Received: 27 October 2021 | Revised: 27 January 2022 | Accepted: 1 February 2022
DOI: 10.1002/rra.3953

SPECIAL ISSUE PAPER

WILEY

Hydropeaking impairs upstream salmonid spawning habitats in a restored Danube tributary

Joachim Pander[1] | Roser Casas-Mulet[1,2] | Juergen Geist[1]

[1]Aquatic Systems Biology Unit, TUM School of Life Sciences, Technical University of Munich, Freising, Germany

[2]Department of Infrastructure Engineering, School of Engineering, University of Melbourne, Melbourne, Victoria, Australia

Correspondence
Juergen Geist, Aquatic Systems Biology Unit, TUM School of Life Sciences, Technical University of Munich, Freising, Germany.
Email: geist@tum.de

Funding information
Alexander von Humboldt-Stiftung; bayklif network funded by the Bavarian State Ministry of Science and the Arts

Abstract

Hydropower is considered an important form of renewable energy, often involving hydropeaking. While the effects of hydropeaking on aquatic communities in areas downstream the dam are well understood, there is a lack of studies investigating potential impacts on tributaries located further upstream. In this study, we tested the effects of hydropeaking operations on upstream tributaries in a restored area of the Danube River, with a focus on the periods of backlog and release of water (up-ramping and down-ramping, respectively) during the filling and release of the reservoir. We used brown trout egg and larval mortality, linked to hydraulic, sedimentary and physiochemical changes in spawning grounds as an indicator. We compared hydropeaking-affected versus non-affected sites in upstream tributaries using HydroEcoSedimentary Tools (HESTs) loaded with clean gravels and brown trout eggs. Egg and larval mortalities were significantly higher in the hydropeaking-affected site with more than 80% egg mortality and almost 100% larval mortality compared to values of 55–63% and 80–85%, respectively, in non-affected sites. Spawning ground quality was significantly altered in the hydropeaking-affected site, where the highest mortalities were observed. Overall, duration of time periods with flow velocities close to zero were a key variable, potentially decreasing oxygen supply for eggs and larvae. Such periods of close to zero flow velocities were driven by backlog periods during the filling of the reservoir, revealing that such events can severely impair ecological integrity of spawning sites in tributaries upstream of dams by slowing the flows in upstream tributaries. Such altered processes can reduce fish population recruitment and need to be considered in future restoration projects.

KEYWORDS
aquatic conservation, brown trout, fish egg survival, flow fluctuations, hydropower operation, river restoration, water–sediment interface

1 | INTRODUCTION

Increasing energy demand and energy decarbonization drive the construction of new hydropower plants in Eastern Europe and developing countries in Asia, Africa and South America (Lehner, Czisch, & Vassolo, 2005; Zarfl, Lumsdon, Berlekamp, Tydecks, & Tockner, 2015). In central Europe, where hydropower has had a long tradition and where its potential is almost fully exploited, power plants

This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.
© 2022 The Authors. *River Research and Applications* published by John Wiley & Sons Ltd.

are being optimized, changing to more effective turbine technologies (Sari et al., 2018) or operation modes (Wagner, Hauer, & Habersack, 2019) that increase the implementation of hydropeaking regimes (Smokorowski, 2021). The need for the operators to run the power plant as efficient as possible makes it attractive for them to use hydropeaking as an operational tool to feed peaks of energy demand and maximise energy production revenue (Venus, Smialek, Pander, Harby, & Geist, 2020). Sudden stops and starts of the turbines to store and release water efficiently typically results in hydropeaking.

Hydropeaking regimes are well known to negatively affect river ecology downstream of power plants (Greimel et al., 2018; Hauer, Siviglia, & Zolezzi, 2017; Moreira et al., 2019; Schmutz et al., 2015). Extreme and sudden changes in discharge can lead to the degradation of river habitat quality (Bruder et al., 2016; Casas-Mulet, Alfredsen, Hamududu, & Timalsina, 2015; Greimel et al., 2018), the alteration of stream thermal regimes (Casas-Mulet, Saltveit, & Alfredsen, 2016; Choi & Choi, 2018), the dewatering of spawning grounds (Casas-Mulet, Saltveit, & Alfredsen, 2015; Grabowski & Isely, 2007), and the stranding of fish (Auer, Zeiringer, Führer, Tonolla, & Schmutz, 2017; Bartoň et al., 2021; Puffer et al., 2015; Schmutz et al., 2015). Fishes are known to be fast colonisers of aquatic habitats (Matthews, 1986; Pander, Mueller, & Geist, 2015b) that can readily spawn during high water phases of hydropeaking at spawning grounds that may then fall fully dry during low water phases (Grabowski & Isely, 2007), leading to increased mortality.

Upstream effects of hydropeaking are less well understood. In the headwater area directly upstream of the power plant, hydropeaking potentially impairs fish habitat by increasing water depth and reducing current speed, leading to more uniform conditions that favour generalist or limnophilic aquatic species and communities (Greimel et al., 2018; Mueller, Pander, & Geist, 2011). During the water storage phase, when the turbines stop, a water backlog may be formed, reducing flow velocity. Low flow velocities may increase fine sediment deposition and potentially affect ecologically relevant processes in the interstitial zone. Most relevant is streambed clogging impairing spawning ground quality (Hauer, Holzapfel, Tonolla, Habersack, & Zolezzi, 2019), altering streambed communities (Bondar-Kunze, Kasper, & Hein, 2021; Casas-Mulet, Alfredsen, et al., 2015; Elgueta et al., 2021; Salmaso, Servanzi, Crosa, Quadroni, & Espa, 2021), and potentially also affecting the river productivity (Greimel et al., 2018; Mueller et al., 2011). An understudied aspect of these processes is the potential effect that such hydropeaking-induced backlogs may have on aquatic habitat of upstream tributaries. This lack of knowledge is surprising given the key role tributaries play as aquatic habitats for spawning, larval development and juvenile growth of many riverine fish species such as rheophilic salmonids and cyprinids (Naus & Reid Adams, 2018; Pracheil, Pegg, & Mestl, 2009).

In this study, we aim at tackling the lack of understanding of upstream effects of hydropeaking, with a focus on tributaries and hydropeaking-induced backlog events. We assessed the upstream effects of hydropeaking of the power plant Ingolstadt in the European River Danube on a structurally restored tributary located within a large floodplain restoration area (Stammel et al., 2012), which is known to provide several spawning grounds for lithophilic fish along its course (Pander et al., 2015b; Pander, Knott, Mueller, & Geist, 2019; Pander, Mueller, & Geist, 2018). We hypothesized that a backlog resulting from hydropeaking operations in the main river will impair spawning ground quality in the upstream tributary. In particular, the changed hydrograph of the tributary will have severe consequences on water depth, current speed, fine sediment deposition and oxygen supply, leading to unfavourable conditions in the interstitial spaces of the spawning grounds and reducing the recruitment success of brown trout in affected sites compared to sites in the same system not affected by hydropeaking.

2 | MATERIAL AND METHODS

2.1 | Site description

The Ottheinrichbach (OHB) River is located in the middle section of a large scale floodplain restoration project at the upper River Danube (mean annual discharge = 333 $m^3 \cdot s^{-1}$) in Bavaria, south-Germany (Fischer & Cyffka, 2014; Pander et al., 2015b; Stammel et al., 2012; 48°44′55,7 N, 11°16′35,7 O; Figure 1a). It was constructed to restore the impaired fish migration within the Danube due to the construction of the power plant Bergheim, to increase groundwater dynamics, to provide additional habitat for keystone organisms and to re-wet one of the last remaining fluvial forests along this large European River (Pander et al., 2015b, Pander, Mueller, Knott, Egg, & Geist, 2017, Pander et al., 2018, Pander et al., 2019; Stammel et al., 2012; Stammel, Fischer, Gelhaus, & Cyffka, 2016). Due to its location in spatial proximity to the hydropower plants Ingolstadt and Bergheim and its important function as a fish nursery (Pander et al., 2015b), the OHB represents an ideal model stream for tributaries located along heavily modified water bodies affected by hydropower generation. Due to hydropeaking of the Ingolstadt Plant, the confluence OHB–Danube is subject to severe flow fluctuations largely driven by the power plants' backlog (Figure 2). The backlog effect reaches from 700 to 1,200 m into the OHB, depending on the discharge of the River Danube, potentially impairing one of the spawning grounds that were newly built in the year 2010 during the floodplain restoration (Figure 3). The OHB has a variable discharge between 0.5 and 5 $m^3 \cdot s^{-1}$ and can be additionally flooded with another 25 $m^3 \cdot s^{-1}$ to mimic natural dynamics of flood scenarios that were historically present in the alluvial forest (Fischer & Cyffka, 2014; Pander et al., 2019; Stammel et al., 2012).

In the OHB, three sites known to function as spawning grounds for lithophilic fish species were chosen for active bioindication with trout eggs (Pander & Geist, 2013). Site 1 (23 m^2) is located in the upper reach of the OHB (48°44′12″N, 11°15′56″E) approximately 280 m downstream of a weir where the OHB is released from the Danube. Site 1 comprises a flow gradient of 0.64% and is not affected by the hydropeaking-induced backlog of the power plant Ingolstadt. Site 2 is located in the middle reach of the OHB (48°44′25″N, 11°18′23″E), has a larger flow gradient (0.80%) and covers 36 m^2.

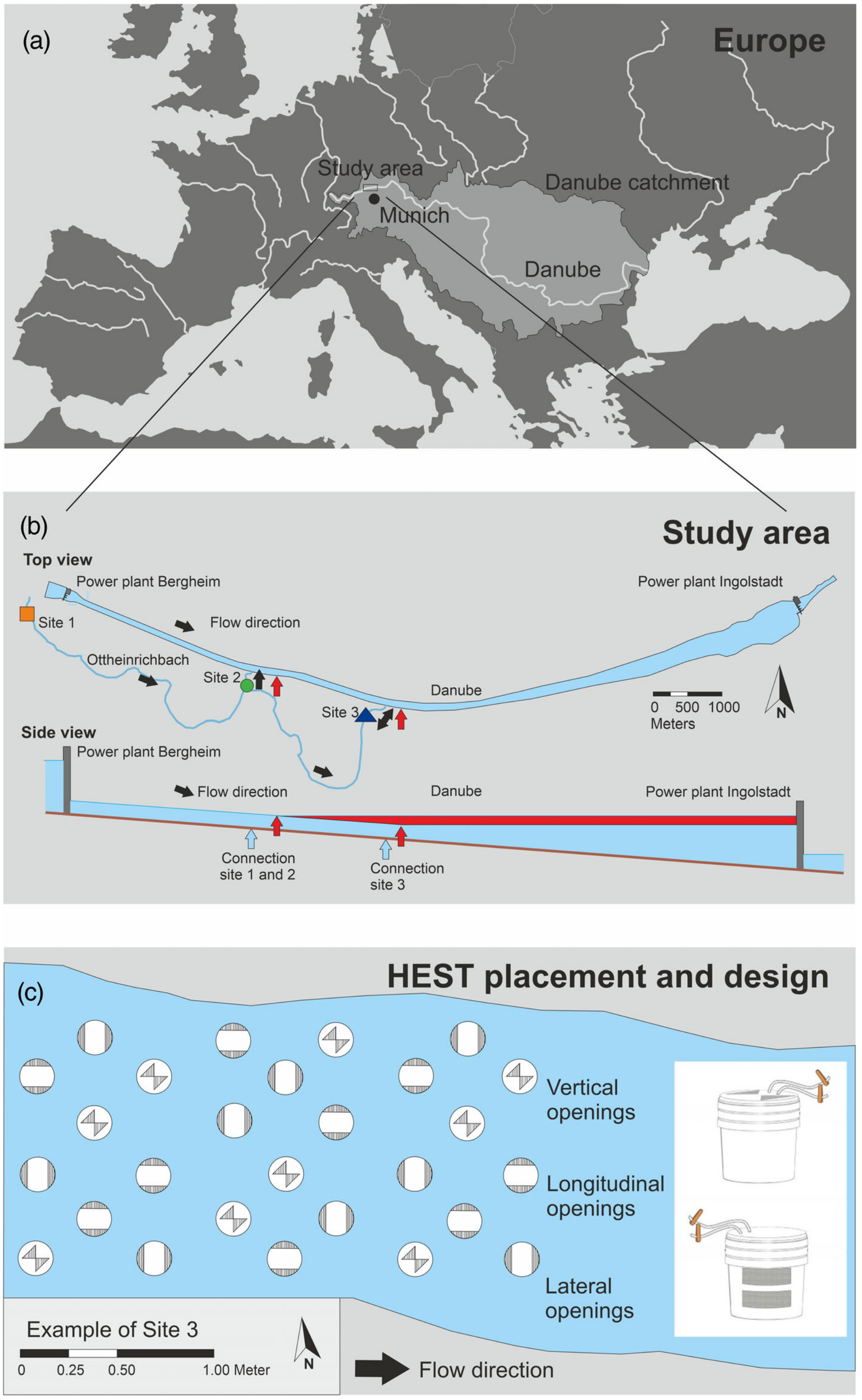

FIGURE 1 Illustration of the study area within Europe (a) and location of the three investigated spawning sites within a large scale floodplain restoration at the Danube River (b) including a schematic top-view on the study area between the power plants Bergheim and Ingolstadt with an indication of the backlog caused by the power plant Ingolstadt in side view. Red arrows indicate the variability of the affected backlog area. Coloured triangle, circle and square indicate the location of the three assessed spawning sites; black arrows indicate the flow directions. Light blue arrows indicate the location of the two principle connections the Ottheinrichbach has to the Danube River. The lowermost Panel (c) indicates placement and construction of the HydroEcoSedimentary Tool (HEST) in site 3 as an example [Color figure can be viewed at wileyonlinelibrary.com]

Despite its location close to a connection to the Danube, it is not influenced by the backlog due to the steepness of the OHBs river course on the lowermost 100 m on its way to the Danube (Figure 1b). Site 3 covers 20 m^2 and is located 200 m upstream of the final confluence of the OHB in spatial proximity to the Danube. This site is highly affected by the backlog of the Danube, comprising strongly fluctuating water levels and changes in current speed and direction (Figure 1b). During low discharge conditions and outflow of the discharge back into the Danube, the OHB site 3 comprises a flow gradient of 0.50%.

2.2 | Hydroecological assessment

In order to assess the potential effects of the hydropeaking-driven backlog, we compared the quality of the spawning grounds between

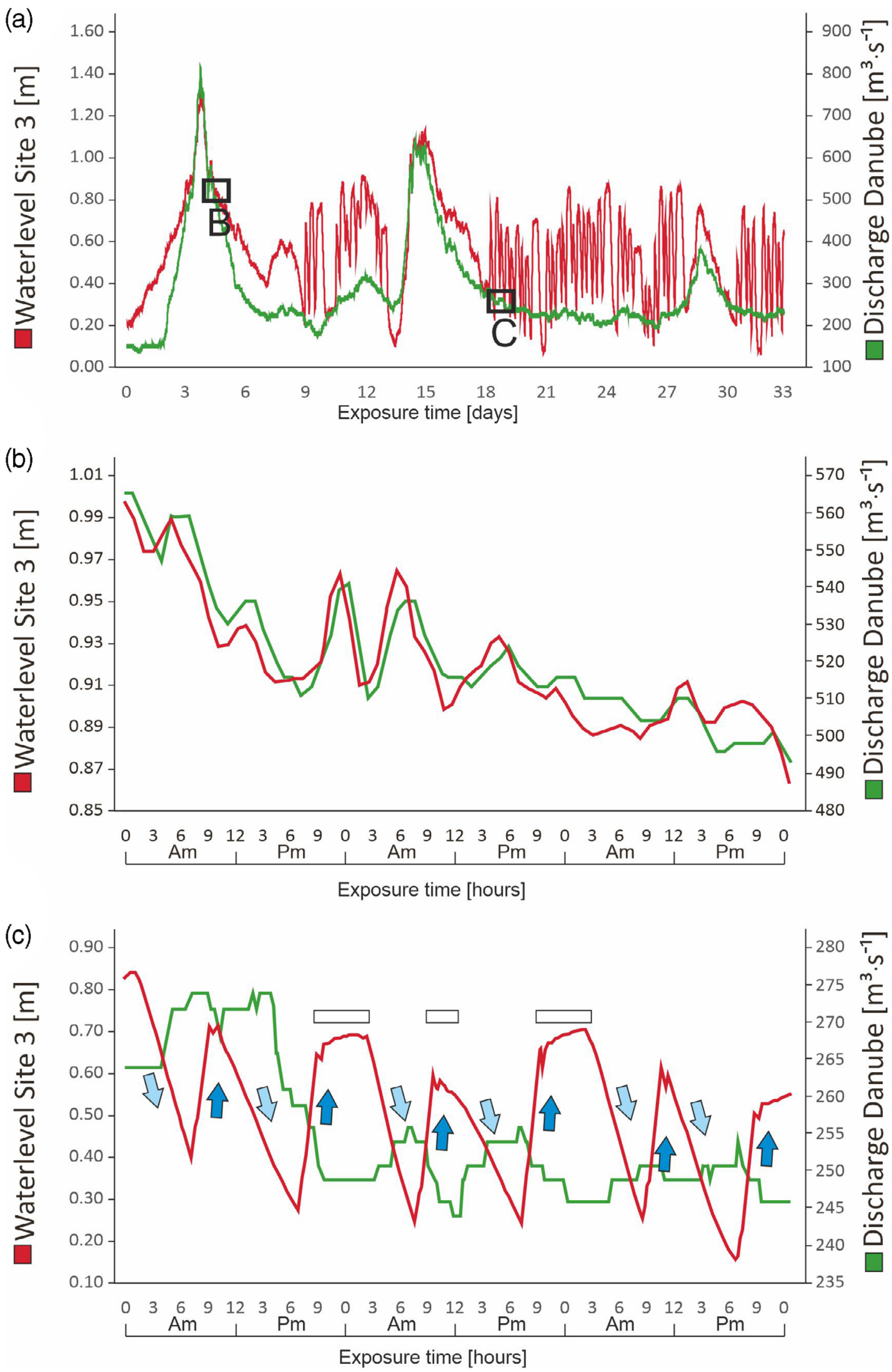

FIGURE 2 Hydrograph of the Danube's discharge during the exposure of the brown trout eggs in comparison to water level changes in the hydropower-affected site 3 (a) as well as for representative medium (b) and low (c) discharge conditions during the egg exposure. Light blue arrows in panel c indicate flow direction towards the Danube (OHB discharges regular into the Danube); blue arrows indicate flow direction from the Danube upstream into the OHB (caused by the backlog of the Danube) and open rectangles in panel c indicate time phases with almost no directed flow [Color figure can be viewed at wileyonlinelibrary.com]

sites. At each site, we installed 27 HydroEcoSedimentary Tools (HESTs) loaded with brown trout eggs (*Salmo trutta fario* L.) (Figure 1c). HESTs were made out of interlocked plastic containers (AUER Packaging GmbH, Amerang, Germany), creating top (T) and bottom (B) compartments. We placed a temperature logger in each compartment, and installed a 1.5 m long Sahleberg® TubeTec silicon tubing of 4.5 mm inner diameter (Sahleberg GmbH, Feldkirchen, Germany) to enable water samples extraction. Three sets of different HEST types were applied to distinguish longitudinal, (L) lateral (X), and vertical (V) infiltration of fines. Each of the infiltration openings was covered with Jaera® perforated metallic plates (2 mm diameter round holes, JAERA GmbH & Co. KG, Laatzen, Germany). For full details of HESTs design, see Casas-Mulet, Pander, Prietzel, and Geist (2021).

Before exposure, each HEST was pre-filled with sediment truncated at the 6.3 mm fraction. We followed granulometry curves from the OHB's natural streambed material, described in Pander et al. (2015b), to mimic the corresponding sediment sizes at each site. Brown trout eggs were purchased from a local fish farm (Forellenhof Nadler, Eching, Germany). Brown trout eggs were inserted in the eye-

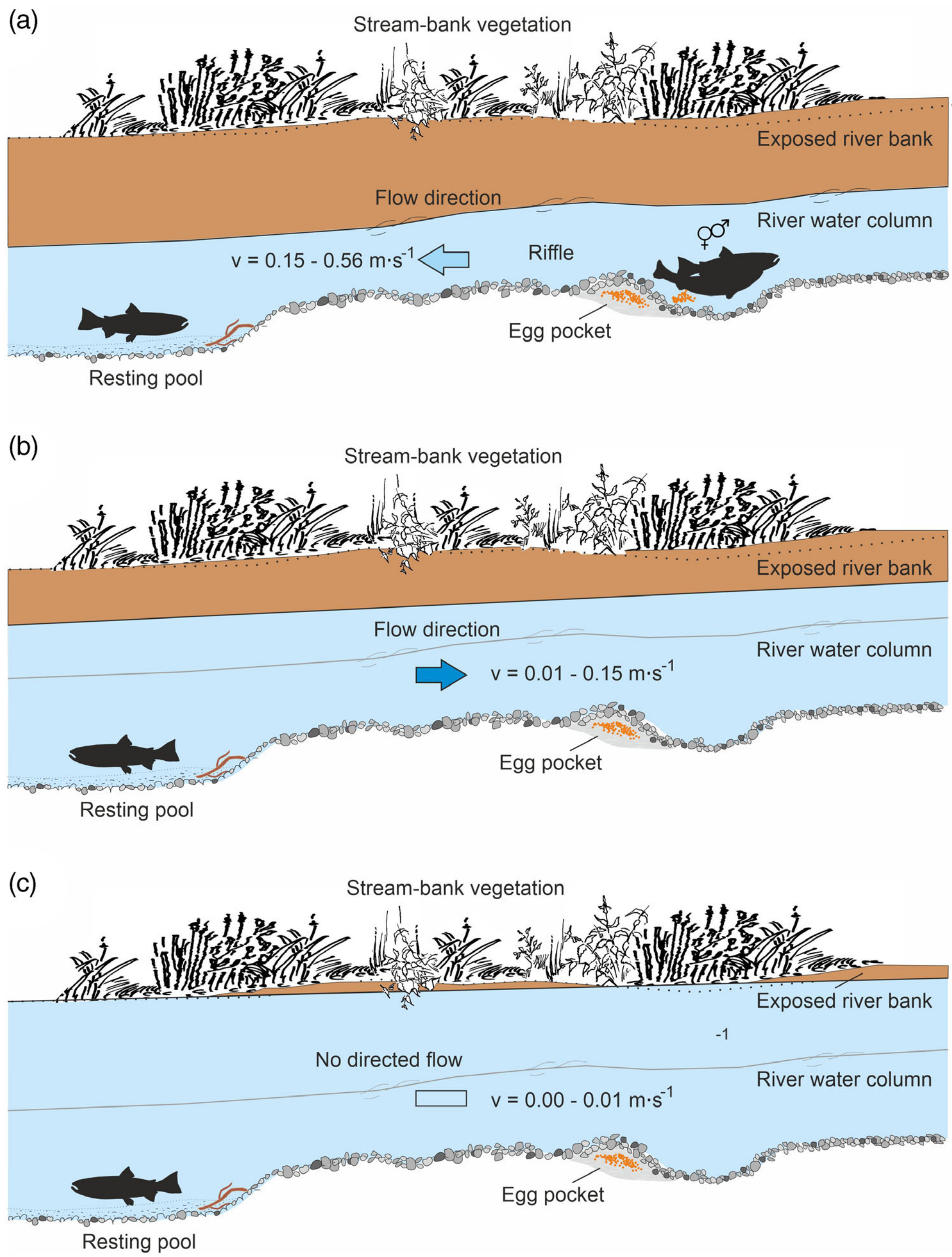

FIGURE 3 Schematic view of the hydropeaking affected site 3 with the indication of the three different stages (a) outflowing conditions (light blue arrows), (b) back flowing conditions (so called backlog, blue arrows), and (c) stagnant conditions (open rectangles) with high water level and almost no directed current [Color figure can be viewed at wileyonlinelibrary.com]

point stage to assess their survival, analogously to their use for bioindication of open (Pander & Geist, 2010) and interstitial water quality (Pander, Schnell, Sternecker, & Geist, 2009). After receiving the eggs from the fish farm, they were acclimatized for 30 min including a temperature adjustment of 2°C in the laboratory of the Aquatic Systems Biology Unit, Freising, Germany. Dead eggs were subsequently removed, and the remaining live eggs were distributed into the HESTs. Each HEST compartment (T and B) was loaded with 30 eggs that were randomly picked and placed by forming a small pit in the HESTs, which was then carefully covered with 5 cm of substrate. The full HESTs were kept submerged in a large tank with aerated water, so the quality of the eggs was preserved during transport until their installation in the river the next day (see Casas-Mulet et al., 2021 for further details).

On 18th December 2018, 27 HESTs were installed at each site into the streambed of the OHB. A hole big enough to fit each of the HESTs was dug with a common spade, keeping disturbance of the surrounding streambed to a minimum. Each HEST was then inserted so that its top was even with the gravel surface, and the river´s natural coarse sediment was used to fill up the gap to the same level. The HESTs were installed in closed mode and after fines were settled, they were opened to start the experiment (Casas-Mulet et al., 2021). After 33 days of exposure, all HESTs were retrieved and immediately assessed in the laboratory for egg and larvae survival. The HEST compartments were opened carefully, data loggers and larger stones were removed, and the sediment content was emptied into a tray, rinsed with water and examined for larvae and eggs. A distinction was made between live and dead eggs as well as between live and dead larvae, as described in Casas-Mulet et al. (2021). All samples were preserved in a solution of 70% (v/v) ethanol.

Ecologically relevant physico-chemical parameters were measured *in situ* for each HEST and in the open water of the river after installation of the HEST and before retrieval. The interstitial water of each HEST was extracted following the procedure described in Casas-Mulet et al. (2021) using 100 mL, Omnifix Solo plastic syringes (B. Braun Melsungen AG, Melsungen, Germany). Samples of interstitial water were immediately transferred into clean 100 mL vials and temperature [°C], dissolved oxygen [$mg \cdot L^{-1}$], electrical conductivity [$\mu S \cdot cm^{-1}$, corrected to 20°C], and pH were measured with a hand-held WTW® Multimeter 340i (WTW GmbH, Weilheim, Germany). In addition, turbidity [NTU] was assessed using a WTW® Turb 355 IR measuring set (Pander, Mueller, & Geist, 2015a). HOBO® temperature loggers (UA-002-064, Onset, US) installed in the HESTs, and in the water column of each site, were used to record continuous (at 30 min intervals) temperature data. Measurements of interstitial water are presented in Table 1. To assess fine sediment deposition in the HESTs, we wet-sieved (Pander et al., 2015a) the sediment contents of each HEST compartment after retrieval. We used an AS 200 Retsch sieving machine (Retsch, Haan, Germany) equipped with sieves ISO 3310-1 of screen sizes 20.0, 6.3, 2.0, 0.85, 0.20 and 0.045 mm. Coarse fractions (> 20.0 mm,> 6.3 mm, > 2.0 mm) were dried at air temperature for 24 hours, and finer fractions (< 2.0 mm) were oven-dried at 100°C for 24 h (Pander et al., 2015a). All fractions were then weighted with a scale (Dini Argeo S.r.l., Modena, Italy) to the nearest 0.1 g. Water depth [m] and near-bed flow velocity [$m \cdot s^{-1}$] was measured with a magnetic inductive flow meter (Ott MF pro, Ott, Kempten, Germany) directly at the HESTs, 5 cm below the water surface as well as 3–5 cm above the HESTs.

2.3 | Data analysis

Total percent mortality was calculated as the difference between the surviving eggs or larvae and the initially loaded egg number for each of the HESTs retrieved from the three sites. For univariate multiple-group comparisons of egg and larval mortality as well as abiotic habitat variables, each dataset was tested for normal distribution (Shapiro–Wilk test) and homoscedasticity (Levene test). Since data did not fulfil the criteria for parametric testing, the non-parametric Kruskal–Wallis test was applied to test for significant differences. A subsequent post-hoc Wilcoxon test with Bonferroni correction for multiple comparisons was used to determine whether values differed significantly between HESTs, compartments and/or infiltration directions. Since no significant differences between longitudinal, lateral and vertical HEST measurements were observed, the data was pooled for further investigation. Univariate statistics were carried out using statistical and graphical open-source software R (R Core Team, 2020, version 4.0.3R, www.R-project.org/, last accessed on 27 July 2021).

To visualise differences of HESTs in egg and larval mortality between the three sites, a non-metric multidimensional scaling (NMDS) using PRIMER v7 (Plymouth Marine Laboratory, Plymouth, UK) was plotted. For this multivariate comparison, a resemblance matrix was calculated using the full data resolution of egg and larval mortality from the different retrieval time points of HESTs at the three sites (Clarke, Gorley, Somerfield, & Warwick, 2014). To test for significant differences of mortality rates between HESTs and between top and bottom compartments, one-way analysis of similarities (ANOSIM) based on Bray–Curtis similarities (Bray & Curtis, 1957) calculated from egg and larval mortality data (Clarke, 1993) were computed. To analyse the interaction between the measured abiotic habitat variables and the ordination of HESTs in the NMDS, the abiotic habitat variables were displayed in the NMDS using the overlay function in PRIMER.

To test for relations between egg mortality and minimum oxygen concentration found in the HESTs, the oxygen concentration was used as predictor variable and plotted against the response variable egg mortality. To avoid false-negative conclusions due to potentially non-linear relations, Spearman rank correlation for monotonic trend were computed and a smooth curve was displayed. This analysis was also performed using R (R Core Team, 2020). For all testing's, a significance level of $p \leq .05$ (= 95% probability) was applied.

3 | RESULTS

3.1 | Brown trout eggs and larval mortality

Univariate comparisons of egg and larval mortality revealed significant differences (Table 2) between the replicates of hydropeaking-affected site 3 and the two non-hydropeaking affected sites 1 and 2 that were

TABLE 1 Abiotic spawning ground characteristics of the assessed sites

	T [°C]	O_2 [$mg \cdot L^{-1}$]	pH [pH]	EC [$\mu S \cdot cm^{-1}$]	Turb [NTU]	D [m]	V [$m \cdot s^{-1}$]	DG [mm]	IR [$kg \cdot d^{-1}$]
Site 1	3.73	11.45 a	8.29 a	558 a	420 a	0.18 a	0.45 a	2.53 a	0.98 a
	0.16–8.67	5.17–12.98	7.66–9.17	488–807	15–1,100	0.07–0.22	0.17–0.77	0.18–5.23	0.02–4.50
Site 2	3.41	11.79 a	8.37 a	628 b	434 a	0.22 b	0.52 b	2.75 a	1.12 a
	−1.13–7.39	9.29–13.12	7.86–9.95	525–811	49–1,065	0.11–0.23	0.25–0.86	0.40–5.86	0.03–3.40
Site 3	3.81	9.69 b	7.97 b	592 c	326 b	0.40 c	0.10 c	1.66 b	0.56 b
	−0.49–8.45	5.03–12.73	7.38–8.72	331–979	39–1,067	0.10–0.76	0.00–0.70	0.06–5.45	0.02–3.40

Note: Significant differences between pairwise comparisons of sites were indicated with letters behind the respective mean values.
Abbreviations: T, temperature [°C]; O_2, dissolved oxygen [$mg \cdot L^{-1}$]; pH, pH-value; EC, electric conductance [$\mu S \cdot cm^{-1}$]; Turb, turbidity [NTU]; D, water depth [m]; V, river bed velocity [$m \cdot s^{-1}$]; DG, mean particle diameter [mm]; IR, sediment infiltration rate [$kg \cdot d^{-1}$].

TABLE 2 Univariate comparisons of egg and larval mortality for the three different sites

Test	Test type	Factor levels/pairwise comparison	*p*-value	
			Egg mortality	Larval mortality
Kruskal–Wallis ANOVA	Main test	Site 1 - site 2 - site 3	$p < .0001$	$p < .0001$
Wilcoxon signed-ranks test	Post hoc test	Site 1 - site 2	$p > .05$	$p > .05$
	Post hoc test	Site 1 - site 3	$p < .01$	$p < .01$
	Post hoc test	Site 2 - site 3	$p < .0001$	$p < .0001$

Note: Site 3 = hydropeaking affected site, sites 1 and 2 = non-hydropeaking affected site. Kruskal–Wallis ANOVA df = 2. Wilcoxon-signed ranks post hoc test was Bonferroni corrected for multiple comparisons.

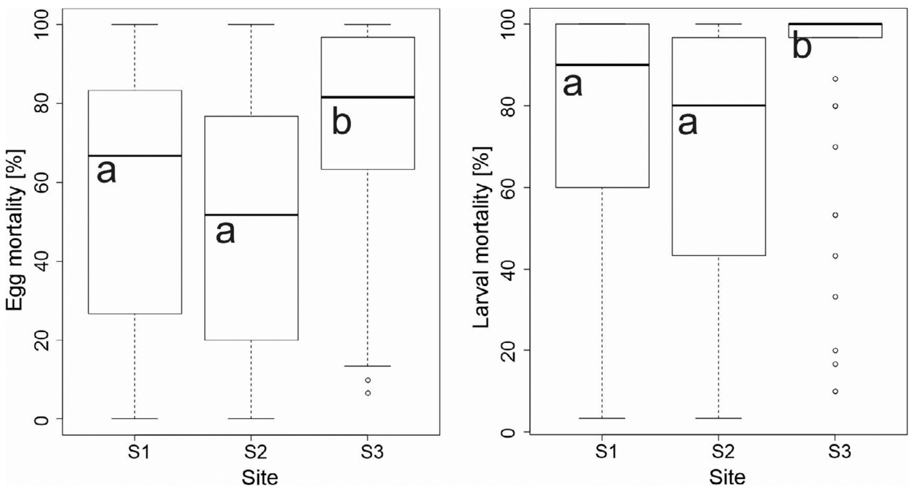

FIGURE 4 Box-whisker-plot (25% quantile, median. 75% quantile, whisker: minimum and maximum values, circles represent outliers) of egg and larval mortality [%] for the three different sites. Letters below the median indicate significant differences between sites

considered as a reference. In the hydropeaking affected site 3, egg and larval mortalities were significantly higher (Figure 4, Table 2), with over 80% egg mortality and almost 100% larval mortality compared to the non-hydropeaking affected sites. Egg and larval mortality in the non-hydropeaking affected site 1 (over 63% egg mortality and 85% larval mortality) and site 2 (55% egg mortality and 80% larval mortality) were not significantly different (Table 2). In site 2, we found the lowest egg and larval mortality of the tested spawning grounds (Figure 4).

Multivariate analyses of brown trout egg and larval mortality (Figure 5 and Table 3) revealed significant differences (ANOSIM global test: R = 0.07, $p < .001$) between reference site 1 and the hydropeaking affected site 3 (ANOSIM: R = 0.06, $p < .01$) as well as between sites 2 and 3 (ANOSIM: R = 0.14, $p < .001$). No significant differences in egg and larval mortality could be found between the non-hydropeaking affected sites 1 and 2 (ANOSIM: R = 0.14, $p > .05$). In addition, significant differences between top and bottom compartments could only be detected in site 3 (ANOSIM: R = 0.07, $p < .05$) with 20.5% higher mortality for eggs and 19.6% for larvae in bottom compartments compared to top compartments (Table 4). Correlating abiotic habitat variables with egg mortality revealed that mortality increased sharply with decreasing oxygen supply in the interstitial zone, with more than 90% egg mortality when oxygen values were below 10 mg·L^{-1} (Figure 6).

3.2 | Abiotic habitat variables at the spawning sites of the OHB

All abiotic habitat variables of sites 1 and 2 differed significantly from those measured in the hydropeaking-affected site 3, except for temperature (Kruskal–Wallis ANOVA $p < .001$ and subsequently applied Wilcoxon signed-ranks post-hoc test, see Table 1). In addition, site 1 differed significantly from site 2 with lower values of electric conductance, depth and current speed (Table 1). However, the differences for some variables between sites concerning electric conductance, pH and turbidity were small and within the range of values required for successful brown trout development. Mean dissolved oxygen values were highest at site 2 (11.79 mg·L^{-1}) and 2 mg·L^{-1} lower at site 3 (Table 1). Mean water depth at site 1 was 0.18 m with a mean flow velocity at the surface of 0.45 m·s^{-1}, whilst site 2 was 0.22 m deep with slightly higher flow velocities at the surface compared to site 1 (0.52 m·s^{-1}). At site 3, water depth changed several times a day and ranged between 0.10 and 0.76 m (daily fluctuations in water level up to 66 cm). The water level change induced by hydropeaking also led to changes in flow velocity and direction at site 3 (Figures 2 and 3). In contrast to site 3, the water level at sites 1 and 2 was rather constant during the day and comprised less water level fluctuations during the investigation period (seasonal fluctuation in site 1 = 15 cm and in site 2 = 12 cm). In sites 1 and 2, the flow

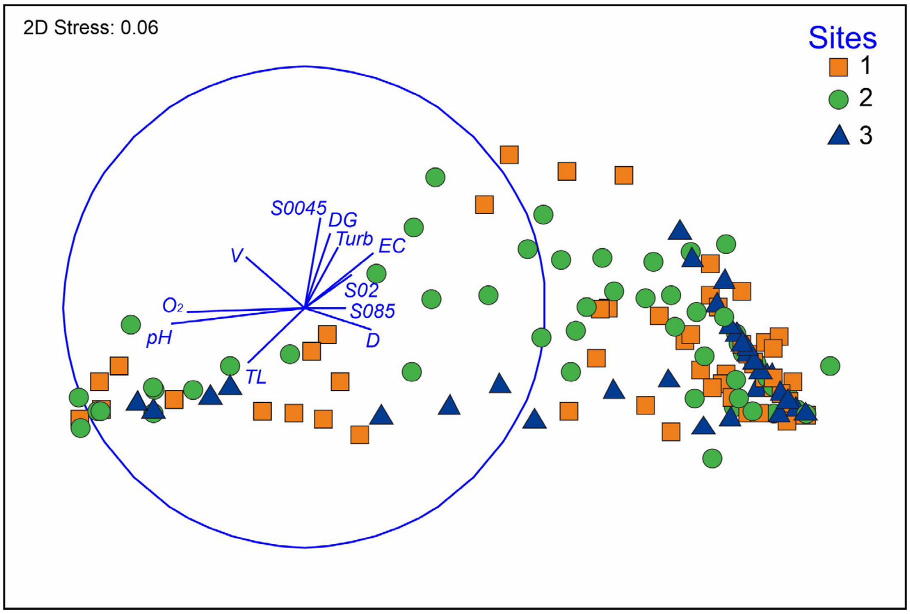

FIGURE 5 Non-metric multidimensional scaling (NMDS) comprising comparisons of egg and larval mortality of the HydroEcoSedimentary Tool (HEST) between the three assessed sites in the Ottheinrichbach. O_2 = dissolved oxygen [mg·L^{-1}], pH = pH-value, TL = temperature data [°C] from loggers exposed in the HEST, D = water depth [m], EC = electric conductance [μS·cm^{-1}] (corrected to 20°C), V = river bed velocity [m·s^{-1}], Turb = turbidity [NTU], DG = mean particle diameter [mm], S0045 = sediment grain size of 0.045 mm, S02 = sediment grain size of 0.20 mm, S085 = sediment grain size of 0.85 mm. Abiotic habitat variables were correlated on the NMDS ordination plot and are displayed as blue lines. The length of the blue lines is proportional to the degree of correlation with the arrangement of egg and larval mortality (the blue circle indicates 100% correlation). 2D-Stress = stress value after Kruskal [Color figure can be viewed at wileyonlinelibrary.com]

TABLE 3 Results of multivariate comparisons of sites with ANOSIM considering T = top compartment as well as B = bottom compartment of the HESTs

Pairwise tests	R-value	*p*-value
Site 1 - site 2	0.011	>.05
Site 1 - site 3	0.059	**<.01**
Site 2 - site 3	0.141	**<.001**
Site 1T - site 2T	−0.003	>.05
Site 1T - site 3T	0.003	>.05
Site 2T - site 3T	0.058	**<.05**
Site 1B - site 2B	0.002	>.05
Site 1B - site 3B	0.119	**<.001**
Site 2B - site 3B	0.255	**<.001**
Site 1B - site 1T	−0.024	>.05
Site 2B - site 2T	−0.022	>.05
Site 3B - site 3T	0.074	**<.01**

Note: Values in bold indicate significant differences between sites or compartments.

direction was always constant and did not change direction. Mean particle diameter was largest at site 2 (2.75 mm) and smallest at site 3 (1.66 mm). Site 2 also comprised the highest infiltration rates (1.12 kg·d^{-1}) of fine sediment, being almost twice as high as at site 3.

TABLE 4 Egg mortality and larval mortality detected in the top and bottom compartments of the HESTs in the three assessed spawning grounds

	Egg mortality [%]		Larval mortality [%]	
	B	T	B	T
Site 1	60.6	56.4	76.4	74.1
	0.0–100.0	0.0–93.3	6.7–100.0	13.3–100.0
Site 2	52.2	46.5	69.6	63.2
	0.0–100.0	3.3–100.0	6.7–100.0	3.3–100.0
Site 3	84.8	64.3	97.9	78.3
	56.7–100.0	6.7–96.7	70.0–100.0	10.0–100.0

Note: Upper layer indicates mean mortality rates for eggs and larvae, respectively, whilst the lower layer indicates minimum and maximum values.

4 | DISCUSSION

Hydropower is a growing source of renewable energy worldwide with negative effects on aquatic habitats and biological communities, particularly fishes (Auer et al., 2017; Bartoň et al., 2021; Casas-Mulet et al., 2016; Grabowski & Isely, 2007; Greimel et al., 2018; Hauer et al., 2017; Moreira et al., 2019; Puffer et al., 2015; Schmutz et al., 2015). An objective evaluation of the “green” and “red” aspects

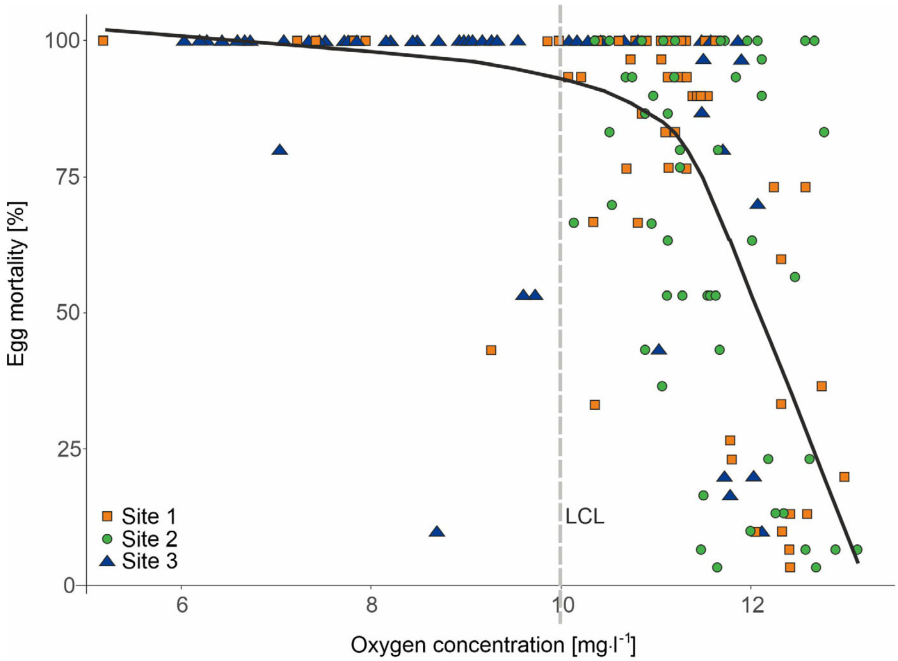

FIGURE 6 Correlation plot of the oxygen concentration measured in the HESTs against egg mortality. The smooth curves are locally weighted regression fits (Cleveland & Devlin, 1988) to the data points. LCL = lower critical limit for egg to fry survival according to Rubin and Glimsäter (1996) reviewed in Smialek, Pander, and Geist (2021) [Color figure can be viewed at wileyonlinelibrary.com]

of hydropower production (Geist, 2021) requires a comprehensive consideration of all effects including those resulting from hydropeaking operation. To the best of our knowledge, this is the first study that describes hydropeaking-induced negative effects to upstream-located tributaries. Specifically, the study illustrates how egg and larval mortalities were increased in hydropeaking impacted spawning grounds compared to those in non-hydropeaking affected sites. Corresponding to the storage duration driven by the hydropeaking operations of the power plant Ingolstadt and the discharge of the Danube, a large backlog (up-ramping) reaching more than 6 km upstream was evident. This backlog can explain the observed change in habitat conditions with discharge flowing back into the OHB and stopping for a certain period of time before running out again. In our dataset, hydropeaking-induced fluctuations in water depth, as also described by Grabowski and Isely (2007), additionally contributed to permanent changes in the hydraulic gradient of site 3. They were strongest during low discharge conditions of the Danube when current directions changed twice a day. Significantly increased water depth, reduced flow velocity and reduced oxygen supply of the HESTs at the hydropeaking affecting site 3, all likely contributed to the reduced hatching rate of eggs and larval survival. The most likely cause of reduced oxygen supply was because, at the peak of the incoming backlog, the current of the river almost completely stops for a certain period impairing the exchange of interstitial water with the open water. Such exchange between open water and interstitial is crucial for oxygen supply and successful egg or larval development (Sternecker, Cowley, & Geist, 2013). It is possible that the stagnant conditions caused by the backlog were responsible for an oxygen deficiency in the interstitial pores, as the subsurface flow was not enough to supply the exposed eggs and larvae with oxygen and to transport the metabolites away. In addition, respiration of organic matter could have led to reduced oxygen availability in the interstitial spaces. At site 3, there was no increased sedimentation of fines detectable compared to site 2 or site 1 where egg and larval development was on average 20%–40% higher. Even though this was not experimentally tested, based on prior literature, we took the assumption that stagnant flow conditions result in an accumulation of a thin layer of the commonly present fines <0.0045 mm on the eggs, hindering oxygen supply and removal of metabolites (Greig, Sear, & Carling, 2005). Once the current started to move outwards again, the fines could have been transported (see Casas-Mulet, Lakhanpal, & Stewardson, 2018) without being detected due to the coarser temporal sampling resolution we obtained from applying the HESTs.

In the present study, it needs to be considered that the hydropeaking regime of the power plant Ingolstadt affected only site 3 and not the other two (sites 1 and 2). However, site 3 represents a crucial access point to suitable habitats of the restored floodplain for key fish species, highlighting the negative effects that hydropeaking can have on such important habitat function. Negative effects on other important habitat functions such as fish migration and accessibility of tributaries is also possible, but was not investigated here.

We acknowledge that this study represents only one season and one hydropeaking affected area, and that, in general, spatial and temporal variability in spawning success can be high. However, this case study helps illustrate that the positive effects of structural river restoration can be limited in highly hydropower-affected environments (Pander & Geist, 2013). If constraints such the one illustrated here in a hydropeaking-imparied tributary cannot be mitigated, restoration success may be lower than expected (Geist & Hawkins, 2016). This is particularly critical for highly specialized riverine fish such as rheophilic salmonids and cyprinids, which are all high on the conservation agenda (Mueller, Bierschenk, Bierschenk, Pander, & Geist, 2020). Such upstream hydropeaking effects can lead to severe bottlenecks in species recruitment, which is a prerequisite for a successful population development, and is an important factor for the functionality of river restoration.

5 | CONCLUSION

To the best of our knowledge, this study is the first to provide evidence on the potential ecological upstream effects of hydropeaking, with a focus on fish habitat quality in tributaries. Spawning grounds can be severely affected by hydropeaking operations carried out in the main river, particularly when these comprise strong water level fluctuations linked to water storage and release phases. The negative effects of hydropeaking in this study were expressed in reduced salmonid hatching rates and larval survival. These could be linked to water level fluctuations causing temporarily increased water depth and reduced current speed at the affected spawning grounds, which may have led to the reduced oxygen availability in the hydropeaking affected site. Accounting for such effects is critical for the survival of gravel-spawning early life stages of many fish species. Particularly for target species of conservation such as rheophilic salmonids and cyprinids, such altered processes can result in reduced population recruitment and need to be considered in the design and implementation of restoration projects.

ACKNOWLEDGEMENTS

We would like to thank Catarina Eirich, Julia Reinbeck and Martin Gauger who contributed to the sampling in the Ottheinrichbach. We are also grateful to all the volunteers and student assistants who helped with the installation and retrieval of the HESTs in the field and later sample processing. We thank the AuenZentrum Neuburg-Ingolstadt for providing water level data, and, in particular to B. Cyffka for coordination of the permissions needed from the landowners. We also would like to thank the water authorities, in particular B. Kuegel from the local water authority, for their kind support of the study. This research was partly funded by the Alexander von Humboldt Foundation through a fellowship awarded to R. C.-M., carried out at TUM. This study was also partly supported by the framework of the project AquaKlif in the bayklif network for investigation of regional climate change funded by the Bavarian State Ministry of Science and the Arts. Open access funding enabled and organized by Projekt DEAL.

Open access funding enabled and organized by Projekt DEAL.

AUTHOR CONTRIBUTIONS

All authors have read and agreed to the published version of the manuscript. Individual contributions are as follows: Conceptualization, Joachim Pander, Roser Casas-Mulet, and Juergen Geist, methodology, Joachim Pander and Roser Casas-Mulet; formal analysis, Joachim Pander; writing—original draft preparation, Joachim Pander and Roser Casas-Mulet; editing and artwork Joachim Pander, review Juergen Geist; project administration, Joachim Pander and Juergen Geist; resources, Juergen Geist, Joachim Pander, and Roser Casas-Mulet; funding acquisition, Juergen Geist and Roser Casas-Mulet.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

ORCID

Joachim Pander https://orcid.org/0000-0002-8322-9374
Roser Casas-Mulet https://orcid.org/0000-0002-7139-8859
Juergen Geist https://orcid.org/0000-0001-7698-3443

REFERENCES

Auer, S., Zeiringer, B., Führer, S., Tonolla, D., & Schmutz, S. (2017). Effects of river bank heterogeneity and time of day on drift and stranding of juvenile European grayling (*Thymallus thymallus* L.) caused by hydropeaking. *Science of the Total Environment*, *575*, 1515–1521. https://doi.org/10.1016/j.scitotenv.2016.10.029

Bartoň, D., Bretón, F., Blabolil, P., Souza, A. T., Vejřík, L., Sajdlová, Z., … Šmejkal, M. (2021). Effects of hydropeaking on the attached eggs of a rheophilic cyprinid species. *Ecohydrology*, *14*(4), e2280. https://doi.org/10.1002/eco.2280

Bondar-Kunze, E., Kasper, V., & Hein, T. (2021). Responses of periphyton communities to abrupt changes in water temperature and velocity, and the relevance of morphology: A mesocosm approach. *Science of the Total Environment*, *768*(145), 200. https://doi.org/10.1016/j.scitotenv.2021.145200

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

Bruder, A., Tonolla, D., Schweizer, S. P., Vollenweider, S., Langhans, S. D., & Wüest, A. (2016). A conceptual framework for hydropeaking mitigation. *Science of the Total Environment*, *568*, 1204–1212. https://doi.org/10.1016/j.scitotenv.2016.05.032

Casas-Mulet, R., Alfredsen, K., Hamududu, B., & Timalsina, N. P. (2015). The effects of hydropeaking on hyporheic interactions based on field experiments. *Hydrological Processes*, *29*(6), 1370–1384. https://doi.org/10.1002/hyp.10264

Casas-Mulet, R., Lakhanpal, G., & Stewardson, M. J. (2018). The relative contribution of near-bed vs. intragravel horizontal transport to fine sediment accumulation processes in river gravel beds. *Geomorphology*, *303*, 299–308. https://doi.org/10.1016/j.geomorph.2017.12.013

Casas-Mulet, R., Pander, J., Prietzel, M., & Geist, J. (2021). The HydroEcoSedimentary tool: An integrated approach to characterise interstitial hydro-sedimentary and associated ecological processes. *River Research and Applications*, *37*(7), 988–1002. https://doi.org/10.1002/rra.3819

Casas-Mulet, R., Saltveit, S. J., & Alfredsen, K. (2015). The survival of Atlantic Salmon (*Salmo salar*) eggs during dewatering in a river subjected to hydropeaking. *River Research and Applications*, *31*(4), 433–446. https://doi.org/10.1002/rra.2827

Casas-Mulet, R., Saltveit, S. J., & Alfredsen, K. T. (2016). Hydrological and thermal effects of hydropeaking on early life stages of salmonids: A modelling approach for implementing mitigation strategies. *Science of the Total Environment*, *573*, 1660–1672. https://doi.org/10.1016/j.scitotenv.2016.09.208

Choi, B., & Choi, S. U. (2018). Impacts of hydropeaking and thermopeaking on the downstream habitat in the Dal River, Korea. *Ecological Informatics*, *43*, 1–11. https://doi.org/10.1016/j.ecoinf.2017.10.016

Clarke, K. R. (1993). Non-parametric multivariate analyses of changes in community structure. *Australian Journal of Ecology*, *18*, 117–143. https://doi.org/10.1111/j.1442-9993.1993.tb00438.x

Clarke, K. R., Gorley, R. N., Somerfield, P. J., & Warwick, R. M. (2014). *Change in marine communities: An approach to statistical analysis and interpretation* (third ed., p. 144). PRIMER-E: Plymouth, UK.

Cleveland, W. S., & Devlin, S. J. (1988). Locally weighted regression: An approach to regression analysis by local fitting. *Journal of the American Statistical Association*, *83*, 596–610. https://doi.org/10.1080/01621459.1988.10478639

Elgueta, A., Górski, K., Thoms, M., Fierro, P., Toledo, B., Manosalva, A., & Habit, E. (2021). Interplay of geomorphology and hydrology drives macroinvertebrate assemblage responses to hydropeaking. *Science of the Total Environment*, *768*(144), 262. https://doi.org/10.1016/j.scitotenv.2020.144262

Fischer, P., & Cyffka, B. (2014). Floodplain restoration on the upper Danube by re-establishingback water dynamics: First results of the hydrological monitoring. *Erdkunde*, *68*, 3–18. https://doi.org/10.3112/erdkunde.2014.01.02

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

Geist, J., & Hawkins, S. J. (2016). Habitat recovery and restoration in aquatic ecosystems: Current progress and future challenges. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *26*(5), 942–962. https://doi.org/10.1002/aqc.2702

Grabowski, T. B., & Isely, J. J. (2007). Effects of flow fluctuations on the spawning habitat of a riverine fish. *Southeastern Naturalist*, *6*(3), 471–478. https://doi.org/10.1656/1528-7092(2007)6[471:EOFFOT]2.0.CO;2

Greig, S. M., Sear, D. A., & Carling, P. A. (2005). The impact of fine sediment accumulation on the survival of incubating salmon progeny: Implications for sediment management. *Science of the Total Environment*, *344*, 241–258. https://doi.org/10.1016/j.scitotenv.2005.02.010

Greimel, F., Schülting, L., Graf, W., Bondar-Kunze, E., Auer, S., Zeiringer, B., & Hauer, C. (2018). *Hydropeaking impacts and mitigation*. Riverine ecosystem management: Science for governing towards a sustainable future. In S. Schmutz & J. Sendzimir (Eds.), *Vienna, Austria, Riverine Ecosystem Management, Aquatic Ecology Series* (Vol. 8, pp. 91–110). Cham, Switzerland: SpringerOpen. https://doi.org/10.1007/978-3-319-73250-3

Hauer, C., Holzapfel, P., Tonolla, D., Habersack, H., & Zolezzi, G. (2019). In situ measurements of fine sediment infiltration (FSI) in gravel-bed rivers with a hydropeaking flow regime. *Earth Surface Processes and Landforms*, *44*(2), 433–448. https://doi.org/10.1002/esp.4505

Hauer, C., Siviglia, A., & Zolezzi, G. (2017). Hydropeaking in regulated rivers–from process understanding to design of mitigation measures. *Science of the Total Environment*, *579*, 22–26. https://doi.org/10.1016/j.scitotenv.2016.11.028

Lehner, B., Czisch, G., & Vassolo, S. (2005). The impact of global change on the hydropower potential of Europe: A model-based analysis. *Energy Policy*, *33*(7), 839–855. https://doi.org/10.1016/j.enpol.2003.10.018

Matthews, W. J. (1986). Fish faunal structure in an Ozark stream: Stability, persistence and a catastrophic flood. *Copeia*, *2*, 388–397. https://doi.org/10.2307/1444997

Moreira, M., Hayes, D. S., Boavida, I., Schletterer, M., Schmutz, S., & Pinheiro, A. (2019). Ecologically-based criteria for hydropeaking mitigation: A review. *Science of the Total Environment*, *657*, 1508–1522. https://doi.org/10.1016/j.scitotenv.2018.12.107

Mueller, M., Bierschenk, A. M., Bierschenk, B. M., Pander, J., & Geist, J. (2020). Effects of multiple stressors on the distribution of fish communities in 203 headwater streams of Rhine, Elbe and Danube. *Science of the Total Environment*, *703*(134), 523. https://doi.org/10.1016/j.scitotenv.2019.134523

Mueller, M., Pander, J., & Geist, J. (2011). The effects of weirs on structural stream habitat and biological communities. *Journal of Applied Ecology*, *48*(6), 1450–1461. https://doi.org/10.1111/J.1365-2664.2011.02035.X

Naus, C. J., & Reid Adams, S. (2018). Fish nursery habitat function of the main channel, floodplain tributaries and oxbow lakes of a medium-sized river. *Ecology of Freshwater Fish*, *27*(1), 4–18. https://doi.org/10.1111/eff.12319

Pander, J., & Geist, J. (2010). Salmonid-egg floating boxes as bioindication for riverine water quality and stocking success. *Journal of Fish Biology*, *76*(10), 2584–2590. https://doi.org/10.1111/j.1095-8649.2010.02645.x

Pander, J., & Geist, J. (2013). Ecological indicators for stream restoration success. *Ecological Indicators*, *30*, 106–118. https://doi.org/10.1016/j.ecolind.2013.01.039

Pander, J., Knott, J., Mueller, M., & Geist, J. (2019). Effects of environmental flows in a restored floodplain system on the community composition of fish, macroinvertebrates and macrophytes. *Ecological Engineering*, *132*, 75–86. https://doi.org/10.1016/j.ecoleng.2019.04.003

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

Pander, J., Mueller, M., & Geist, J. (2015b). Succession of fish diversity after reconnecting a large floodplain to the upper Danube River. *Ecological Engineering*, *75*, 41–50. https://doi.org/10.1016/j.ecoleng.2014.11.011

Pander, J., Mueller, M., & Geist, J. (2018). Habitat diversity and connectivity govern the conservation value of restored aquatic floodplain habitats. *Biological Conservation*, *217*, 1–10. https://doi.org/10.1016/j.biocon.2017.10.024

Pander, J., Mueller, M., Knott, J., Egg, L., & Geist, J. (2017). Is it Worth the Money? The Functionality of Engineered Shallow Stream Banks as Habitat for Juvenile Fishes in Heavily Modified Water Bodies. *River Research and Applications*, *33*, 63–72. https://doi.org/10.1002/rra.3065

Pander, J., Schnell, J., Sternecker, K., & Geist, J. (2009). The "egg sandwich": A method for linking spatially resolved salmonid hatching rates with habitat variables in stream ecosystems. *Journal of Fish Biology*, *74*, 683–690. https://doi.org/10.1111/j.1095-8649.2008.02145.x

Pracheil, B. M., Pegg, M. A., & Mestl, G. E. (2009). Tributaries influence recruitment of fish in large rivers. *Ecology of Freshwater Fish*, *18*(4), 603–609. https://doi.org/10.1111/j.1600-0633.2009.00376.x

Puffer, M., Berg, O. K., Huusko, A., Vehanen, T., Forseth, T., & Einum, S. (2015). Seasonal effects of hydropeaking on growth, energetics and movement of juvenile Atlantic salmon (*Salmo salar*). *River Research and Applications*, *31*(9), 1101–1108. https://doi.org/10.1002/rra.2801

R Core Team. (2020). *R: A language and environment for statistical computing. R foundation for statistical computing*. Vienna, Austria: RFS Computing. http://www.r-project.org/index.html (last accessed on 27. July 2021)

Rubin, J.-F., & Glimsäter, C. (1996). Egg-to-fry survival of the sea trout in some streams of Gotland. *Journal of Fish Biology*, *48*, 585–606. https://doi.org/10.1111/j.1095-8649.1996.tb01454.x

Salmaso, F., Servanzi, L., Crosa, G., Quadroni, S., & Espa, P. (2021). Assessing the impacts of hydropeaking on river benthic macroinvertebrates: A state-of-the-art methodological overview. *Environments*, *8*(7), 67. https://doi.org/10.3390/environments8070067

Sari, M. A., Badruzzaman, M., Cherchi, C., Swindle, M., Ajami, N., & Jacangelo, J. G. (2018). Recent innovations and trends in in-conduit hydropower technologies and their applications in water distribution systems. *Journal of Environmental Management*, *228*, 416–428. https://doi.org/10.1016/j.jenvman.2018.08.078

Schmutz, S., Bakken, T. H., Friedrich, T., Greimel, F., Harby, A., Jungwirth, M., … Zeiringer, B. (2015). Response of fish communities to hydrological and morphological alterations in hydropeaking rivers of Austria. *River Research and Applications*, *31*(8), 919–930. https://doi.org/10.1002/rra.2795

Smialek, N., Pander, J., & Geist, J. (2021). Environmental threats and conservation implications for Atlantic salmon and brown trout during their critical freshwater phases of spawning, egg development and juvenile emergence. *Fisheries Management and Ecology*, *28*, 437–467. https://doi.org/10.1111/fme.12507

Smokorowski, K. E. (2021). The ups and downs of hydropeaking: A Canadian perspective on the need for, and ecological costs of, peaking hydropower production. *Hydrobiologia*, *849*, 1–21. https://doi.org/10.1007/s10750-020-04480-y

Stammel, B., Cyffka, B., Geist, J., Müller, M., Pander, J., Blasch, G., … Weißbrod, M. (2012). Floodplain restoration on the upper Danube (Germany) by re-establishing water and sediment dynamics: A scientific monitoring as part of the implementation. *River Research and Applications*, *20*, 55–70. https://doi.org/10.1127/1868-5749/2011/020-0033

Stammel, B., Fischer, P., Gelhaus, M., & Cyffka, B. (2016). Restoration of ecosystem functions and efficiency control: Case study of the Danube floodplain between Neuburg and Ingolstadt (Bavaria/Germany). *Environmental Earth Science*, *75*, 1–14. https://doi.org/10.1007/s12665-016-5973-y

Sternecker, K., Cowley, D. E., & Geist, J. (2013). Factors influencing the success of salmonid egg development in river substratum. *Ecology of Freshwater Fish*, *22*(2), 322–333. https://doi.org/10.1111/eff.12020

Venus, T. E., Smialek, N., Pander, J., Harby, A., & Geist, J. (2020). Evaluating cost trade-offs between hydropower and fish passage mitigation. *Sustainability*, *12*(20), 8520. https://doi.org/10.3390/su12208520

Wagner, B., Hauer, C., & Habersack, H. (2019). Current hydropower developments in Europe. *Current Opinion in Environmental Sustainability*, *37*, 41–49. https://doi.org/10.1016/j.cosust.2019.06.002

Zarfl, C., Lumsdon, A. E., Berlekamp, J., Tydecks, L., & Tockner, K. (2015). A global boom in hydropower dam construction. *Aquatic Sciences*, *77*(1), 161–170. https://doi.org/10.1007/s00027-014-0377-0

How to cite this article: Pander, J., Casas-Mulet, R., & Geist, J. (2023). Hydropeaking impairs upstream salmonid spawning habitats in a restored Danube tributary. *River Research and Applications*, *39*(3), 389–400. https://doi.org/10.1002/rra.3953