

**RESEARCH ARTICLE**

WILEY

# Making up the bed: Gravel cleaning as a contribution to nase (*Chondrostoma nasus* L.) spawning and recruitment success

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**Funding information**

VERBUND Innkraftwerke GmbH, Grant/Award Number: N/A

**Abstract**

1. Spawning substrate quality is a major factor influencing the early ontogeny of European nase (*Chondrostoma nasus*), a target species of conservation.
2. Analogous to findings from salmonids, restoration of spawning grounds was hypothesized to enhance spawning, development and thus recruitment success of nase, by improving the substrate quality, and subsequently spawning site use, egg infiltration and protection of larvae in the interstitial zones before emergence. These assumptions were tested using a comparative approach by cleaning 50% of the area of each spawning ground in two Bavarian rivers.
3. Substrate cleaning resulted in an immediate reduction of ~70% fine sediment content with improvements still detectable 2 months later. Spawning nase used the restored areas of spawning grounds preferentially, which was evident in the number of spawning fish and the significantly higher number of eggs laid.
4. Infiltration of eggs into the interstitial zone was distinctly more successful in the opened interstices of the cleaned spawning substrate, where they were found down to a depth of 20 cm. The same was true for larvae, which could be found down to 30 cm and up to 13 days after hatching. Moreover, higher peaks in the drift density of emerging larvae from the restored spawning substrate were detected (2.5 compared with 1.7 larvae  $m^{-3}$  discharge for the River Mangfall and 0.3 compared with 0.03 larvae  $m^{-3}$  for the River Sims).
5. These results clearly indicate that gravel cleaning is a successful short-term restoration tool for nase spawning grounds. It is a quick, cheap and effective method for the conservation management of nase, which may also be applicable to other riverine species with a similar ecology and incubation time, such as *Barbus barbus*, *Squalius cephalus*, *Leuciscus leuciscus* and *Phoxinus phoxinus*. This especially holds true if streams lack internal dynamics and suffer from high loads of fine sediment and colmation.

**KEYWORDS**

early-life stages, fine sediment, fish larvae, freshwater fish conservation, lithophilic cyprinids, river restoration, spawning ground

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## 1 | INTRODUCTION

Habitat quality is a major factor in the survival of fish populations (Lapointe et al., 2013) and its widespread degradation has been identified as the main cause for the slow recovery of fish fauna in large rivers in Europe (Aarts, Van den Brink, & Nienhuis, 2004). This is primarily evident in the functionality of gravel banks used as spawning grounds by lithophilic fish species, which is often reduced owing to fine sediment infiltration from erosion by land use and animal activity (e.g. livestock, crayfish burrowing; Davies, Biggs, Williams, & Thompson, 2009) or restricted internal stream sediment dynamics (Auerswald & Geist, 2018). Excessive amounts of fine sediment introduction into the stream bed cause adverse effects by physically clogging substrate porosity (Geist & Auerswald, 2007) and through biogeochemical processes owing to the reduced oxygen supply (Greig, Sear, & Carling, 2005; Sear et al., 2017), which ultimately affect egg survival, hatching and the emergence of larvae (Jensen, Steel, Fullerton, & Pess, 2009; Kemp, Sear, Collins, Naden, & Jones, 2011; Sternecker & Geist, 2010). Consequently, the reproductive success of lithophilic fish species is often impaired. Synergistic effects between fine-sediment ingress and increased temperature explain greater susceptibilities of spring-spawning species compared with winter spawners (water temperature-related processes; Sternecker, Denic, & Geist, 2014).

To date, studies analysing substrate-related effects and stream-bed restoration success on egg and larval survival have mainly focused on economically important salmonids (Kondolf, 2000; Phillips, Lantz, Claire, & Moring, 1975; Pulg, Barlaup, Sternecker, Trepl, & Unfer, 2013; Soulsby, Youngson, Moir, & Malcolm, 2001; Sternecker, Cowley, & Geist, 2013). Surprisingly, this topic has rarely been considered in lithophilic cyprinids, which also comprise species such as nase, barbel (*Barbus barbus* L.), chub (*Squalius cephalus* L.), dace (*Leuciscus leuciscus* L.) and common minnow (*Phoxinus phoxinus* L.), that have declined in recent decades, especially in Bavaria, Germany (Mueller, Pander, & Geist, 2018; Pander & Geist, 2018). From this group, the European nase (subsequently referred to as 'nase') is threatened throughout its entire native distribution area (Peñáz, 1996), ranging from Central Europe north of the Alps to Eastern Europe in the basins of the Black Sea, southern Baltic Sea and southern North Sea (Kottelat & Freyhof, 2007). Although *Chondrostoma nasus* does not receive any special conservation recognition in the European Habitats Directive (Council of the European Communities, 1992), five other species of the genus *Chondrostoma* are listed in Annex II, requiring Member States to designate special areas of conservation for important sites where these species occur. However, severe declines of nase have occurred locally, which is evident in Bavaria where nase is listed as 'endangered' according to the Red List (Bohl, Kleisinger, & Leuner, 2003).

Owing to its complex life cycle, which depends on the availability, quality and connectivity of various habitats for the different life stages, nase populations are threatened by river damming and channelization and the related consequences of blocked migration routes and degraded habitats, especially spawning grounds

(Ovidio & Philippart, 2008; Peñáz, 1996). Therefore, nase has become a target species for conservation in Central European rivers (Schiemer, Keckeis, & Kamler, 2002). Successful spawning of nase is divided into four crucial steps. First, spawning grounds need to be accessible. Nase is known to be a potamodromus species, aggregating in dense swarms to migrate in spawning runs from rivers to tributaries (De Leeuw & Winter, 2008; Melcher & Schmutz, 2010; Rakowitz, Berger, Kubecka, & Keckeis, 2008). Consequently, river damming often hinders the accessibility of functional spawning grounds (Aarts et al., 2004). Second, hydromorphological conditions at spawning grounds need to meet their spawning habitat requirements. Nase prefer shallow riffles with fast currents for egg deposition (e.g. Melcher & Schmutz, 2010), requiring stable conditions throughout the period of egg incubation (Hauer, Unfer, Schmutz, & Habersack, 2007). In addition, these riffles need to be in the immediate vicinity of pools as, apart from the spawning event itself, nase show a spatial separation of sexes during the days of spawning, with females resting in the pools while males maintain position on the spawning grounds (Peñáz, 1996). Third, after spawning, eggs need to develop successfully on the spawning grounds. Recent findings suggest that most eggs develop under the gravel surface in the interstitial zone (Duerregger et al., 2018), providing a protected environment. In contrast, deposition of eggs on the gravel surface exposes them to predation and uncontrolled drift (Keckeis, Bauer-Nemschkal, & Kamler, 1996; Persat & Olivier, 1995). Finally, hatched larvae need to emerge successfully from spawning gravel, so infiltration of fines into the stream bed during early ontogeny can reduce emergence success and affect subtle endpoints, such as larval size at emergence (Nagel, Pander, Mueller, & Geist, 2020).

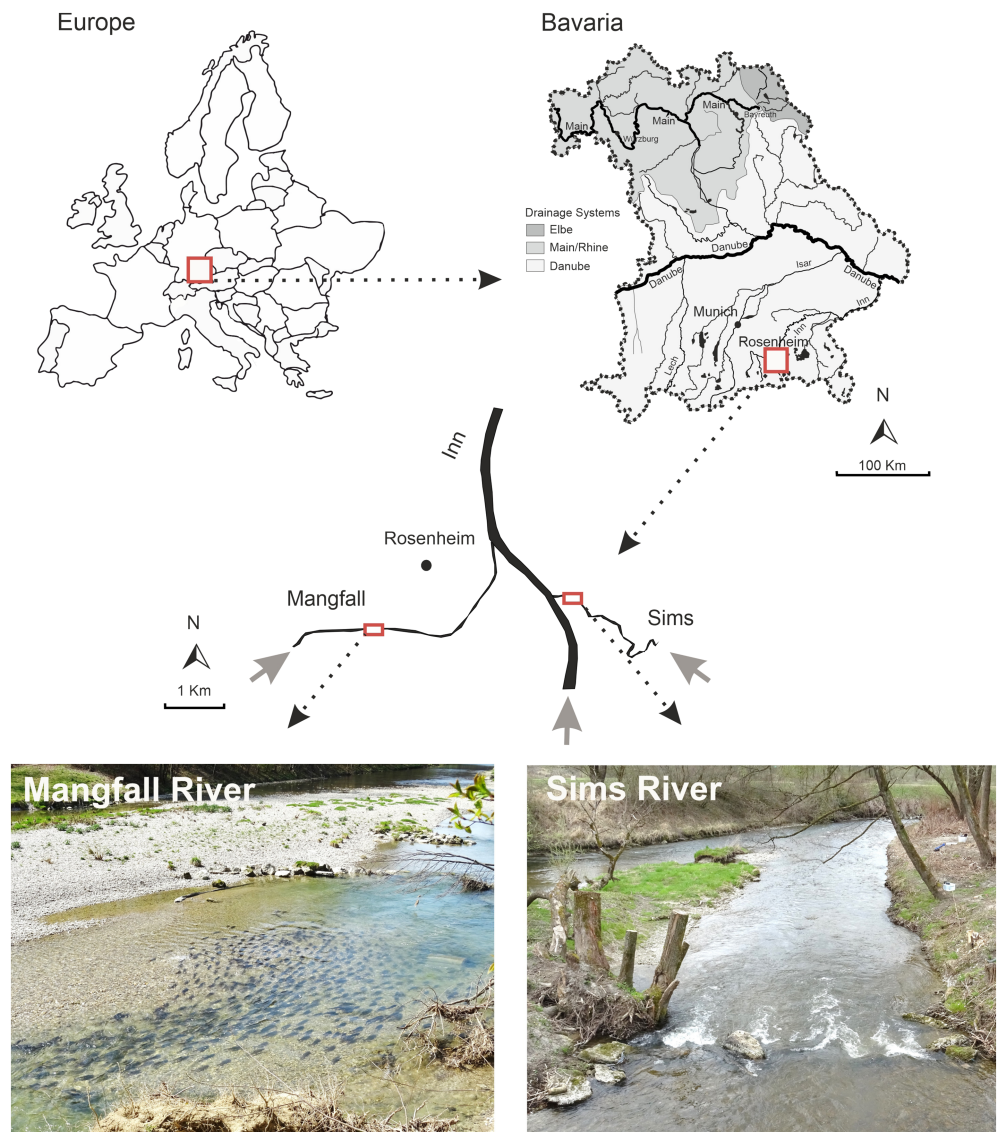
Measurements to improve spawning success by restoration of spawning grounds have been widely discussed in the scientific literature (Taylor et al., 2019) and are used to support fish populations by many organizations such as local fishing associations and regulatory authorities. Primary target species mostly comprise salmonids such as brown trout (*Salmo trutta* L.; Pulg et al., 2013; Sternecker, Wild, & Geist, 2013; Zeh & Dönni, 1994), European grayling (*Thymallus thymallus* L.; Zeh & Dönni, 1994) and salmon (Cramer, 2012; Mih & Bailey, 1981). Implemented and recommended measures for restoration include cleaning of colmated gravel, e.g. using an excavator (Pander, Mueller, & Geist, 2015; Pulg et al., 2013) or jetting lance (Bašić, Britton, Rice, & Pledger, 2017) and addition of gravel of various size classes (e.g. Barlaup, Gabrielsen, Skoglund, & Wiers, 2008; Cramer, 2012; Pander et al., 2015) as well as structural improvements of the stream bed using current deflectors or boulders (Gore, Crawford, & Addison, 1998; Gortz, 1998; Pander et al., 2015). To date, little is known on whether the results from these studies are also applicable to lithophilic cyprinids. Therefore, there is a great need to extend knowledge on the interaction of spawning substrate and reproduction success to those species, as an increasing number of studies, mainly conducted under laboratory conditions, have demonstrated the effects of spawning substrate composition on the early life

stages of these species, e.g. on the interstitial movement (Vilizzi & Copp, 2013) and emergence timing (Bašić, Britton, Rice, & Pledger, 2018) of European barbel, as well as hatching and emergence success of nase (Duerregger et al., 2018; Nagel et al., 2020). Moreover, as the success of stream-bed restoration in salmonids is often limited by the short duration of the effects (Mueller, Pander, & Geist, 2014), these measures may be more effective for cyprinid species with a shorter egg incubation period. Consequently, the aim of this study was to test how the restoration of nase spawning grounds influences (i) the fine sediment content of spawning substrates, (ii) spawning site use, (iii) infiltration of eggs and larvae into the interstitial zone and (iv) development and timing of emergence, as measured by the numbers and size of downstream drifting larvae. Specifically, we hypothesized that restoring the spawning grounds will result in a reduced fine sediment content in the spawning substrates, increased habitat use by the spawners and a greater depth range of eggs and larvae within the interstitial zone and subsequent differences in their development and timing of emergence.

## 2 | METHODS

### 2.1 | Study area

To test for the effects of substrate cleaning on the reproduction and recruitment of nase, two spawning areas with well-known morphology (see Duerregger et al., 2018) in the River Mangfall ( $12^{\circ}6'23.52''$  E;  $47^{\circ}50'46.66''$  N) and the River Sims ( $12^{\circ}9'1.02''$  E;  $47^{\circ}51'4.20''$  N) – two tributaries of the River Inn in Bavaria (Germany) – were chosen for investigation (Figure 1). These sites are among the most important known spawning grounds in the entire catchment area of the River Inn according to observations on the size of spawning populations in previous years. The Mangfall has a river length of 58 km, draining a catchment area of 1,099 km<sup>2</sup> before it discharges into the River Inn at about 3.3 km downstream of the investigated spawning ground. The mean annual flow of the Mangfall is 17.6 m<sup>3</sup> s<sup>-1</sup>, but as the investigated spawning ground is located in a diverted river section, discharge at this site is relatively stable at 1.5 m<sup>3</sup> s<sup>-1</sup> throughout the year ([www.hnd-bayern.de](http://www.hnd-bayern.de)). The Mangfall is



**FIGURE 1** Map and photographs of the study area; grey arrows indicate flow direction. Note the spawning nase on the photograph of the River Mangfall

assigned as a 'heavily modified water body' with a moderate to poor ecological potential ([www.umweltatlas.bayern.de](http://www.umweltatlas.bayern.de)) according to the European Water Framework Directive (Council of the European Communities, 2000). The Sims has a river length of 8 km, draining a catchment area of 94 km<sup>2</sup>. Directly downstream of the investigated spawning ground, the Sims meets the River Rohrdorfer Ache before it also discharges into the River Inn. Mean annual flow of the Sims is at 1.89 m<sup>3</sup> s<sup>-1</sup> ([www.hnd-bayern.de](http://www.hnd-bayern.de)). The ecological status for the Sims is assessed as 'moderate' ([www.umweltatlas.bayern.de](http://www.umweltatlas.bayern.de)). In both rivers, their hydromorphological dynamics are restricted owing to controlled discharge by weirs located upstream of the spawning grounds, resulting in fine sediment (<0.85 mm) contents above 10%.

## 2.2 | Abiotic measurements

Hydromorphological conditions in the spawning grounds were characterized by measuring water depth (cm) and current velocity (m s<sup>-1</sup>) 10 cm above the substrate and 10 cm below the water surface in close proximity to each spawning box (see Section 2.5) on the day of installation. Importantly, no significant differences in the restored and the untreated site of each spawning ground were detected (Table 1). At the same points redox potential (mV) at 10 cm substrate depth was measured *in situ*, as described by Geist and Auerswald (2007) 6 days after the first spawning event using a hand-held pH 3110 meter (WTW, Weilheim, Germany). Measurements were also made of oxygen concentration (mg L<sup>-1</sup>), pH, electric conductance (μS cm<sup>-1</sup>) (with a hand-held Multi 3430; WTW, Weilheim, Germany) as well as turbidity (NTU) (using a hand-held PhotoFlex Turb equipment; WTW, Weilheim, Germany) each time drift nets were placed. Temperature was measured hourly using data loggers in each river (Lascar Electronics Ltd; [www.lascarelectronics.com](http://www.lascarelectronics.com)). These data were used to calculate degree-days (dd), by multiplying the mean daily water temperature with the days of incubation.

## 2.3 | Fine sediment content of spawning substrate

Initial substrate quality was assessed with three freeze-cores at each site before restoration. At this time, fine sediment content (<0.85 mm) of spawning substrates was similar in both halves of the spawning grounds in the River Mangfall (treatment site, 12.2 ± 2.7%; control site, 10.9 ± 1.0%) and in the River Sims (treatment site, 10.1 ± 1.0%; control site, 9.2 ± 1.3%). Another three freeze-cores at each site were taken 1 day after the restoration to account for changes in the substrate composition related to restoration. Subsequently, this sampling procedure was repeated ~40 and ~60 days after the restoration. Sediment samples from freeze-cores were wet-sieved in the fractions of >20–63, >6.3–20, >2.0–6.3, >0.85–2.0 and ≤0.85 mm using an electronic sieving-tower (Fritsch, Idar-Oberstein, Germany). Afterwards, discrete fractions were dried and weighed to determine percentages by mass.

## 2.4 | Restoration of spawning grounds

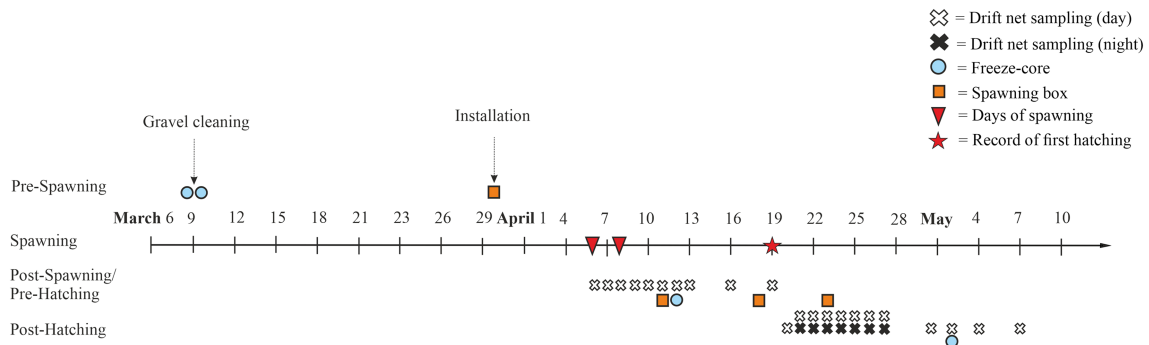
Substrate restoration took place at the beginning of March, 5 weeks before the expected spawning runs of nase (Figure 2), as other studies showed that gravel cleaning is only effective for short periods if streams transport high loads of fine sediment (Meyer, Niepagenkemper, Molls, & Spaenhoff, 2008; Pander et al., 2015). Spawning grounds were divided lengthways into two parts of equal size, in which only one part was randomly selected for restoration while the other was left untreated to serve as a reference for naturally occurring conditions (Figure 3). This resulted in four investigated sites in total: Mangfall restored, Mangfall untreated, Sims restored and Sims untreated. Subsequently, the substrate of one half of each spawning ground was loosened and cleaned down to a depth of 50 cm by an excavator following the approach of Pulg et al. (2013) and Sternecker, Wild, and Geist (2013).

**TABLE 1** Abiotic parameters of the investigated spawning grounds

	Mangfall		Sims	
	Restored	Untreated	Restored	Untreated
Flow velocity surface (m s <sup>-1</sup> )	1.0 ± 0.2 <sup>a</sup>	0.9 ± 0.3 <sup>a</sup>	1.0 ± 0.1 <sup>a</sup>	0.9 ± 0.1 <sup>a</sup>
Flow velocity stream bed (m s <sup>-1</sup> )	1.0 ± 0.1 <sup>a</sup>	1.0 ± 0.3 <sup>a</sup>	0.5 ± 0.1 <sup>b</sup>	0.5 ± 0.1 <sup>b</sup>
Water depth (cm)	30.2 ± 3.4 <sup>a</sup>	27.9 ± 3.4 <sup>a</sup>	47.1 ± 5.2 <sup>b</sup>	42.9 ± 3.4 <sup>b</sup>
Redox potential interstitial (mV)	473 ± 24 <sup>ab</sup>	478 ± 16 <sup>a</sup>	467 ± 10 <sup>ab</sup>	447 ± 19 <sup>b</sup>
O <sub>2</sub> (mg L <sup>-1</sup> )	11.2 ± 1.0 <sup>a</sup>		10.1 ± 1.0 <sup>b</sup>	
pH	8.6 ± 0.2 <sup>a</sup>		8.8 ± 0.2 <sup>a</sup>	
Electric conductance (μS cm <sup>-1</sup> )	485 ± 43 <sup>a</sup>		453 ± 30 <sup>b</sup>	
Water temperature (°C)	13.3 ± 3.0 <sup>a</sup>		13.7 ± 3.2 <sup>a</sup>	
Turbidity (NTU)	1.7 ± 0.6 <sup>a</sup>		6.9 ± 2.4 <sup>b</sup>	

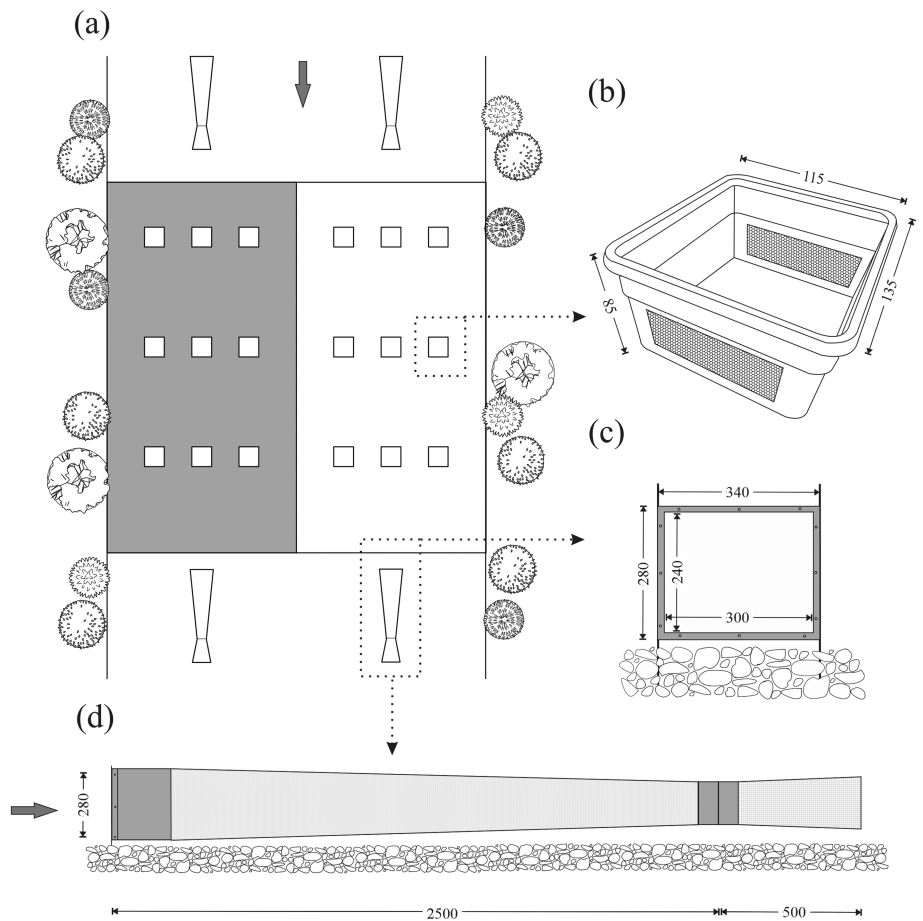
Note: Values are given as means ± SD. Lower case letters indicate statistical differences between the restored and untreated sites of the spawning grounds in both rivers (regarding flow velocity, water depth and interstitial redox) and the water physico-chemistry of the two investigated rivers respectively.





**FIGURE 2** An example of the timeline of the experimental setup in the River Mangfall

**FIGURE 3** Schematic overview of the experimental setup on investigated spawning grounds (a). The grey part refers to the untreated site and the white part to the restored one. Squares show the positioning of the spawning boxes (b); trapeze-shaped symbols show the position of the drift nets (c and d). Dimensions are given in millimetres. Grey arrows indicate flow direction



### 2.5 | Spawning site use

To evaluate substrate-related preferences in the use of spawning sites visual observations were conducted on the days of spawning counting the numbers of spawners per area. In addition, to quantify the number of eggs deposited immediately after spawning, as well as to estimate the decrease in the number of eggs at nase spawning grounds over incubation time, plastic boxes ('spawning boxes'; 16.5 cm x 14.5 cm x 8.5 cm, ROTHO clear boxes, ROTHO Kunststoff AG, Würenlingen, Switzerland) were used (Figure 3). Spawning boxes were comparable with those used in Duerregger et al. (2018), but of

smaller size to limit the disturbance of the interstitial to a minimum. One week before the expected spawning event, determined by gathering nase in further downstream areas, nine spawning boxes were equally distributed in each half of the spawning grounds, resulting in a total of 36 spawning boxes (Figures 2 and 3). Spawning boxes were retrieved every 5–7 days after spawning by randomly removing three boxes from the restored site in the spawning grounds and three boxes with corresponding positions from the untreated sites (Figure 2). Larvae had already started hatching by the scheduled date for the third retrieving interval, which is why only six out of nine boxes were assessed per treatment and river.

## 2.6 | Infiltration of eggs and larvae into the interstitial zone

To quantify the horizontal distribution of eggs in the interstitial zone, three 30 cm deep freeze-cores equally distributed from downstream to upstream in each half of the spawning grounds were taken 6 days after spawning. Subsequently, freeze-cores were defrosted in layers of 10 cm and separately checked for eggs. The same method was applied 26 days after the first spawning event to check for remaining larvae in the interstitial zone. Sediment samples from freeze-cores were also used to evaluate changes in the substrate composition.

## 2.7 | Development and timing of emergence

To evaluate the number of eggs that were not capable of entering the interstices of the stream bed, drift nets located downstream and upstream of each half of the spawning grounds were used, the latter to check for potential bias from spawning activity upstream of the investigated sites (Figure 3). Sampling devices were constructed using rectangular aluminium frames for the mouth (30 × 24 cm) and tear-proof polyester (mesh size ~800 µm) for the nets. The same method was applied to measure the timing of emerging larvae after spawning. To determine the amount of water filtered by every sampling device, flow velocity was measured six times in each frame (three at the upper end and three at the lower end) using an electromagnetic flow meter (Ott MF pro, Ott, Kempton, Germany) each time drift nets were set. Drift-net sampling started the day on which nase arrived at the spawning grounds and was continued on the following days for 1 h each day in the period from 12.00 to 17.00 (Figure 2). Two days after the first hatched larvae were caught, drift-net sampling was additionally conducted in the hour between dusk and darkness (20:30–21:30) to check for light-dependent emergence patterns of larvae, as results of Persat and Olivier (1995) demonstrated that drift of nase larvae under experimental conditions is highest in the 2 h after dusk. This sampling schedule was maintained for 1 week and then changed back to only daylight sampling for one more week (Figure 2). Collected larvae were then preserved in 96% ethanol to determine total length (±0.1 mm) of all morphologically intact larvae using a stereo-microscope Olympus SZX10 (Olympus Deutschland GmbH, Hamburg, Germany) with a magnification of 6.3 and the cellSens-Software (Olympus Corporation; www.olympus-lifescience.com).

## 2.8 | Data analysis

To compare abiotic conditions on spawning grounds, Shapiro-Wilk and Levene tests were applied to check for normal distribution and homogeneity of variances prior to statistical significance tests. Where the analysed data did not follow a normal distribution or homogeneity of variances, differences were tested with unpaired

two-sample Wilcoxon tests (Wilcoxon rank sum test) for the comparison of two groups and with Kruskal–Wallis tests and post-hoc Mann–Whitney U tests for the comparison of more than two groups. As the data structure of the interstitial redox potential followed a normal distribution, significant differences were tested with ANOVA and *post-hoc* Tukey tests.

To quantify the fine sediment content of spawning substrate, cumulative texture lines were computed. In addition, arithmetic means (± standard deviation) were calculated for the fine sediment content of each investigated site at each date of sampling. Preferences in spawning-site use were tested with each spatially independent spawning box as a replicate (Table S1). As these data did not follow a normal distribution and homogeneity of variances, differences in the egg count were tested for each river separately with Kruskal–Wallis tests. To assess the infiltration of eggs and larvae into the interstitial zone, the numbers of eggs and larvae in each substrate horizon are presented as arithmetic means (± standard deviation). This holds true for all values given in this study unless stated otherwise.

Drift densities (number of eggs or larvae caught in 1 m<sup>3</sup> of filtered water) were calculated separately for each drift sampling device. In some drift samples from the River Sims, nase eggs and larvae were also found in the reference nets located upstream of the spawning ground. In this case, drift densities from reference nets were subtracted from drift densities downstream of the investigated spawning ground. Differences in the density of drifting eggs and larvae were tested for each river separately using linear mixed effect models (LMMs) with the function 'lmer' in the package 'lme4' in R (R Core Team, 2017). First, the response variable 'egg drift density' was linked to the fixed factor 'treatment' only. Second, to account also for daylight-depending patterns in the emergence of larvae, the response variable 'larval drift density' was linked to fixed factors 'treatment' and 'daylight' (day or night sampling). In all models sampling date (days after first spawning for eggs, days after first hatching for larvae) was set as a random effect to account for temporal correlation between measurements.

Linear mixed effect models were also used to test for significant effects of treatment, river and daylight on the size of emerging larvae, as model assumptions regarding normal distribution of model residuals and homogeneity of variances were met (Table S1). To account also for the interaction effects of treatment and river a second model was computed, in which the response variable 'larval length at emergence' was additionally linked to the interaction terms of these predictors. For both models, sampling date (days after first hatching) was set as a random effect. Model fit was assessed using standard graphical validation for LMMs in R (Zuur, Ieno, Walker, Saveliev, & Smith, 2009). The significance of effects was tested using a Wald  $\chi^2$  test in the R 'car' package (Fox & Weisberg, 2011).

Distribution of larval length over time was visualized in weighted scatter plots using the function 'geom\_count' from the package 'ggplot2' in R (R Core Team, 2017). All statistical analyses were performed using R (version 3.5.1, R Core Team, 2017). Significance levels were set to  $P < 0.05$  for all statistical analysis.

### 3 | RESULTS

#### 3.1 | Fine sediment content of spawning substrate

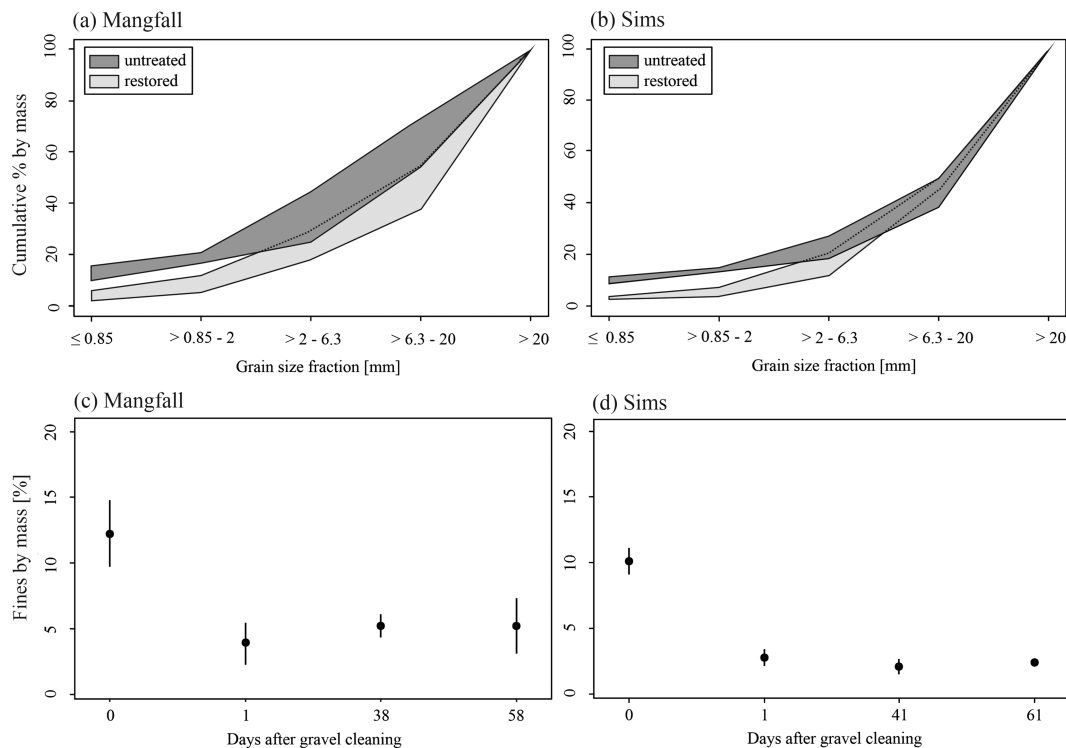
Freeze-core samples taken before and one day after the restoration revealed an immediate reduction of fines (<0.85 mm) from 12.2 ( $\pm$  2.6)% (w/w) to 3.6 ( $\pm$  1.6)% in the River Mangfall (Figure 4a,c) and from 10.1 ( $\pm$  1.0)% to 2.7 ( $\pm$  0.6)% in the River Sims (Figure 4b, d). Freeze-core samples taken  $\sim$ 40 days after gravel cleaning showed a further decline of fines in the River Sims (2.1  $\pm$  0.6%; Figure 4b), possibly owing to self-cleaning effects of the loose gravel, which has previously been reported in a study by Sternecker, Wild, and Geist (2013) analysing the effects of substrate restoration on spawning grounds of brown trout. Freeze-cores taken another 20 days later indicated that the substrate cleaning was still effective, as only marginal increases in fine sediment content (Mangfall, 5.1  $\pm$  2.1%; Sims, 2.4  $\pm$  0.3%) could be detected (Figure 4c, d).

#### 3.2 | Spawning site use

In the River Mangfall, spawning of nase occurred on 6 and 8 April 2018. When spawning began, the water temperature was at 10.3°C and discharge at 1.5 m<sup>3</sup> s<sup>-1</sup> (www.hnd-bayern.de; Water Authority Rosenheim, pers. comm., May 2018). In the River Sims, spawning

occurred on 9 and 10 April 2018, at a water temperature of 11.3°C and a discharge of 1.47 m<sup>3</sup> s<sup>-1</sup> (www.hnd-bayern.de).

Visual observations in the River Mangfall (conducted on 8 April 2018) recorded 281 spawning nase on the spawning ground, from which 148 individuals (53%) were counted within the restored site (density = 2.4 fish m<sup>-2</sup>) and 133 within the untreated one (density = 2.1 fish m<sup>-2</sup>). This observation was much more pronounced in the River Sims, where visual observations (conducted on 9 April 2018) counted 180 spawning nase, of which 160 (89%) were within the restored site (density = 3.3 fish m<sup>-2</sup>), and only 20 within the untreated one (density = 0.4 fish m<sup>-2</sup>). The observed visual effect on spawning site use was also evident in the number of deposited eggs in the spawning boxes, which was significantly higher at the restored sites compared with the untreated sites in both the River Mangfall (Kruskal–Wallis test:  $\chi^2$  = 5.77; d.f. = 1;  $P$  < 0.05) and the River Sims (Kruskal–Wallis test:  $\chi^2$  = 6.56; d.f. = 1;  $P$  < 0.05; Figure 5). In the River Mangfall, the number of eggs deposited at the restored site of the spawning ground was seven times higher (1,354  $\pm$  1,394) compared with eggs deposited at the untreated site (262  $\pm$  185). In the River Sims, this difference was even greater (restored 725  $\pm$  811, untreated 38  $\pm$  44). Combining the numbers of eggs deposited across sites and rivers, the mean number of eggs was twice as high in the first retrieval event (806  $\pm$  1,249) compared with the second (383  $\pm$  420), which occurred 6 days later; however, this difference was not statistically significant (Kruskal–Wallis test:  $\chi^2$  = 0.003; d.f. = 1;  $P$  = 0.95).

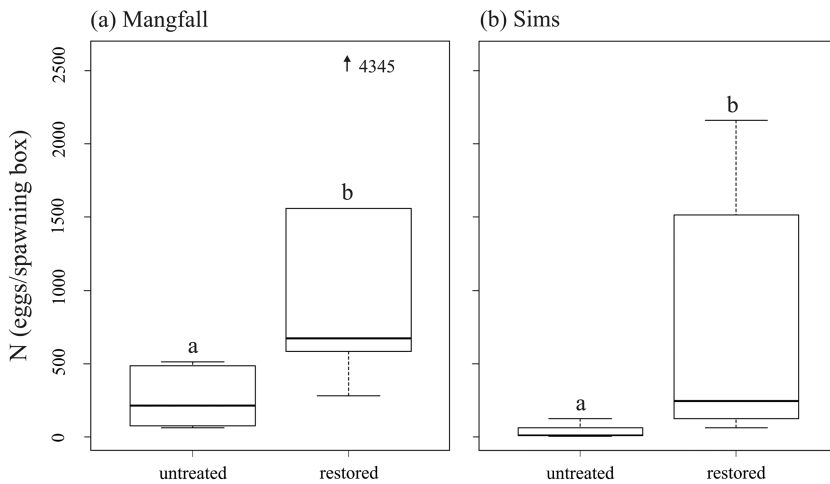


**FIGURE 4** Direct effects of gravel cleaning on substrate composition in (a) the River Mangfall and (b) the River Sims ( $n$  = 3 each per river and treatment); grey shaded areas indicate the range between minimum and maximum values. Average ( $\pm$  standard deviation) development of fine sediment content (<0.85 mm) during the period of investigation in (c) the River Mangfall and (d) the River Sims ( $n$  = 3 per observation)

### 3.3 | Infiltration of eggs and larvae into the interstitial zone

Egg counts from freeze-core samples taken in the River Mangfall 6 days after spawning resulted in great differences between the restored ( $147 \pm 121$ ) and the untreated site ( $4 \pm 1$ ). The same was demonstrated for the River Sims (restored  $28 \pm 7$ , untreated  $1 \pm 1$ ). In both rivers, eggs were detected down to a depth of 20 cm in the substrate, almost exclusively at the restored sites (Table 2). At the untreated site, only one egg in the River Mangfall was detected deeper than 10 cm in the substrate. Freeze-cores taken 26 days after spawning revealed no remaining eggs, but larvae down to 30 cm in the substrate (Table 3). Comparable with egg counts in the River Mangfall, the substrate layers of the restored site of this spawning ground contained most larvae ( $39 \pm 31$ ) whereas only a few ( $7 \pm 4$ ) were detected in substrate layers of the untreated site. In the River Sims, only four larvae were found, all in freeze-cores from the restored site.

Drifting eggs were found downstream of all investigated sites, indicating that not all eggs were capable of infiltrating into the interstices of the stream bed or attaching to the substrate surface. Egg drift was highest during the days of spawning and declined consistently afterwards (Figure 6a, c). In the River Mangfall, the mean density (mean of the restored and untreated site) of drifting eggs was  $0.61 \pm 0.45 \text{ eggs m}^{-3}$  on the first day of spawning (6 April 2018) and increased to the overall peak of  $4.86 \pm 1.54 \text{ eggs m}^{-3}$  on the second day of spawning (8 April 2018; Figure 6a). The last eggs were found 189 dd after the first day of spawning. Egg drift densities from the restored site were significantly higher compared with the untreated site ( $\chi^2_{(1)} = 5.98; P < 0.05$ ). Mean drift density in the River Sims was  $3.63 \pm 3.55 \text{ eggs m}^{-3}$  on the first day of spawning (9 April 2018). Comparable with the River Mangfall, the overall peak was reached on the second day of spawning (10 April 2018) with  $9.57 \pm 3.13 \text{ eggs m}^{-3}$  (Figure 6c). At this time, the total numbers drifting downstream were estimated to be 50,000 eggs per hour. The last eggs were



**FIGURE 5** Distribution of eggs on the spawning grounds ( $n = 6$  each). Box - 25% quantile, median, 75% quantile; whisker - minimum and maximum value. Extreme outlier is marked with a black arrow. Different letters above boxes indicate significant differences

**TABLE 2** Vertical distribution of eggs in freeze-cores (FC) taken 6 days after first spawning

Horizon (cm)	Mangfall						Sims					
	Restored			Untreated			Restored			Untreated		
0-10	91	17	213	7	2	3	23	21	14	0	0	3
>10-20	22	2	96	0	1	0	14	5	7	0	0	0
>20-30	0	0	0	0	0	0	0	0	0	0	0	0
FC weight (g)	1,828	3,480	3,004	4,566	1,960	2,381	5,045	2,161	2,666	3,913	3,448	3,492

**TABLE 3** Vertical distribution of larvae in freeze-cores (FC) taken 26 days after first spawning

Horizon (cm)	Mangfall						Sims					
	Restored			Untreated			Restored			Untreated		
0-10	6	19	48	7	10	1	3	0	0	0	0	0
>10-20	0	10	23	0	2	2	0	0	0	0	0	0
>20-30	0	2	9	0	0	0	0	0	1	0	0	0
FC weight (g)	5,045	2,161	2,666	3,913	3,448	3,492	2,742	4,314	2,107	2,971	4,055	2,895



detected 159 dd after the first day of spawning (6 April 2018). No statistical differences could be detected, although egg drift densities from the restored site in the River Sims exceeded those from the untreated site in every sample ( $\chi^2_{(1)} = 3.37$ ;  $P = 0.07$ ).

### 3.4 | Timing of emergence

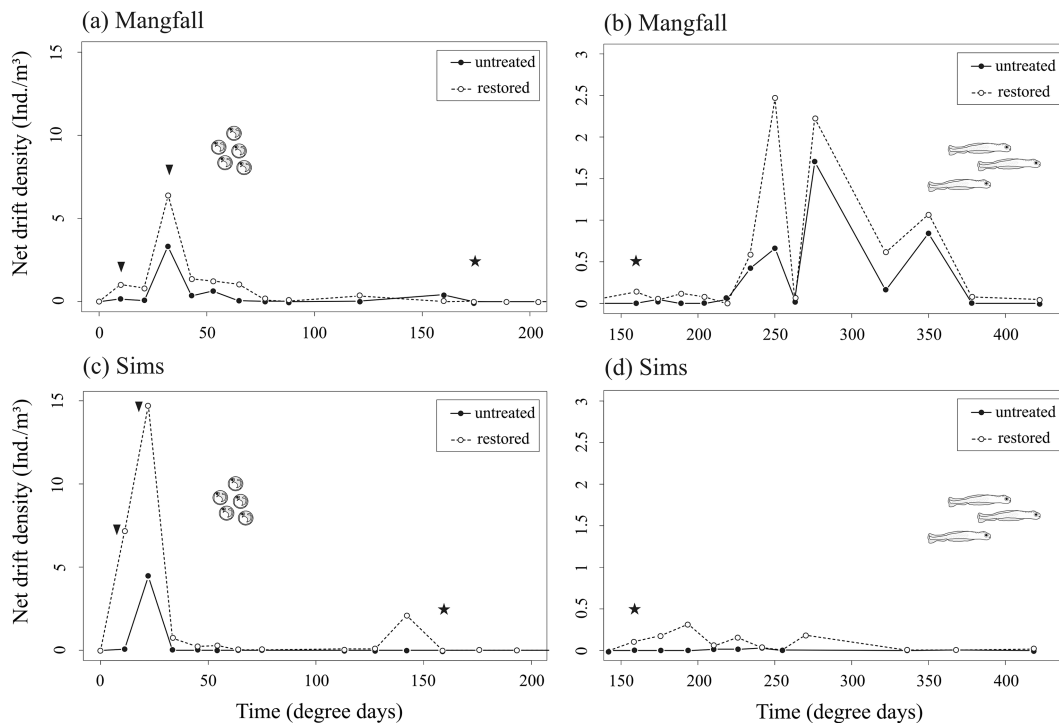
The timing pattern of emergence was different between the two rivers, but similar trends were observed when comparing the restored and the untreated sites. In the River Mangfall, larval drift started at 160 dd with a few individual larvae ( $0.07 \pm 0.07$  larvae  $m^{-3}$ ) and remained at a comparably low level until numbers began to increase distinctly after 250 dd ( $1.57 \pm 0.91$  larvae  $m^{-3}$ ). The overall peak was reached 12 days after the record of the first hatched larvae at 276 dd with a density of  $1.96 \pm 0.26$  larvae  $m^{-3}$  drifting downstream from the spawning ground (Figure 6b). At this time, the total numbers drifting downstream were estimated to be 10,500 larvae per hour. Subsequently, numbers began to decrease until the termination of the field observations on 7 May 2018. Densities of drifting larvae from the restored site were higher in almost every sample, although no significant influence of the factor treatment could be detected ( $\chi^2_{(1)} = 2.30$ ;  $P = 0.08$ ). Larvae in the River Sims were first recorded after 159 dd ( $0.06 \pm 0.06$  larvae  $m^{-3}$ ). Contrary to the River Mangfall, the overall peak was already reached 2 days later at 194 dd with a mean density of  $0.16 \pm 0.16$  drifting larvae  $m^{-3}$  (Figure 6d). In the following days only a few individual larvae were caught. Drift densities

from the restored site were significantly higher compared with the untreated site ( $\chi^2_{(1)} = 14.62$ ;  $P < 0.001$ ).

Although larval drift densities during daylight (Mangfall,  $0.60 \pm 0.76$ ; Sims,  $0.06 \pm 0.06$ ) exceeded those during darkness in both rivers (Mangfall,  $0.28 \pm 0.30$ ; Sims,  $0.06 \pm 0.05$ ), no significant differences could be detected (Mangfall,  $\chi^2_{(1)} = 3.61$ ;  $P = 0.06$ ; Sims,  $\chi^2_{(1)} = 0.04$ ;  $P = 0.84$ ).

### 3.5 | Larval size at emergence

From a total of 3,139 larvae caught, 1,699 were morphologically intact and used for determination of total length. In the River Mangfall, 1,090 larvae (day 724; night 366) were measured from the treated site compared with 443 from the untreated site (day 311; night 132). From the treated site in the River Sims, 136 larvae were measured (day 110; night 26) compared with 30 from the untreated site (day 18; night 12). In all larvae measured, total length ranged between 7.2 and 15.0 mm. Larval length was significantly influenced by the factor daylight ( $\chi^2_{(1)} = 16.65$ ;  $P < 0.001$ ), whereas treatment and river only showed a significant effect in the interaction term of these factors ( $\chi^2_{(1)} = 4.03$ ;  $P < 0.05$ ). Only marginal differences in larval length were detected between the treated and untreated site, in the River Mangfall (restored,  $11.1 \pm 1.4$ ; untreated,  $10.9 \pm 1.3$ ), as well as the River Sims (restored,  $10.0 \pm 1.3$ ; untreated,  $9.9 \pm 1.0$ ). At all sites, larval length increased over time (Figure 7) and was higher during the night ( $11.1 \pm 1.2$ ) compared with daylight sampling ( $10.7 \pm 1.4$ ). In



**FIGURE 6** Drift densities of eggs (6a, c) and larvae (6b, d) from spawning grounds in the River Mangfall and the River Sims. Solid lines and filled dots indicate drift densities of organisms caught downstream of the untreated sites; dashed lines and circles indicate those caught downstream of the restored sites. Black triangles indicate spawning events, black stars show the catch of first larvae

addition, larval length was greater in the River Mangfall ( $11.0 \pm 1.4$ ) compared with the River Sims ( $9.9 \pm 1.3$ ).

## 4 | DISCUSSION

The results of this experimental restoration clearly indicate that cleaning of spawning gravel affects all crucial steps of the reproduction and recruitment success of nase as evident from increased use of spawning sites and numbers of eggs released as well as deeper infiltration of eggs and greater shelter of larvae in the interstitial zone, all resulting in greater larval recruitment.

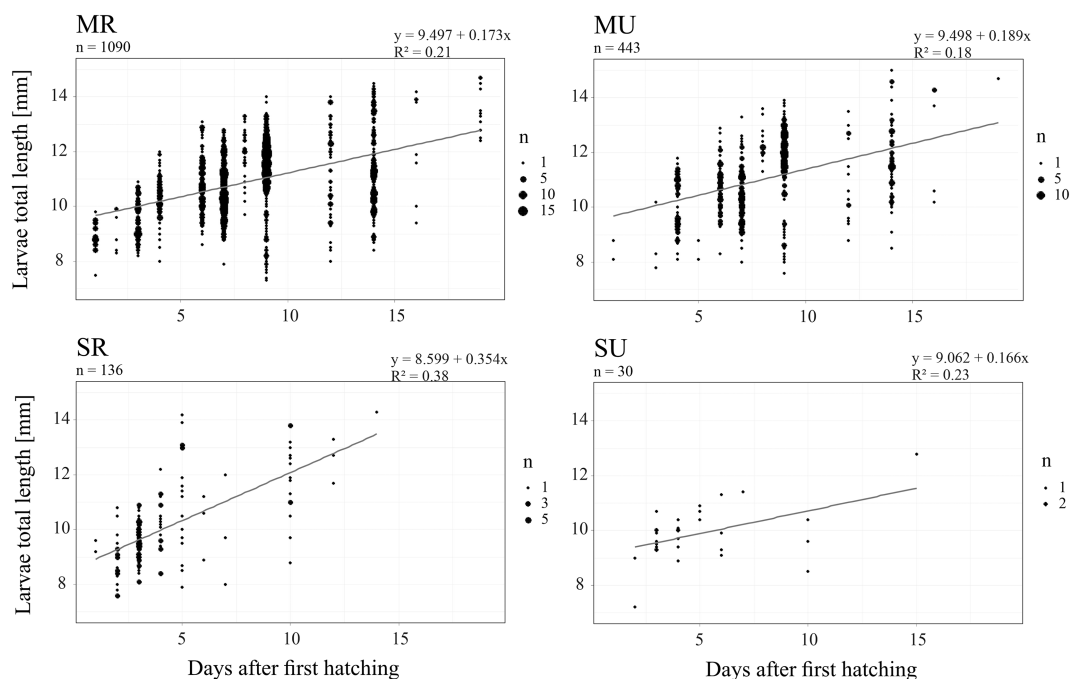
### 4.1 | Effects on nase spawning site use

In both rivers investigated, significantly higher numbers of eggs were found in restored parts of the spawning grounds, suggesting that the improved substrate quality, as indicated by the results of freeze-core samples, is a major factor influencing spawning habitat use. This interpretation is also supported by the number of spawning nase counted in the respective halves of spawning grounds, which was up to eight times higher in the restored parts. Although the number of nase counted in the spawning ground of the River Mangfall was only slightly higher in the restored site, the significantly higher numbers of eggs laid indicate that this site was preferred for egg release. The importance of substrate quality in spawning ground use has been demonstrated previously for salmonid species, e.g. with evidence of coho salmon (*Oncorhynchus kisutch* W.) spawning on substrates with certain

gravel–pebble ratios (Mull & Wilzbach, 2007), as well as brook trout (*Salvelinus fontinalis* M.) preferring spawning substrate with reduced fine sediment content (Bernier-Bourgault & Magnan, 2002). Spawning sites of nase are commonly characterized by shallow, fast-flowing riffles with a high proportion of gravel and pebbles (Keckeis, 2001; Melcher & Schmutz, 2010), yet the results of this study indicate that other substrate-related parameters, such as colmation or bulk-density, might also influence spawning site acceptance at the microhabitat level. It is conceivable that males check for substrate quality before spawning events by breaking up the gravel with their tails, which has been described by Ahnelt and Keckeis (1994) as a pre-spawning preparation in nase. Zoogeomorphic effects of spawning activity have also been reported for another lithophilic cyprinid, the European barbel (Gutmann Roberts, Bašić, Britton, Rice, & Pledger, 2020). This clearly demonstrates the value that assessing microhabitat use may have for future river management and restoration projects, as shown by Santos, Rivaes, Boavida, and Branco (2018).

### 4.2 | Effects on the infiltration of eggs and larvae in the interstitial zone

Higher numbers of eggs and larvae were also found in the interstitial zone of the restored sites in both rivers, indicating that loosened and cleaned spawning substrate provides important interstices for both developmental stages. This confirms recent findings from Duerregger et al. (2018) that post-spawning eggs seep down into the interstitial zone and post-hatching larvae retreat to greater depths. The importance of a loose and porous interstitial for the early ontogeny of nase



**FIGURE 7** Weighted scatter plots showing the size of larvae caught while drifting downstream from the restored (MR) and untreated (MU) spawning ground in the River Mangfall and the restored (SR) and untreated (SU) spawning ground in the River Sims

becomes evident in the reduced risk of predation and uncontrolled drift of eggs and larvae developing in sheltered interstices in the gravel bed. In contrast, these risks are elevated for eggs directly exposed on the gravel surface (Keckeis et al., 1996; Persat & Olivier, 1995). Spawning ground restoration by gravel cleaning clearly supports the egg and larval infiltration mechanism, as indicated by the higher number of eggs and larvae in deep interstitial layers of up to 20 and 30 cm, respectively, which were found almost exclusively in the restored halves of spawning grounds. As studies on European barbel and common minnow show that eggs of these species can also be found in substrate layers down to 20 cm (barbel: Pinder, Clough, Morris, & Fletcher, 2009) and 30 cm, respectively (common minnow: Bless, 1996), it is likely that the benefits of gravel cleaning observed in this study might be transferable to other species with a similar ecology and incubation time, such as barbel, chub, dace and common minnow.

However, while gravel cleaning might be a good choice for species with a short incubation phase, this is still only a temporary solution (Mueller et al., 2014). In contrast, it is highly doubtful that single instream measures provide a sufficient conservation tool for aquatic biota that depend on a loose and well-oxygenated stream bed for a much longer period of time, such as freshwater pearl mussels (Denic & Geist, 2015). For these species sufficient habitat conditions can only be established when integrative catchment concepts, comprising management of land use and flow dynamics, are developed (Denic & Geist, 2015).

Generally, nase eggs are characterized by a cover of adhesive villi on the *zona radiata externa* (Patzner, Weidinger, & Riehl, 2006), supporting egg adhesive ability even in fast-flowing areas of spawning grounds. However, not all eggs are capable of remaining on spawning grounds, as high densities of suspended eggs drifting downstream were found during the days of spawning, exceeding those reported by Hofer and Kirchhofer (1996), in which the mean density of drifting eggs peaked at 3.17 eggs m<sup>-3</sup>. Peaks in the drift of eggs were higher from the restored sites of spawning grounds, which can be explained by the significantly higher number of eggs laid on these sites.

In a study on egg populations of dace, another lithophilic cyprinid with a similar egg attachment mechanism (Petz-Glechner, Patzner, & Riehl, 1998), the number of downstream drifting eggs directly linked to the initial egg population was estimated to be 2% in the wild (Mills, 1981). Species-specific differences in the density and length of adhesive villi have already been reported (Riehl & Patzner, 1998); however, it remains unclear whether there are also intraspecific differences, as previously demonstrated by Keckeis, Bauer-Nemeschkal, Menshutkin, Nemeschkal, and Kamler (2000), for egg size of nase, or effects of water chemistry on the attachment mechanism that might explain differences in the adhesiveness of eggs between the two rivers investigated. Moreover, it remains to be tested whether eggs drifting from spawning grounds can settle and develop elsewhere, or whether they are completely lost to the population. The latter seems likely in cases where streams transport high loads of fines, as observed by Nagel et al. (2020), where even 10% fine sediment content in the incubation substrate (<0.85 mm) caused elevated mortality

of nase eggs. However, drifting eggs can also contribute indirectly to the recruitment success by distracting predators from eggs developing in more favourable conditions on spawning grounds. In any case, our findings highlight the importance of a loose and porous interstitial on spawning grounds, as the chances of a successful development of eggs with a reduced adhesive ability is elevated if the stream bed provides sufficient porous space for egg infiltration.

### 4.3 | Development success and timing of emergence

In both rivers, larval emergence was distinctly higher from the restored sites of spawning grounds, which can be linked to the preferred use of these sites by spawning nase. Subsequently, higher numbers of eggs laid develop in a greater interstitial space, which results in higher numbers of emerging larvae. It seems likely that the observed effects are not only a matter of a higher number of eggs laid, but also a result of more favourable conditions for the early ontogeny of nase, as the hatching rate of nase larvae increases with reduced fine sediment content in the incubation substrate (Nagel et al., 2020). However, the variability in the development success between the two rivers was high, with a peak density of larvae emerging in the River Mangfall 12 times higher than in the River Sims. We assume that this could be related to several factors such as substrate composition or compaction, differences in water chemistry or biological causes such as a reduced egg adhesive ability of the Sims population, as indicated by the high densities of downstream drifting eggs and consequently lower numbers of eggs remaining on the spawning ground. As larval emergence in the River Sims was almost exclusively observed at the restored site, it is possible that this population has fundamental problems in recruitment success under naturally occurring conditions that might threaten its survival. In the River Mangfall, emergence activity was detected from the record of the first larvae until the end of the investigation, but the peak of emergence was observed 155 dd after the first record of hatching. This suggests that post-hatching nase larvae use the interstitial zone as a sheltered habitat for further development and emerge several days after hatching, which is consistent with findings from a laboratory experiment, in which the time of hatching and emergence in nase larvae differed by up to 156 dd (Nagel et al., 2020).

Generally, nase larvae are described as negatively phototactic (Peñáz, 1974). However, contrary to findings of Hofer and Kirchhofer (1996) in the wild and results from Persat and Olivier (1995) under experimental conditions, a shift to increasing drift activity of nase larvae during darkness in both rivers was not observed. Taking into account the high emergence success in the River Mangfall (derived by the high numbers of drifting larvae and findings of Duerregger et al., 2018), we assume that the main driver of dispersal in this spawning ground can be related to the reaction of larvae to population density effects after hatching (Lechner, Keckeis, & Humphries, 2016). The aggregation of eggs and larvae on spawning grounds can attract predators, such as chub – which were observed on spawning grounds after spawning of nase – waterfowl and

macroinvertebrates (Keckeis et al., 1996; Persat & Olivier, 1995). A dispersal movement from spawning grounds can reduce these risks as well as the competition for space (Copp, Faulkner, Doherty, Watkins, & Majecki, 2002).

This interpretation is also supported by a study on brown trout (Daufresne, Capra, & Gaudin, 2005) that demonstrated that downstream drift was reduced following displacement of 80% of the hatched fry. Moreover, the observed size difference in nase larvae drifting during daylight compared with those drifting during darkness suggests that daylight larval drift is mainly composed of small hatched embryos of eggs attached to the stream bed. Larvae are probably flushed away by the current immediately after hatching (passive drift entry) in contrast to larger individuals actively emerging from the substrate during the night (active drift entry). In addition, it remains unclear whether the observed size difference of larvae between the rivers investigated is a result of the time when larvae were caught in relation to the date of hatching or an inherited phenomenon caused by differing genetic constitution of the spawning populations. The latter seems unlikely, as there are no migration barriers between the spawning grounds in the River Sims and the River Mangfall, and Wetjen, Hübner, Seehausen, and Schulz (2020) very recently detected only limited geographical differences in the genetic structure of nase populations in Germany, where migration between populations was not interrupted. In contrast, a time-related effect seems more likely, as larval emergence in the River Sims stopped ~7 days earlier compared with the River Mangfall and a linear increase in growth of nase larvae following hatching is well described (Schludermann, Keckeis, & Nemeschkal, 2009). Effects of greater larval sizes from the restored parts of spawning grounds were not observed in the present study; however, the effects of smaller larval sizes with increasing amounts of fines in the incubation substrate were found in studies under experimental conditions for nase (Nagel et al., 2020) and for salmonids likewise (Sternecker & Geist, 2010).

#### 4.4 | Conservation implications

Identifying life-stage specific deficiencies in habitat quality is one of the most crucial steps in developing sound conservation plans (Geist, 2011; Pander & Geist, 2013), yet knowledge of the autecological requirements of threatened European freshwater fish species is still not sufficient (Smialek et al., 2019). The results of this study reveal that spawning ground restoration for nase clearly supports the reproduction and recruitment success of this species, by reducing the amount of fines in the spawning substrates and thereby increasing the porosity of the stream bed. Consequently, the improved substrate quality results in a preferred use of the restored site, which is evident in the higher numbers of spawning nase and eggs laid on the spawning grounds. Considering subsequent development stages, the restoration-induced increase in stream-bed porosity leads to higher numbers of eggs and larvae infiltrating the interstitial zone, where larvae can successfully use the interstices as shelter, increasing

emergence success and size at emergence. Other studies have observed only short-term effects of spawning substrate restoration and raise doubt concerning the effectiveness of this measure for species with a relatively long interstitial phase such as salmonids or freshwater pearl mussels (Mueller et al., 2014; Pander et al., 2015). In contrast to those species, the predictability and synchrony of nase spawning runs in concert with a relatively short interstitial phase of less than 1 month, allowing a high accuracy in the timing of spawning ground restoration and therefore greater restoration success. It is therefore important to consider spawning ground restoration as a quick, cheap and effective tool for the restoration and conservation management of nase and other species with a similar ecology and incubation time, such as barbel, chub, dace and common minnow. This holds especially true if streams lack internal dynamics and transport high fine-sediment loads. It is essential, however, to consider the spatial and temporal restriction of gravel cleaning effects as well as possible adverse consequences that may occur in downstream areas as a result of fine sediment wash-out when implementing this measure (Pander et al., 2015). The extent of both depends on the individual geomorphology, flow dynamics and fine-sediment loads and is therefore highly river- and site-specific (Pander et al., 2015). Consequently, long-term improvements for stream bed-dependent aquatic biota can only be achieved if all causes of fine-sediment clogging in the stream bed are addressed. This includes the reduction of fine-sediment loads from catchment-dependent land use as well as restricted gravel relocation caused by structural instream modifications (Geist & Hawkins, 2016). Rethinking common land-use practices, as well as re-establishing natural flow dynamics, is therefore crucial to support a self-sustaining process of reducing sediment input on the one hand and sediment mobilization and relocation on the other.

#### ACKNOWLEDGEMENTS

We are grateful for the financial support of this study by Verbund Innkraftwerke GmbH, particularly to G. Loy who initiated and supported this project. We would also like to thank E. Schulz, A. Huber (Kreisfischereiverein Rosenheim e.V.) and R. Zillmer (Anglerbund Rosenheim) for their permission to restore nase spawning grounds and their assistance in field work. B. Gum (Fischereifachberatung Oberbayern) and T. Bittl (Wasserwirtschaftsamt Rosenheim) are also thanked for their support of the study. We would like to thank all helping hands for the assistance during the study, particularly J. Sinicki for her support with length measurements. Open access funding enabled and organized by Projekt DEAL.

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#### REFERENCES

- Aarts, B. G. W., Van den Brink, F. W. B., & Nienhuis, P. H. (2004). Habitat loss as the main cause of the slow recovery of fish faunas of regulated large rivers in Europe: The transversal floodplain gradient. *River Research and Applications*, 20, 3–23. <https://doi.org/10.1002/rra.720>



- Ahnelt, H., & Keckeis, H. (1994). Breeding tubercles and spawning behaviour in *Chondrostoma nasus* (Teleostei: Cyprinidae): A correlation. *Ichthyological Exploration of Freshwaters*, 5, 321–330.
- Auerswald, K., & Geist, J. (2018). Extent and causes of siltation in a headwater stream bed: Catchment soil erosion is less important than internal stream processes. *Land Degradation and Development*, 29, 737–748. <https://doi.org/10.1002/ldr.2779>
- Barlaup, B. T., Gabrielsen, S. E., Skoglund, H., & Wiers, T. (2008). Addition of spawning gravel: A means to restore spawning habitat of Atlantic salmon (*Salmo salar* L.), and anadromous and resident brown trout (*Salmo trutta* L.) in regulated rivers. *River Research and Applications*, 24, 543–550. <https://doi.org/10.1002/rra.1127>
- Bašić, T., Britton, J. R., Rice, S. P., & Pledger, A. G. (2017). Impacts of gravel jetting on the composition of fish spawning substrates: Implications for river restoration and fisheries management. *Ecological Engineering*, 107, 71–81. <https://doi.org/10.1016/j.ecoleng.2017.06.057>
- Bašić, T., Britton, J. R., Rice, S. P., & Pledger, A. G. (2018). Does sand content in spawning substrate result in early larval emergence? Evidence from a lithophilic cyprinid fish. *Ecology of Freshwater Fish*, 28, 110–122. <https://doi.org/10.1111/eff.12435>
- Bernier-Bourgault, I., & Magnan, P. (2002). Factors affecting redd site selection, hatching, and emergence of brook charr, *Salvelinus fontinalis*, in an artificially enhanced site. *Environmental Biology of Fishes*, 64, 333–341. <https://doi.org/10.1023/A:1016006303854>
- Bless, R. (1996). *Einsichten in die Ökologie der Elritze Phoxinus phoxinus (L.): Praktische Grundlagen zum Schutz einer gefährdeten Fischart. Bundesforschungsanstalt für Naturschutz und Landschaftsökologie*. Münster: Landwirtschaftsverlag.
- Bohl, E., Kleisinger, H., & Leuner, E. (2003). Rote Liste gefährdeter Fische (Pisces) und Rundmäuler (Cyclostomata) Bayerns. *Bayerisches Landesamt für Umwelt*, 166, 52–55.
- Copp, G. H., Faulkner, H., Doherty, S., Watkins, M. S., & Majecki, J. (2002). Diel drift behaviour of fish eggs and larvae, in particular barbel, *Barbus barbus* (L.), in an English chalk stream. *Fisheries Management and Ecology*, 9, 95–103. <https://doi.org/10.1046/j.1365-2400.2002.00286.x>
- Council of the European Communities. (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 Communities*, L206, 7–50.
- Council of the European Communities. (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 Communities*, L327, 1–73.
- Cramer, M. L. (Ed.) (2012). *Stream habitat restoration guidelines*. Olympia, WA: The Washington Departments of Fish and Wildlife, Natural Resources, Transportation and Ecology, Washington State Recreation and Conservation Office, Puget Sound Partnership, and the US Fish and Wildlife Service.
- Daufresne, M., Capra, H., & Gaudin, P. (2005). Downstream displacement of post-emergent brown trout: Effects of development stage and water velocity. *Journal of Fish Biology*, 67, 599–614. <https://doi.org/10.1111/j.0022-1112.2005.00759.x>
- Davies, B., Biggs, J., Williams, P., & Thompson, S. (2009). Making agricultural landscapes more sustainable for freshwater biodiversity: A case study from southern England. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 19, 439–447. <https://doi.org/10.1002/aqc.1007>
- De Leeuw, J. J., & Winter, H. V. (2008). Migration of rheophilic fish in the large lowland rivers Meuse and Rhine, the Netherlands. *Fisheries Management and Ecology*, 15, 409–415. <https://doi.org/10.1111/j.1365-2400.2008.00626.x>
- Denic, M., & Geist, J. (2015). Linking stream sediment deposition and aquatic habitat quality in pearl mussel streams: Implications for conservation. *River Research and Applications*, 31, 943–952. <https://doi.org/10.1002/rra.2794>
- 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, 920–932. <https://doi.org/10.1111/eff.12403>
- Fox, J., & Weisberg, S. (2011). *An R companion to applied regression* (2nd ed.). Thousand Oaks CA: Sage.
- Geist, J. (2011). Integrative freshwater ecology and biodiversity conservation. *Ecological Indicators*, 11, 1507–1516. <https://doi.org/10.1016/j.ecolind.2011.04.002>
- Geist, J., & Auerswald, K. (2007). Physicochemical stream bed characteristics and recruitment of the freshwater pearl mussel (*Margaritifera margaritifera*). *Freshwater Biology*, 52, 2299–2316. <https://doi.org/10.1111/j.1365-2427.2007.01812.x>
- 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, 942–962. <https://doi.org/10.1002/aqc.2702>
- Gore, J. A., Crawford, D. J., & Addison, D. S. (1998). An analysis of artificial riffles and enhancement of benthic community diversity by physical habitat simulation (PHABSIM) and direct observation. *Regulated Rivers: Research and Management*, 14, 69–77. [https://doi.org/10.1002/\(SICI\)1099-1646\(199801/02\)14:1<69::AID-RRR477>3.0.CO;2-D](https://doi.org/10.1002/(SICI)1099-1646(199801/02)14:1<69::AID-RRR477>3.0.CO;2-D)
- Gortz, P. (1998). Effects of stream restoration on the macroinvertebrate community in the River Esrom, Denmark. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 8, 115–130. [https://doi.org/10.1002/\(SICI\)1099-0755\(199801/02\)8:1<115::AID-AQC263>3.0.CO;2-L](https://doi.org/10.1002/(SICI)1099-0755(199801/02)8:1<115::AID-AQC263>3.0.CO;2-L)
- 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>
- Gutmann Roberts, C., Bašić, T., Britton, J. R., Rice, S., & Pledger, A. G. (2020). Quantifying the habitat and zoogeomorphic capabilities of spawning European barbel *Barbus barbus*, a lithophilous cyprinid. *River Research and Applications*, 36, 259–279. <https://doi.org/10.1002/rra.3573>
- Hauer, C., Unfer, G., Schmutz, S., & Habersack, H. (2007). The importance of morphodynamic processes at riffles used as spawning grounds during the incubation time of nase (*Chondrostoma nasus*). *Hydrobiologia*, 579, 15–27. <https://doi.org/10.1007/s10750-006-0406-7>
- Hofer, K., & Kirchhofer, A. (1996). Drift, habitat choice and growth of the nase (*Chondrostoma nasus*, Cyprinidae) during early life stages. In *Conservation of endangered freshwater fish in Europe* (pp. 269–278). Basel: Birkhäuser.
- Jensen, D. W., Steel, E. A., Fullerton, A. H., & Pess, G. R. (2009). Impact of fine sediment on egg-to-fry survival of Pacific salmon: A meta-analysis of published studies. *Reviews in Fisheries Science*, 17, 348–359. <https://doi.org/10.1080/10641260902716954>
- Keckeis, H. (2001). Influence of river morphology and current velocity conditions on spawning site selection of *Chondrostoma nasus* (L.). *Large Rivers*, 341–356. <https://doi.org/10.1127/lr/12/2001/341>
- Keckeis, H., Bauer-Nemeschkal, E., Menshutkin, V. V., Nemeschkal, H. L., & Kamler, E. (2000). Effects of female attributes and egg properties on offspring viability in a rheophilic cyprinid, *Chondrostoma nasus*. *Canadian Journal of Fisheries and Aquatic Sciences*, 57, 789–796. <https://doi.org/10.1139/f00-006>
- Keckeis, H., Bauer-Nemeschkal, E., & Kamler, E. (1996). Effects of reduced oxygen level on the mortality and hatching rate of *Chondrostoma nasus* embryos. *Journal of Fish Biology*, 49, 430–440. <https://doi.org/10.1111/j.1095-8649.1996.tb00039.x>
- Kemp, P., Sear, D., Collins, A., Naden, P., & Jones, I. (2011). The impacts of fine sediment on riverine fish. *Hydrological Processes*, 25, 1800–1821. <https://doi.org/10.1002/hyp.7940>

- Kondolf, G. M. (2000). Assessing salmonid spawning gravel quality. *Transactions of the American Fisheries Society*, 129, 262–281. [https://doi.org/10.1577/1548-8659\(2000\)129<0262:ASSGQ>2.0.CO;2](https://doi.org/10.1577/1548-8659(2000)129<0262:ASSGQ>2.0.CO;2)
- Kottelat, M., & Freyhof, J. (2007). *Handbook of European freshwater fishes*. Cornol: Publications Kottelat.
- Lapointe, N. W., Cooke, S. J., Imhof, J. G., Boisclair, D., Casselman, J. M., Curry, R. A., ... Power, M. (2013). Principles for ensuring healthy and productive freshwater ecosystems that support sustainable fisheries. *Environmental Reviews*, 22, 110–134.
- Lechner, A., Keckeis, H., & Humphries, P. (2016). Patterns and processes in the drift of early developmental stages of fish in rivers: A review. *Reviews in Fish Biology and Fisheries*, 26, 471–489. <https://doi.org/10.1007/s11160-016-9437-y>
- Melcher, A. H., & Schmutz, S. (2010). The importance of structural features for spawning habitat of nase *Chondrostoma nasus* (L.) and barbel *Barbus barbus* (L.) in a pre-Alpine river. *River Systems: Integrating Landscapes, Catchment Perspectives, Ecology, Management*, 19, 33–42. <https://doi.org/10.1127/1868-5749/2010/019-0033>
- Meyer, E. I., Niepagenkemper, O., Molls, F., & Spaenhoff, B. (2008). An experimental assessment of the effectiveness of gravel cleaning operations in improving hyporheic water quality in potential salmonid spawning areas. *River Research and Applications*, 24, 119–131. <https://doi.org/10.1002/rra.1051>
- Mih, W. C., & Bailey, G. C. (1981). The development of a machine for the restoration of stream gravel for spawning and rearing of salmon. *Fisheries*, 6, 16–20.
- Mills, C. A. (1981). Egg population dynamics of naturally spawning dace, *Leuciscus leuciscus* (L.). *Environmental Biology of Fishes*, 6, 151–158. <https://doi.org/10.1007/BF00002778>
- Mueller, M., Pander, J., & Geist, J. (2014). The ecological value of stream restoration measures: An evaluation on ecosystem and target species scales. *Ecological Engineering*, 62, 129–139. <https://doi.org/10.1016/j.ecoleng.2013.10.030>
- Mueller, M., Pander, J., & Geist, J. (2018). Comprehensive analysis of >30 years of data on stream fish population trends and conservation status in Bavaria, Germany. *Biological Conservation*, 226, 311–320. <https://doi.org/10.1016/j.biocon.2018.08.006>
- Mull, K. E., & Wilzbach, M. A. (2007). Selection of spawning sites by coho salmon in a northern California stream. *North American Journal of Fisheries Management*, 27, 1343–1354. <https://doi.org/10.1577/M06-054.1>
- Nagel, C., Pander, J., Mueller, M., & Geist, J. (2020). Substrate composition determines emergence success and development of European nase larvae (*Chondrostoma nasus* L.). *Ecology of Freshwater Fish*, 29, 121–131. <https://doi.org/10.1111/eff.12500>
- Ovidio, M., & Philippart, J. C. (2008). Movement patterns and spawning activity of individual nase *Chondrostoma nasus* (L.) in flow-regulated and weir-fragmented rivers. *Journal of Applied Ichthyology*, 24, 256–262. <https://doi.org/10.1111/j.1439-0426.2008.01050.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., & Geist, J. (2018). The contribution of different restored habitats to fish diversity and population development in a highly modified river: A case study from the river Günz. *Water*, 10, 1202. <https://doi.org/10.3390/w10091202>
- 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, 239–255. <https://doi.org/10.1002/rra.2732>
- Patzner, R. A., Weidinger, C., & Riehl, R. (2006). Die Eier heimischer Fische: 18. Nase - *Chondrostoma nasus* (Linnaeus, 1758) (Cyprinidae). *Oesterreichs Fischerei*, 59, 163–168.
- Peñáz, M. (1974). Early development of the nase carp, *Chondrostoma nasus* (Linnaeus, 1758). *Zoologische Listy*, 23, 275–288.
- Peñáz, M. (1996). *Chondrostoma nasus* – Its reproduction strategy and possible reasons for a widely observed population decline – A review. In *Conservation of endangered freshwater fish in Europe* (pp. 279–285). Basel: Birkhäuser.
- Persat, H., & Olivier, J. M. (1995). The first displacements in the early stages of *Chondrostoma nasus* under experimental conditions. *Folia Zoologica*, 44, 43–50.
- Petz-Glechner, R., Patzner, R. A., & Riehl, R. (1998). Die Eier heimischer Fische. 12. Hasel-*Leuciscus leuciscus* (L. 1758) und Stroemer-*Leuciscus souffia agassizi* (V. 1844) (Cyprinidae). *Oesterreichs Fischerei*, 51, 83–89.
- Phillips, R. W., Lantz, R. L., Claire, E. W., & Moring, J. R. (1975). Some effects of gravel mixtures on emergence of coho salmon and steelhead trout fry. *Transactions of the American Fisheries Society*, 104, 461–466. [https://doi.org/10.1577/1548-8659\(1975\)104<461:SEOGMO>2.0.CO;2](https://doi.org/10.1577/1548-8659(1975)104<461:SEOGMO>2.0.CO;2)
- Pinder, A. C., Clough, S., Morris, K., & Fletcher, R. (2009). An investigation into the spawning and recruitment success of barbel in the River Wensum. APEM 410776, Environment Agency, 1–20.
- Pulg, U., Barlaup, B. T., Sternecker, K., Trepl, L., & Unfer, G. (2013). Restoration of spawning habitats of brown trout (*Salmo trutta*) in a regulated chalk stream. *River Research and Applications*, 29, 172–182. <https://doi.org/10.1002/rra.1594>
- Rakowitz, G., Berger, B., Kubecka, J., & Keckeis, H. (2008). Functional role of environmental stimuli for the spawning migration in Danube nase *Chondrostoma nasus* (L.). *Ecology of Freshwater Fish*, 17, 502–514. <https://doi.org/10.1111/j.1600-0633.2008.00302.x>
- R Core Team. (2017). R: A language and environment for statistical computing. Vienna: R Foundation for Statistical Computing. Retrieved from <https://www.R-project.org/>
- Riehl, R., & Patzner, R. A. (1998). Minireview: The modes of egg attachment in teleost fishes. *The Italian Journal of Zoology*, 65, 415–420. <https://doi.org/10.1080/11250009809386857>
- Santos, J. M., Rivaes, R., Boavida, I., & Branco, P. (2018). Structural microhabitat use by endemic cyprinids in a Mediterranean-type river: Implications for restoration practices. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 28, 26–36. <https://doi.org/10.1002/aqc.2839>
- Schiemer, F., Keckeis, H., & Kamler, E. (2002). The early life history stages of riverine fish: Ecophysiological and environmental bottlenecks. *Comparative Biochemistry and Physiology Part A: Molecular and Integrative Physiology*, 133, 429–449. [https://doi.org/10.1016/S1095-6433\(02\)00246-5](https://doi.org/10.1016/S1095-6433(02)00246-5)
- Schludermann, E., Keckeis, H., & Nemeschkal, H. L. (2009). Effect of initial size on daily growth and survival in freshwater *Chondrostoma nasus* larvae: A field survey. *Journal of Fish Biology*, 74, 939–955. <https://doi.org/10.1111/j.1095-8649.2009.02182.x>
- Sear, D. A., Pattison, I., Collins, A. L., Smallman, D. J., Jones, J. I., & Naden, P. S. (2017). The magnitude and significance of sediment oxygen demand in gravel spawning beds for the incubation of salmonid embryos. *River Research and Applications*, 33, 1642–1654. <https://doi.org/10.1002/rra.3212>
- Smialek, N., Pander, J., Mueller, M., Van Treeck, R., Wolter, C., & Geist, J. (2019). Do we know enough to save European riverine fish? – A systematic review on autecological requirements during critical life stages of 10 rheophilic species at risk. *Sustainability*, 11, 5011. <https://doi.org/10.3390/su11185011>
- Soulsby, C., Youngson, A. F., Moir, H. J., & Malcolm, I. A. (2001). Fine sediment influence on salmonid spawning habitat in a lowland agricultural stream: A preliminary assessment. *Science of the Total Environment*, 265, 295–307. [https://doi.org/10.1016/S0048-9697\(00\)00672-0](https://doi.org/10.1016/S0048-9697(00)00672-0)
- Sternecker, K., Cowley, D. E., & Geist, J. (2013). Factors influencing the success of salmonid egg development in river substratum. *Ecology of Freshwater Fish*, 22, 322–333. <https://doi.org/10.1111/eff.12020>

- 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, 2749–2758. <https://doi.org/10.1002/ece3.1128>
- Sternecker, K., & Geist, J. (2010). The effects of stream substratum composition on the emergence of salmonid fry. *Ecology of Freshwater Fish*, 19, 537–544. <https://doi.org/10.1111/j.1600-0633.2010.00432.x>
- Sternecker, K., Wild, R., & Geist, J. (2013). Effects of substratum restoration on salmonid habitat quality in a subalpine stream. *Environmental Biology of Fishes*, 96, 1341–1351. <https://doi.org/10.1007/s10641-013-0111-0>
- Taylor, J., Rytwinski, T., Bennett, J. R., Smokorowski, K. E., Lapointe, N., Clarke, R., ... Cooke, S. (2019). The effectiveness of spawning habitat creation or enhancement for substrate-spawning temperate fish: A systematic review. *Environmental Evidence*, 8, 19. <https://doi.org/10.1186/s13750-019-0162-6>
- Vilizzi, L., & Copp, G. H. (2013). Interstitial movement and emergence of barbel, *Barbus barbus*, free embryos and larvae. *Journal of Fish Biology*, 82, 1057–1063. <https://doi.org/10.1111/jfb.12033>
- Wetjen, M., Hübner, D., Seehausen, O., & Schulz, R. (2020). Genetic diversity of endangered *Chondrostoma nasus* in the River Rhine system: Conservation genetics considerations on stocking and reintroduction. *Knowledge and Management of Aquatic Ecosystems*, 421, 25. <https://doi.org/10.1051/kmae/2020016>
- Zeh, M., & Dönni, W. (1994). Restoration of spawning grounds for trout and grayling in the river High-Rhine. *Aquatic Sciences*, 56, 59–69. <https://doi.org/10.1007/BF00877435>
- Zuur, A., Ieno, E. N., Walker, N., Saveliev, A. A., & Smith, G. M. (2009). *Mixed effects models and extensions in ecology with R*. New York: Springer Science & Business Media. <https://doi.org/10.1007/978-0-387-87458-6>

#### SUPPORTING INFORMATION

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

**How to cite this article:** Nagel C, Mueller M, Pander J, Geist J. Making up the bed: Gravel cleaning as a contribution to nase (*Chondrostoma nasus* L.) spawning and recruitment success. *Aquatic Conserv: Mar Freshw Ecosyst*. 2020;30:2269–2283. <https://doi.org/10.1002/aqc.3458>