org/10.1016/j.watres.2020.116379

Barbour, M. T., Gerritsen, J., Snyder, B. D., & Stribling, J. B. (1999). *Rapid bioassessment protocols for use in streams and wadeable rivers: Periphyton, benthic macroinvertebrates, and fish* (2nd ed.). U.S. Environmental Protection Agency.

Belletti, B., Garcia de Leaniz, C., Jones, J., Bizzi, S., Börger, L., Segura, G., Castelletti, A., van de Bund, W., Aarestrup, K., Barry, J., Belka, K., Berkhuysen, A., Birnie-Gauvin, K., Bussettini, M., Carolli, M., Consuegra, S., Dopico, E., Feierfeil, T., Fernández, S., & Zalewski, M. (2020). More than one million barriers fragment Europe's rivers. *Nature*, *588*, 436–441. https://doi.org/10.1038/s41586-020-3005-2

Birnie-Gauvin, K., Aarestrup, K., Riis, T. M., Jepsen, N., & Koed, A. (2017). Shining a light on the loss of rheophilic fish habitat in lowland rivers as a forgotten consequence of barriers, and its implications for management. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *27*(6), 1345–1349. https://doi.org/10.1002/aqc.2795

Bray, J. R., & Curtis, J. T. (1957). An ordination of the upland forest communities of southern Wisconsin. *Ecological Monographs*, *27*(4), 325–349. https://doi.org/10.2307/1942268

Clarke, K. R., & Gorley, R. N. (2015). *PRIMER v7: User manual/tutorial*. PRIMER-E Ltd.

Clarke, K. R., Gorley, R. N., Somerfield, P. J., & Warwick, R. M. (2014). *Change in marine communities: An approach to statistical analysis and interpretation* (3rd ed.). PRIMER-E Ltd.

DIN EN 14011. (2003). *Water quality—Sampling of fish with electricity*. Beuth Verlag.

DIN EN 14757. (2005). *Water quality—Sampling of fish with multi-mesh gillnets*. Beuth Verlag.

DIN EN 15204. (2006). *Water quality—Guidance standard on the enumeration of phytoplankton using inverted microscopy (Utermöhl technique)*. Beuth Verlag.

Dudgeon, D., Arthington, A. H., Gessner, M. O., Kawabata, Z. I., Knowler, D. J., Lévêque, C., Naiman, R. J., Prieur-Richard, A. H., Soto, D., Stiassny, M. L., & Sullivan, C. A. (2006). Freshwater biodiversity: Importance, threats, status and conservation challenges. *Biological Reviews*, *81*(2), 163–182. https://doi.org/10.1017/S1464793105006950

Duerregger, A., Pander, J., Palt, M., Mueller, M., Nagel, C., & Geist, J. (2018). The importance of stream interstitial conditions for the early-life-stage development of the European nase (*Chondrostoma nasus* L.). *Ecology of Freshwater Fish*, *27*(4), 920–932. https://doi.org/10.1111/eff.12403

Dynesius, M., & Nilsson, C. (1994). Fragmentation and flow regulation of river systems in the northern third of the world. *Science*, *266*(5186), 753–762. https://doi.org/10.1126/science.266.5186.753

European Commission. (1992). Council directive 92/43/EEC of 21 May 1992 on the conservation of natural habitats and of wild fauna and flora. *Official Journal of the European Union*, *206*, 7–50.

European Parliament. (2000). Directive 2000/60/EC of the European Parliament and of the Council of 23 October 2000 establishing a framework for community action in the field of water policy. *Official Journal of the European Commission*, *327*, 1–73.

Feld, C. K., & Hering, D. (2007). Community structure or function: Effects of environmental stress on benthic macroinvertebrates at different spatial scales. *Freshwater Biology*, *52*, 1380–1399. https://doi.org/10.1111/j.1365-2427.2007.01749.x

Geist, J. (2021). Green or red: Challenges for fish and freshwater biodiversity conservation related to hydropower. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *31*(7), 1551–1558. https://doi.org/10.1002/aqc.3597

Geist, J., & Auerswald, K. (2007). Physicochemical stream bed characteristics and recruitment of the freshwater pearl mussel (*Margaritifera margaritifera*). *Freshwater Biology*, *52*(12), 2299–2316. https://doi.org/10.1111/j.1365-2427.2007.01812.x

Greenwood, M. J., Harding, J. S., Niyogi, D. K., & McIntosh, A. R. (2012). Improving the effectiveness of riparian management for aquatic invertebrates in a degraded agricultural landscape: Stream size and land-use legacies. *Journal of Applied Ecology*, *49*, 213–222. https://doi.org/10.1111/j.1365-2664.2011.02092.x

Herbert, M. E., & Gelwick, F. P. (2003). Spatial variation of headwater fish assemblages explained by hydrologic variability and upstream effects of impoundment. *Copeia*, *2003*(2), 273–284. https://doi.org/10.1643/0045-8511(2003)003[0273:SVOHFA]2.0.CO;2

Jurvelius, J., Kolari, I., & Leskelä, A. (2011). Quality and status of fish stocks in lakes: Gillnetting, seining, trawling and hydroacoustics as sampling methods. *Hydrobiologia*, *660*, 29–36. https://doi.org/10.1007/s10750-010-0385-6

Knott, J., Mueller, M., Pander, J., & Geist, J. (2019). Fish passage and injury risk at a surface bypass of a small-scale hydropower plant. *Sustainability*, *11*(21), 6037. https://doi.org/10.3390/su11216037

Knott, J., Mueller, M., Pander, J., & Geist, J. (2020). Seasonal and diurnal variation of downstream fish movement at four small-scale hydropower plants. *Ecology of Freshwater Fish*, *29*, 74–88. https://doi.org/10.1111/eff.12489

Knott, J., Mueller, M., Pander, J., & Geist, J. (2023a). Ecological assessment of the world's first shaft hydropower plant. *Renewable and Sustainable Energy Reviews*, *187*, 113727. https://doi.org/10.1016/j.rser.2023.113727

Knott, J., Mueller, M., Pander, J., & Geist, J. (2023b). Bigger than expected: Species-and size-specific passage of fish through hydropower screens. *Ecological Engineering*, *188*, 106883. https://doi.org/10.1016/j.ecoleng.2022.106883

Knott, J., Mueller, M., Pander, J., & Geist, J. (2024). Data from: Habitat quality and biological community responses to innovative hydropower plant installations at transverse in-stream structures. *Dryad Digital Repository* https://doi.org/10.5061/dryad.x69p8czrh

Knott, J., Nagel, C., & Geist, J. (2021). Wasted effort or promising approach—Does it make sense to build an engineered spawning ground for rheophilic fish in reservoir cascades? *Ecological Engineering*, *173*, 106434. https://doi.org/10.1016/j.ecoleng.2021.106434

Malmqvist, B., & Rundle, S. (2002). Threats to the running water ecosystems of the world. *Environmental Conservation*, *29*(2), 134–153. https://doi.org/10.1017/S0376892902000097

Mbaka, J. G., & Wanjiru Mwaniki, M. (2015). A global review of the downstream effects of small impoundments on stream habitat conditions and macroinvertebrates. *Environmental Reviews*, *23*(3), 257–262. https://doi.org/10.1139/er-2014-0080

Mueller, M., & Geist, J. (2016). Conceptual guidelines for the implementation of the ecosystem approach in biodiversity monitoring. *Ecosphere*, *7*(5), e01305. https://doi.org/10.1002/ecs2.1305

Mueller, M., Knott, J., Pander, J., & Geist, J. (2022). Experimental comparison of fish mortality and injuries at innovative and conventional small hydropower plants. *Journal of Applied Ecology*, *59*(9), 2360–2372. https://doi.org/10.1111/1365-2664.14236

Mueller, M., Pander, J., & Geist, J. (2011). The effects of weirs on structural stream habitat and biological communities. *Journal of Applied Ecology*, *48*, 1450–1461. https://doi.org/10.1111/j.1365-2664.2011.02035.x

Mueller, M., Pander, J., & Geist, J. (2014). A new tool for assessment and monitoring of community and ecosystem change based on multivariate abundance data integration from different taxonomic groups. *Environmental Systems Research*, *3*, 12. https://doi.org/10.1186/2193-2697-3-12

O'Connor, J. E., Duda, J. J., & Grant, G. E. (2015). 1000 dams down and counting. *Science*, *348*(6234), 496–497. https://doi.org/10.1126/science.aaa9204

Pander, J., Mueller, M., & Geist, J. (2015). A comparison of four stream substratum restoration techniques concerning interstitial conditions and downstream effects. *River Research and Applications*, *31*(2), 239–255. https://doi.org/10.1002/rra.2732

Pauwels, I. S., Baeyens, R., Toming, G., Schneider, M., Buysse, D., Coeck, J., & Tuhtan, J. A. (2020). Multi-species assessment of injury, mortality, and physical conditions during downstream passage through a large Archimedes hydrodynamic screw (Albert canal, Belgium). *Sustainability*, *12*(20), 8722. https://doi.org/10.3390/su12208722

R Core Team. (2022). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. https://www.R-project.org/

Sachs, J. D., Schmidt-Traub, G., Mazzucato, M., Messner, D., Nakicenovic, N., & Rockström, J. (2019). Six transformations to achieve the sustainable development goals. *Nature Sustainability*, *2*(9), 805–814. https://doi.org/10.1038/s41893-019-0352-9

Schiermeir, Q. (2018). Dam removal restores rivers. *Nature*, *557*(7705), 290–291. https://doi.org/10.1038/d41586-018-05182-1

Sternecker, K., Denic, M., & Geist, J. (2014). Timing matters: Species-specific interactions between spawning time, substrate quality, and recruitment success in three salmonid species. *Ecology and Evolution*, *4*(13), 2749–2758. https://doi.org/10.1002/ece3.1128

Surber, E. W. (1930). A quantitative method of studying the food of small fishes. *Transactions of the American Fisheries Society*, *60*, 158–163. https://doi.org/10.1577/1548-8659(1930)60[158:AQMOST]2.0.CO;2

Taylor, C. A., Knouft, J. H., & Hiland, T. M. (2001). Consequences of stream impoundment on fish communities in a small North American drainage. *Regulated Rivers: Research & Management*, *17*(6), 687–698. https://doi.org/10.1002/rrr.629

Utermöhl, H. (1931). Neue Wege in der quantitativen Erfassung des Planktons (mit besonderer Berücksichtigung des Ultraplanktons). *Internationale Vereinigung für Theoretische und Angewandte Limnologie*, *5*(2), 567–596. https://doi.org/10.1080/03680770.1931.11898492

Vannote, R. L., Minshall, G. W., Cummins, K. W., Sedell, J. R., & Cushing, C. E. (1980). The river continuum concept. *Canadian Journal of Fisheries and Aquatic Sciences*, *37*(1), 130–137. https://doi.org/10.1139/f80-017

Ward, J. V., & Stanford, J. A. (1983). The serial discontinuity concept of lotic ecosystems. In T. D. Fontaine & S. M. Bartell (Eds.), *Dynamics of lotic ecosystems* (pp. 347–356). Ann Arbor Science Publishers.

Zarfl, C., Lumsdon, A. E., Berlekamp, J., Tydecks, L., & Tockner, K. (2015). A global boom in hydropower dam construction. *Aquatic Sciences*, *77*, 161–170. https://doi.org/10.1007/s00027-014-0377-0

Zhou, L., Wang, G., Kuang, T., Guo, D., & Li, G. (2019). Fish assemblage in the Pearl River estuary: Spatial-seasonal variation, environmental influence and trends over the past three decades. *Journal of Applied Ichthyology*, *35*(4), 884–895. https://doi.org/10.1111/jai.13912

SUPPORTING INFORMATION

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

Table S1 Arithmetic mean values (am), standard deviation (SD) and minimum (min) and maximum (max) values (in parentheses) of the recorded physical and hydromorphological parameters at the five study sites averaged over all investigated transects upstream (U) and downstream (D) of the transverse structures before and after hydropower plant construction.

Table S2. Statistical *p*-values according to Bonferroni-corrected post-hoc pairwise Mann–Whitney *U* tests or post-hoc Tukey HSD tests of the recorded physical and hydromorphological parameters for the pairwise comparison of the assessed upstream (U) and downstream (D) sections at the five study sites before and after hydropower plant construction.

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