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Quantifying the habitat and zoogeomorphic capabilities of spawning European barbel *Barbus barbus*, a lithophilous cyprinid

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Abstract

Suitable gravel availability is critical for the spawning success of lithophilous fishes, including redd builders. Redd construction during spawning can alter substrate characteristics, thereby influencing hydraulic conditions and sediment transport, highlighting the importance of spawning as a zoogeomorphic activity. Here, interactions between redd-building fish and their spawning environment were investigated for European barbel *Barbus barbus* with a comparative approach across three English rivers: Teme (western), Great Ouse (eastern) and Idle (central). Sediment characteristics of spawning habitats were similar across the rivers, including subsurface fine sediment (<2 mm) content (≈20% dry weight), but elevated subsurface silt content and coarser surface sediments were found in the river Teme. Water velocities were similar at spawning sites despite differences in channel width and depth. Redds were characterized by a pit and tailspill, with no differences in surface grain-size characteristics between these and the surrounding riverbed, but with topographic alteration (dimensions and tailspill amplitude) in line with those of salmonids. Estimates of the fraction of the bed that spawning barbel were capable of moving exceeded 97% in all rivers. Estimated reproductive potential varied significantly between the rivers Idle and Teme (3,098 to 9,715 eggs/m^2), which was largely due to differences in barbel lengths affecting fecundity. Larger barbel, capable of producing and depositing more eggs, but in more spatially extensive redds, meaning fewer redds per given surface area of riverbed. Predictions of barbel egg mortality based on sand content were low across both rivers. The effects of silt on barbel egg and larvae development are unknown, but the levels detected here would significantly impact salmon egg mortality. Similarities in fish length to redd area and the size of moveable grains by spawning barbel and salmon suggest they have similar geomorphic effects on sediments, although fine sediment tolerance is highly divergent.

KEYWORDS

cyprinid, habitat, redd, reproduction, spawning, zoogeomorphology

1 | INTRODUCTION

Geological, morphological and hydrological processes in rivers have important implications for sustaining biological communities (Bravard et al., 1997; Elosegi, Díez, & Mutz, 2010). Lithophilous fishes are especially dependent on the physical environment for their spawning success, as construction of redds for egg deposition and incubation means egg survival and larval emergence rates can be impacted by suboptimal spawning substratum (Goode, Luce, & Buffington, 2012; Greig, Sear, & Carling, 2007; Lapointe, Bergeron, Berube, Pouliot, & Johnston, 2004). The preferred spawning substrata of lithophilous salmonid fishes are relatively well understood (e.g., Kondolf, 2000; Armstrong, Kemp, Kennedy, Ladle, & Milner, 2003; Louhi, Mäki-Petäys, & Erkinaro, 2008; Table 1). The sediment mixture, particularly the ratio of framework gravel sizes to matrix sand, silt and clay sizes, ultimately defines the quality of spawning substratum (Wu, 2000). Generally, large quantities of fine sediment (<2 mm diameter; "fines") reduce substrate porosity and permeability with negative effects on substrate embeddedness, oxygen transfer, temperature control, metabolite removal and larval emergence. High quantities of fines are therefore associated with reduced egg burial depths, poor egg survival and emergence rates and other lethal (Kemp, Sear, Collins, Naden, & Jones, 2011; Sear et al., 2016) or sublethal impacts (Chapman et al., 2014; Franssen et al., 2012).

Knowledge of spawning substratum preferences amongst non-salmonid lithophilous fishes is comparatively poor, with a paucity of information on how river hydrology interacts with sediment composition to influence larval emergence success and recruitment (Mann, 1996, Bašić et al., 2017, Duerregger et al., 2018; Table 1). This is despite the high ecological and recreational importance of many of these fishes (Winfield & Nelson, 1991), such as the European barbel *Barbus barbus* (barbel hereafter) (Britton & Pegg, 2011). Studies of barbel have focussed on the extent of pre-spawning movements (Baras, 1997; Baras & Cherry, 1990; Baras, Lambert, & Philippart, 1994), with knowledge of spawning requirements limited to studies suggesting preferences for shallow (≈37 cm) and fast-flowing water with loose gravels near overhanging vegetation (Melcher & Schmutz, 2010). Barbel are a lithophilous, aggregative fish, typically inhabiting the middle reaches of European rivers from southeastern England and France in the west to the Black Sea basin in the east (Britton & Pegg, 2011). Spawning generally occurs in spring and summer, with the timing dependent on water temperature (Britton & Pegg, 2011). Fork lengths (FL) of mature female barbel vary between 209 (Vilizzi, Copp, & Britton, 2013) and 836 mm (Britton, Davies, & Pegg, 2013).

The spawning behaviours of salmonids and barbel have some similarities, especially redd construction where similar-sized females (Kondolf & Wolman, 1993) excavate pits in the substrate using rapid, lateral flexions of their bodies, prior to gamete deposition, fertilization and burial (salmonids: Burner, 1951; barbel: Baras, 1994). Despite similarities in spawning mechanisms, there is no quantitative information on the habitat and redd characteristics of spawning barbel. While these knowledge gaps can, at least in part, be informed by the salmonid literature (Table 1), there are important differences between the fishes, including timing of spawning seasons, incubation duration, egg sizes and burial depth. Globally, salmonids can spawn across the year, with timing dependent on latitude (Beechie, Moir, & Pess, 2008); in Britain, salmonid eggs are deposited in redds in winter, with emergence in the following spring. Thus, their eggs are exposed to fines for longer periods than the eggs of fast-incubating spring/summer spawning cyprinids (Bašić et al., 2017). Exception to this longer period of exposure to fines in salmonids includes spring-spawning steelhead trout *Oncorhynchus mykiss* with a 7 to 10 day incubation period (Goode et al., 2013; Phillips, Lantz, Claire, & Moring, 1975) versus 12 to 20 days in barbel (Bašić, Britton, Rice, & Pledger, 2018) under similar sediment but different temperature conditions (steelhead: 7–11°C, barbel: 16–18°C). Another key difference is the egg diameter, with salmonid eggs generally larger than cyprinid eggs (5–9 mm vs. 0.5–3.0 mm, respectively) (salmon: Aulstad & Gjedrem, 1973; Beacham & Murray, 1993; barbel: Pinder, 2001), indicating higher metabolic demand for salmonid eggs (Rombough, 2007). Salmonid eggs are also often buried deeper (salmonids: 11–30 cm depth; cyprinids 3–17 cm depth; Table 1), with oxygen availability decreasing as sediment depth increases (Freixa et al., 2016). Because of these differences, the effects of fine sediment on spawning success of barbel remains unclear and although Bašić et al. (2018) revealed delayed larval emergence from substratum with high sand content (>30% sand by mass), impacts on egg-to-emergence survival were not detected.

Understanding how spawning fishes influence river geomorphology and hydrology is also important, especially where significant numbers of large-bodied spawning fish are involved in redd construction, as observed in salmonid spawning events (Hassan, Tonina, & Buxton, 2015; Moore et al., 2007). Redd construction is a form of zoogeomorphology (Butler, 1995) whereby animals act as geomorphological agents to move sediments and change morphology, sediments and hydraulics. Female salmonids excavate a pit in the riverbed, during redd construction, that results in localized coarsening of the bed surface within the depression (Kondolf & Wolman, 1993). Sediment displaced during pit creation is transported and deposited downstream, forming the tailspill—a mound of sediment typically coarser than both the pit floor and surrounding bed (DeVries, 1997; Lapointe, Eaton, Driscoll, & Latulippe, 2000; Montgomery et al., 1996; Rennie & Millar, 2000). Such alterations to the physical environment can have important implications for sediment mobility in rivers (Buxton, Buffington, Tonina, Fremier, & Yager, 2015; Montgomery et al., 1996), with the extent of disturbance by some species equivalent to the displacement of gravels caused by flood events (Gottesfeld, Hassan, Tunnicliffe, & Poirier, 2004). Spawning salmonids can also alter hyporheic exchange and add marine-derived nutrients into the riverbed (Buxton, Buffington, Yager, Hassan, & Fremier, 2015). There are, however, some biological controls on redd building, with different species and sizes of fish having different zoogeomorphological effects (Moore et al., 2007; Riebe, Sklar, Overstreet, & Wooster, 2014).

The geomorphic impact of spawning barbel is yet to be quantified, but recent studies have revealed that their foraging behaviour can alter the size distribution and/or structure and so, mobility of fluvial sediments (Pledger, Rice, & Millett, 2014, 2017; Rice, Pledger,

TABLE 1 Summary of spawning habitat preferences of non-salmonid (Cyprinidae and Petromyzontiformes) and salmonid lithophils

Order	Species	Egg burial depth (cm) Top	Bottom	Water depth (cm)	Near bed velocity (cm/s)	D_{50} (mm)	Fines content (%) <1 mm	<2 mm
Cyprinids	Alburnoides bipunctatus				20–50[j]			
	Barbus barbus		20[m]	12–88[k] 40[m] 15–24[b]	16–96[k] 50[m] 25–49[j] 28–43[b]	2–60[k]	0.1–1.0[c]	3–46[c]
	Chondrostomus nasus	0[f]	30[f]	16–83[k] 10–61[f]	20–97[k] 30–130[f]	20–200[k] 17–28[f]		
	Squalius cephalus			10–30[e] 138[a]	15–75[e] 5[a]	23–55[a]		
	Phoxinus phoxinus		30[d]					
	Leuciscus leuciscus				30[l]			25[l]
	Notropsis lutipinnis	7[o]	8[o]	10–23[o]	21–31[o]			
	Tiaroga cobitis	8[p]	11[p]	5.8–19.4[p]				
	Luxilus albeolus	2[q]						
	Luxilus cerasinus	0[q]						
	Agosia chrysogaster	0[r]	1[r]	5–20				
Petromyzontiformes	Petromyzon marinus	8[n]	10[n]	10–17[h] 13–179[i]	19–39[h] 50–150[i]			2[h]–25[g]
Salmonids	Salmo salar	15[e]	30[e]	20–50[k] 17–76[a] 15–55[m]	35–65[k] 35–80[a] 35–80[m]	15–16.6[i] 20–30[a] 16–64[k] 10–38[m]	5.4[a] 10[k] 15[o] 3–19[m]	5–17[m]
	Salmo trutta	0[p]	25[p]	15–45[k] 6–82[a]	20–55[k] 11–80[a]	5.8–50[i] 8–128[a] 16–64[k]	8–12[a]	10[k]
	Oncorhynchus kisutch	15[e]	35[e]			5.4–35[i]	7.5–21[h]	
	Oncorhynchus keta	15[e] 9.8[n]	35[e] 48.9[n]			9.6–62[i] 12–23[n]		
	Oncorhynchus tshawytscha	15[e]	50[e]	30–950[g]	25–225[g]	10.8–69[i]		11[c]
	Oncorhynchus gorbuscha	15[e]	35[e]			6.5–11[i]		
	Oncorhynchus nerka	10[e]	25[e]		10–15[j]	14.5–48[i]		
	Oncorhynchus clarkii	10[e]	20[e]	6–27[l]		3.2–25.4[l]	3–17.9[l]	19[c]
	Oncorhynchus mykiss	10[e]	25[e]			10.5–46.3[i]	12[h]	16[c]
	Salvelinus confluentus	10[e]	20[e]					11[c]
	Salvelinus fontinalis	5[e]	15[e]	30–70[d]		7.2–10.7[i]		10–22[f]

Note: Non-salmonid (Cyprinids and Petromyzontiformes) sources: Arlinghaus & Wolter, 2003[a]; Baras, 1994[b]; Bašić, Britton, Rice, & Pledger, 2017[c]; Bless, 1992[d]; Cowx & Welcomme, 1998[e]; Duerregger et al., 2018[f]; Gardner, Coghlan, & Zydlewski, 2012[g]; Hogg, Coghlan, Zydlewski, & Simon, 2014[h]; Manion & Hanson, 1980[i]; Mann, 1996[j]; Melcher & Schmutz, 2010[k]; Mills, 1981[l]; Pinder, Clough, Morris, & Fletcher, 2009[m]; Smith & Marsden, 2009[n]; McAuliffe & Bennett, 1981[o]; Vives & Minckley, 1990[p]; Maurakis & Woolcott, 1993[q]; Minckley & Barber, 1971[r]. Salmonid sources: Armstrong et al., 2003[a]; Bowerman, Neilson, & Budy, 2014[b]; Bryce, Lomnicky, & Kaufmann, 2010[c]; Curry, Noakes, & Morgan, 1995[d]; DeVries, 1997[e]; Franssen et al., 2012[f]; Hanrahan, Dauble, & Geist, 2004[g]; Kondolf, 2000[h]; Kondolf & Wolman, 1993[i]; Lorenz & Eiler, 1989[j]; Louhi et al., 2008[k]; Magee, McMahon, & Thurow, 1996[l]; Moir, Soulsby, & Youngson, 2002[m]; Montgomery, Buffington, Peterson, SchuettHames, & Quinn, 1996[n]; O'Connor & Andrew, 1998 [o]; Ottaway, Carling, Clarke, & Reader, 1981[p].

Toone, & Mathers, 2018), with larger fish having greater effects (Pledger, Rice, & Millett, 2016). For example, large-bodied cyprinids, including adult barbel (>500 mm), disturbed 26% of riffle substrates per day, and displaced clasts up to 90 mm in size (Pledger et al., 2017). Thus, due to their size and abundance in some rivers, we hypothesize that spawning barbel are effective zoogeomorphic agents

and that the impacts of their spawning activities may be similar to those of redd-excavating salmonids.

The aim of this study was to investigate the two-way interaction between barbel and their spawning environment. Three questions are addressed: what flow and substrate characteristics are selected by spawning barbel, what is the likely reproductive potential of selected sites and what are the impacts of spawning on substrate characteristics? Using a comparative approach across three English rivers, the Teme (western England), Great Ouse (eastern England) and Idle (central England), objectives were to: (a) assess grain-size characteristics of surface (n = 3 rivers) and subsurface (n = 2 rivers) sediments at barbel spawning sites and use these in conjunction with salmonid spawning models to predict the reproductive potential of barbel spawning sites and estimate egg survival; (b) quantify flow characteristics (water velocity and depth) and oxygen availability at barbel spawning sites; (c) characterize barbel redds and identify how their construction alters surface sediment composition and (d) use published data on barbel spawning and measurements from this study to determine how effective salmon-derived models are at estimating barbel reproductive potential and egg survival. The application of salmonid models to barbel is considered appropriate given the paucity of knowledge on barbel spawning requirements, and the similarities in female lengths and their redd building characteristics. However, we acknowledge that future work is needed to develop barbel-specific models, given the differences in physiology, timing of spawning season, density of spawners, incubation duration and egg survival rates. The salmonid models thus provide initial, first-order estimates of barbel reproductive potential and egg survival.

2 | MATERIALS, METHODS AND DATA ANALYSIS

2.1 | Study sites

The study was conducted in the rivers Great Ouse, Teme and Idle, three gravel-bed rivers located in the east, west and centre of England, respectively (Table 2). All three rivers run through predominantly agricultural landscapes and maintain low gradients (<0.33%; Downs & Thorne, 1998; Neal et al., 2000; Severn Rivers Trust, 2012). Study reaches were representative of the "Barbel Zone" (Huet, 1959; Figure 1) and hosted translocated, natural or stocked barbel populations (Table 2). Other lithophilous fish occupy the study reaches (Table 2) and utilize the same sites and gravels as barbel during spawning. The reproductive success of barbel is limited in some of the indigenous British range of Eastern England, such as in the river Great Ouse, where populations are supported by hatchery-reared or translocated fish (Antognazza, Andreou, Zaccara, & Britton, 2016; Bašić et al., 2017). In contrast, populations in their non-indigenous British range of Western England tend to have greater reproductive success (Gutmann Roberts & Britton, 2018).

Study sites were selected on the Teme, Idle and Great Ouse (n = 13, 20 and 13, respectively; Figure 1) on the basis of direct spawning observations, and/or because they matched existing qualitative descriptions of spawning habitats—riffles with "coarse" substratum and shallow, "moderate to high-velocity flow" (Baras & Cherry, 1990; Hunt & Jones, 1975; Lucas & Batley, 1996). Sampling occurred under baseflow conditions on the river Idle in April 2011, Great Ouse in September 2014 and 2015 and Teme in May to July 2015 to 2017. Thus, sampling occurred either before or after barbel spawning, to avoid disturbing spawning aggregations and ensure collection of ecologically relevant data.

2.2 | Riffle surface and subsurface sediment and analyses

To assess the size distribution of surface sediments at coarse-grained spawning riffles, 300- to 400-count Wolman samples (Rice & Church, 1996) were used at each site on each river. Grains were selected using a systematic grid-sampling scheme, by pacing across the width of each spawning riffle and, at each step, blindly selecting a grain to measure with a gravelometer and then taking a step downstream and returning in the opposite direction.

TABLE 2 Geomorphological, ecological and biological characteristics of the three study rivers

|	Idle	Great Ouse	Teme
River location	Nottinghamshire	Bedfordshire	Shropshire, Herefordshire and Worcestershire
Type	Gravel-bed	Gravel-bed	Sandstone/mudstone
Drainage/catchment area (km^2)	842	8,600	1,648
Water source	Surface and groundwater	Groundwater	Surface and groundwater
Length of river (km)	42	230	134
Geology	Sandstone, coal measures, magnesium limestone	Limestone, mudstone	Sandstone and mudstone
Dominant morphologies	Pool-riffle	Pool-riffle	Pool-riffle
Predominant barbel populations	Natural	Stocked	Translocated
Common fish species	*Rutilus rutilus, Abramis brama*	*Rutilus rutilus, Abramis brama*	*Squalius cephalus, Leuciscus leuciscus, Phoxinus phoxinus, Alosa* spp., *Petromyzon marinua*
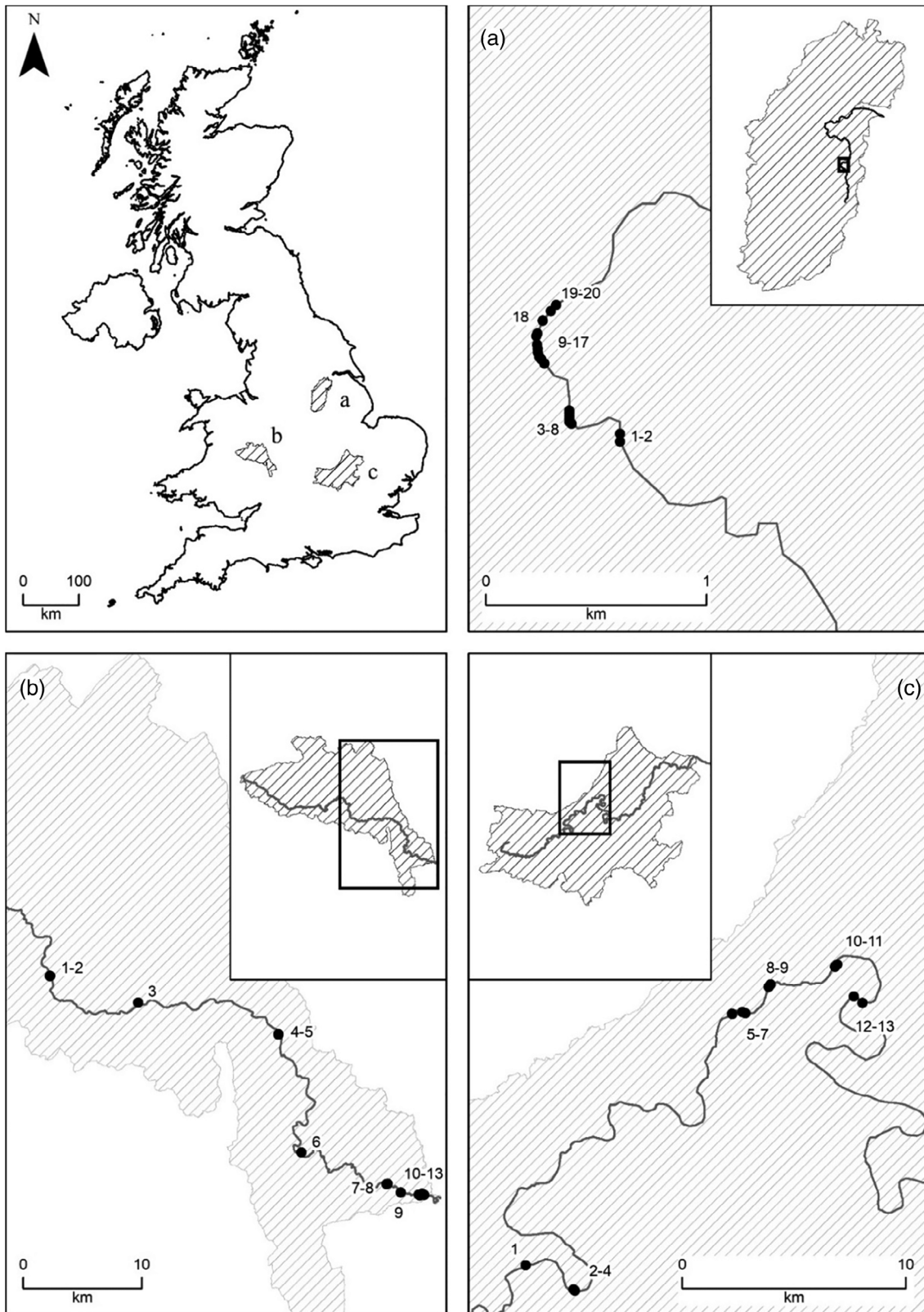
FIGURE 1   Locations of river catchments and study sites inset within the rivers (a) Idle, (b) Teme and (c) Great Ouse

Subsurface sediments were characterized from 10 samples collected at random from within 10 sites in the river Teme and 13 sites in the river Great Ouse, using a McNeil sampler and Koski plunger (coring tube dimensions: 16 × 26 cm; Bunte, Abt, & Station, 2001). Three sites sampled for surface sediments (sites 4, 5 and 9) in the river Teme could not be sampled for subsurface sediments due to issues

preventing access. Surface sediment was removed from the McNeil sampler by hand and then single core samples of subsurface sediments were stored in individual air-tight containers and transported to the laboratory for processing. No subsurface samples were collected from the Idle. In the laboratory, bulk sediment samples were oven-dried for 24 hr at 100°C and sieved into half-phi size fractions using a sieve shaker before weighing on Ohaus Navigator scales, recorded to the nearest 0.1 g. Fines from individual samples were then recombined, mixed and subsampled (10 g), before Loss On Ignition (LOI, %) was performed to determine organic content (Heiri, Lotter, & Lemcke, 2001).

Surface and subsurface samples were characterized using grain-size percentiles (where D_5, D_{10}, D_{25}, D_{50}, D_{75}, D_{84}, D_{90} and D_{95} are the grain sizes [mm] for which 5, 10, 25 50, 75, 84, 90 and 95% of the particles are finer, respectively) from cumulative distribution curves, with mean grain size, sorting, skewness and kurtosis values calculated using Trask's method (1932; Equations 1 to 4).

$$\text{Mean} = \frac{D_{25} + D_{75}}{2} \tag{1}$$

$$\text{Sorting} = \sqrt{\frac{D_{25}}{D_{75}}} \tag{2}$$

$$\text{Skewness} = \frac{D_{25} * D_{75}}{D_{50}{}^2} \tag{3}$$

$$\text{Kurtosis} = \frac{D_{75} - D_{25}}{2 * (D_{90} - D_{10})} \tag{4}$$

To determine the degree of surface armouring, surface D_{50} was divided by subsurface D_{50} with ratios exceeding 1.0 indicative of armoured beds. Summary statistics were used to compare mean values between rivers.

Proportions by mass of fine sediment (<2 mm), sand (0.064–2 mm diameter), silt (≤0.064 mm) and organic matter were determined only for subsurface sediments. Surface and subsurface sediment parameters (D_5, D_{50}, D_{95}, mean grain size, sorting, skewness, kurtosis and percentage of fine sediment) were compared between rivers using one-way ANOVAs, following normality and homogeneity tests. Subsurface proportions of sand, silt and organic matter for each river were compared with one-way ANOVAs, with Tukey's post hoc tests. All analyses were carried out in R version 3.4.0 (R Core Team, 2017).

2.3 | Characterizing site dimensions, flow, oxygen availability and analysis

Measurements of water velocity were made using a Valeport Open Channel Flow Meter (Model 801), set to provide a mean value measured over 60 seconds. Measurements were made at the same 20, 10 and 13 riffles on the rivers Idle, Teme and Great Ouse respectively, where surface sediments were collected. Velocity was measured at two depths: near the bed surface (≈2.5 cm from the bed; m/s) and at 0.6 depth (distance from the water surface; m/s). Sampling occurred at the intersections of multiple flow-parallel (n = 4) and flow-perpendicular (Idle = 5, Teme = 4; Great Ouse = 4) transects, which were systematically distributed across each of the site widths and lengths, respectively. This gave 20 transect intersection points (points hereafter) for 20 sites on the river Idle, 16 points for the 10 sites on the river Teme and 16 points for 13 sites on the river Great Ouse. Concomitantly, a depth measurement was made at each point and multiple wetted width and site length measurements (Idle: n = 4; Teme: n = 1–4, Great Ouse: n = 4) were made per site. Data were collected from the Idle in April 2011, Teme in August and September 2015 and the Great Ouse in August 2016.

Measurements of dissolved oxygen (mg/L) were taken during the daytime. For the Great Ouse (August 2016; 4 sites, 9 replicates per site) and Idle (April 2011; 20 sites, 4 replicates per site), measurements were made approximately 1 cm below the water surface using a Hanna probe. For the Teme (May to August 2015; 5 sites, 2–4 replicates per site), data were extracted from the Environment Agency (2017) water quality monitoring data. All data were collected under summertime baseflow conditions.

Summary statistics were used to quantify water velocity (near-bed and 0.6 depth), depth and oxygen concentrations. For all metrics, site means derived from within-site measurements were averaged to give river-averaged values.

2.4 | Barbel redd characteristics and their impact on surface sediment

The characteristics of six barbel redds at four sites (site 4 at Stanford Bridge: 2 redds; 3 sites at Powick; 10, 11, 12: 4 redds) on the River Teme were measured between May 2015 and June 2017, 2 to 8 days post-spawning. Sample size was constrained by a combination of low numbers of observed redds, accessibility and high turbidity within the river Teme, that reduced visibility and the ability to accurately measure the redds. Three redds measured in 2017 were confirmed as barbel redds by rapid egg assessments that involved disturbing the top 50 mm of tailspill sediment using a pencil in a circular motion, with a hand-held aquaria net placed behind the redd to collect the eggs that were then identified by their colour and morphology (APEM, 2009; Pinder et al., 2016). The other three redds were not conclusively identified as barbel redds, but it was considered unlikely that they were constructed by other lithophils present in the Teme, given that minnow *Phoxinus phoxinus* are too small for their gravel movements to be mistaken for barbel and chub *Squalius cephalus* are not redd constructors (South East River Trust, 2018; Table 2). Sea lamprey *Petromyzon marinus* are found in the river Teme but generally spawn later in the year and create a more circular redd with large grains deposited around the edge (Pinder, Hopkins, Scott, & Britton, 2016). Shad *Alosa* spp. are surface spawners and are thus unlikely to influence bed morphology (Acolas et al., 2004).

Single length and width measurements were made of the two component parts of each redd pit and tailspill (Supporting Information, Figure S1)—the pit (the excavated hole or depression in the bed) and the tailspill (an area where grains, mobilized from the pit during spawning are deposited). Single depth measurements from the water surface to the pit bottom, tailspill top and adjacent river bed (datum) were recorded and used to calculate pit depth and tailspill height by subtracting the depth of adjacent river bed. Length, width and depth measurements were made to the nearest cm (±0.5 cm). Surface sediment samples were collected from each of the pit and tailspill areas to investigate differences in grain-size distributions between these areas and the surrounding riverbed. This was achieved via 30-count Wolman samples. Only 30 clasts were measured in each redd area due to the small redd areas (A_{PIT} = 1.2 ± 0.2 m^2, $A_{TAILSPILL}$ = 2.3 ± 0.3 m^2; mean ± 95% CI) and to minimize redd disturbance. The largest grains visually observed on the tailspill surfaces were measured (mm) to investigate the maximum particle size moved by barbel during redd construction.

The areas (A, m^2) of pits and tailspills were calculated with Equation (5) as ellipses as per Ottaway et al. (1981) from measured values of pit and tailspill lengths and widths.

$$A = \text{length} * \text{width} * \pi \tag{5}$$

The total area of each redd was calculated by combining pit (A_{PIT}) and tailspill ($A_{TAILSPILL}$) areas. The net volume (V) of each pit and tailspill was then calculated as,

$$V = \left(\frac{4}{3} * \pi * \text{depth} * \frac{\text{length}}{2} * \frac{\text{width}}{2} \right) \div 2 \tag{6}$$

assuming that both component parts were half-ellipsoid (McCart, 1969) and the pit depth and tailspill heights were used as vertical parameters in calculations. Volume of sediment displaced during spawning was assumed to be the volume of the tailspill.

Pair-wise Student's t tests in R (R Core Team, 2017 were carried out to compare surface sediment characteristics (D_5, D_{50}, D_{95}, mean, sorting, skewness, kurtosis and percent fines) between the pit, tailspill and surrounding riverbed.

2.5 | Barbel reproductive potential and geomorphological controls

To assess the reproductive potential of barbel spawning sites, a salmonid-specific model was parameterised, as there was no barbel- or cyprinid-specific model available. For salmonids, fork length (FL) is positively correlated with redd area and the maximum size of particles that can be moved by spawning fish (Crisp & Carling, 1989), which can in turn be used to estimate reproductive potential (Riebe et al., 2014). These measurements are taken from dead or dying spawned fish, something not possible for barbel as their post-spawning mortality is very low and they tend to disperse after spawning (Gutmann

Roberts, Bašić, & Pledger, 2019; Hancock, Jones, & Shaw, 1976). To provide a consistent set of predictions based on FL, a salmonid relationship from Riebe et al. (2014) was used to estimate barbel redd area (m^2; "A_{REDD}"; Equation 7), rather than only using our measured redd dimensions.

$$A_{REDD} = 3.3 \left[\frac{FL}{600} \right]^{2.3} \tag{7}$$

An ANOVA was carried out to compare predicted redd area (from the eight fork lengths measured in the Teme) to the six measured redds.

The maximum or threshold particle size (D_T, mm) that a barbel of a given length (mm) can displace during redd construction was estimated using Equation (8) (Riebe et al., 2014).

$$D_T = 115 \left(\frac{FL}{600} \right)^{0.62} \tag{8}$$

Barbel fork lengths for estimating D_T (Equation 8) were derived from the river Teme (n = 8 females sampled from between sites 10 and 13; Gutmann Roberts, Hindes, & Britton, 2019), river Great Ouse (n = 29 sampled from between sites 6 and 7; Twine, 2013) and river Idle (n = 4 sampled from near sites 1 and 2; Pledger, 2015). Then, using D_T calculated for the mean FL of barbel from these rivers (Equation 8), the fraction of moveable particles (F_M) on riffles was calculated:

$$F_M = \left[1 + e^{-1.702z} \right]^{-1} \tag{9}$$

$$z = \left[\frac{\log\left(\frac{D_T}{D_{50}} \right)}{\log\left(\frac{D_{84}}{D_{50}} \right)} \right] \tag{10}$$

Equation (9) approximates a cumulative log-normal distribution (Riebe et al., 2014) and z represents the difference between D_T and D_{50} expressed as a multiple of the SD (Bowling, Khasawneh, Kaewkuekool, & Cho, 2009), where log (D_{50}) and log (D_{84}/D_{50}) are the mean and SD of the log-normal grain-size distribution.

Next, the spawning capacity, expressed as the potential number of redds per riffle area (N_{REDDS}; redds m^{-2}, Equation 11; Riebe et al., 2014), was calculated using redd area estimates (A_{REDD}) and the proportion of riffle covered in moveable particles (F_M).

$$N_{REDDS} = \frac{F_M}{A_{REDD}} \tag{11}$$

Reproductive potential of barbel at a site, N_{EGGS} (eggs m^{-2}, Equation 12; Riebe et al., 2014), was calculated using fecundity estimates F (A). The fecundity ($F(A)$; Equation 13a) of fish of a given length (mm), can be predicted from salmonid input parameters (Riebe et al., 2014; Quinn, 2005).

$$N_{EGGS} = \frac{F_M F}{A_{REDD}} \tag{12}$$

$$F(A) = 8.1\,FL - 1450 \tag{13a}$$

The reproductive potential of barbel at each of the sites was also calculated using the barbel-specific redd measurements from this study, with the mean redd area ($A_{PIT} + A_{TAILSPILL}$ from Equation 5) used instead of A_{REDD} (Equation 7), and using the threshold grain-size D_T from the largest grain measured from barbel redd tailspills. A barbel fecundity-length relationship (F(B), Equation 13b) was also determined from 15 manually stripped females from the river Trent at a hatchery (Calverton fish farm, unpublished) and from data on 33 barbel (length minimum–maximum: 314–740 mm) extracted from Hancock (1979).

$$F(B) = 0.8e^{-6}FL^{3.8} \tag{13b}$$

This enabled a comparison of reproductive potential predicted from salmonid models (12) using salmonid- vs. barbel-specific input parameters for A_{REDDS}, D_T and F. High-density barbel spawning observations (Baras, 1994) were also used to estimate the maximum number of redds per square metre (N_{REDDS}) across a site in the river Meuse, where the fraction of moveable particles is assumed to be 1, due to high and even coverage of redds and in the absence of any grain-size data or redd measurements. Baras (1994) reported 2 years of data, but only successful spawning observations from 1990 were used as this year had the most successful spawning attempts and therefore provides a maximum estimation of spawning potential. The observations are from a 150 m^2 spawning riffle with 71 "successful" spawning attempts in one season, with data on 19 female barbel, with data from 5 females omitted in the original study due to lack of certainty around observations. Assuming no redd superimposition, the spawning riffle area divided by the number of redds (assumed to be number of successful spawning attempts) provides an estimate of redd area.

Barbel egg survival estimates provide indications of the potential suitability of subsurface spawning substratum in the study rivers; however, the absence of suburface sediment data for the river Idle meant these calculations were only completed for the rivers Great Ouse and Teme. To predict the potential effect of bed sediment condition (specifically fines content) on barbel recruitment at individual sites within the two study rivers, egg survival was estimated using salmonid models (Equations 14 and 15; Peterson & Metcalfe, 1981).

$$SI = \frac{S_c}{16} + \frac{S_f}{8} \tag{14}$$

$$Survival\,(\%) = 83 - 29\,SI - 6(SI * Silt\,(\%)) \tag{15}$$

Subsurface sand content was parameterized using a sand index (SI), which gives weighting to finer sands compared to the larger sands due to their greater effect on reproductive success. SI calculations (Equation 14; Lapointe et al., 2004) use the proportion of coarse sand

(S_c = 0.5–2 mm) and fine to medium sand (S_f = 0.06–0.5 mm). Given the lack of information on the synergistic effects of silt- and sand-sized particles on barbel egg development and emergence, Equations (14) and (15) were used and derived from salmonid data. The salmonid model (Equation 15) was used for the sediments found in the river and also against the SI only by inputting 0% silt for all sites to determine the effect of silt. Published data from Bašić et al. (2018) were used to relate the SI to observed barbel survival, which was then compared with values predicted from Equation (15). Successful incubation was defined as at least 50% estimated survival, as per Kondolf (2000).

Comparisons of survival potential between the two rivers were carried out using a one-way ANOVA, following normality and homogeneity tests. Values given throughout the results are means (±95% confidence intervals), unless stated otherwise.

3 | RESULTS

3.1 | Barbel spawning site characteristics

Spawning riffle areas varied across rivers, from 37 ± 7 m^2 in the Great Ouse to 108 ± 10 and 500 ± 249 m^2 in the Idle and the Teme, respectively. Riffle surfaces utilized by spawning barbel across the three rivers were generally coarse (D_{50} = 23.41 ± 4.87 mm), well sorted (0.66 ± 0.03) and characterized by positively skewed (0.97 ± 0.05) and leptokurtic (0.24 ± 0.01) distributions. Fine sediments across the three rivers made up on average 2.3 ± 0.9% of the surface bed material.

There was no significant difference in the surface sediment D_5 between rivers (ANOVA; $F_{2,\,43}$ = 0.57, p = 0.57), with mean values ranging from 5.4 to 6.7 mm (Figure 2). The D_{50} varied significantly between the three rivers (ANOVA; $F_{2,\,43}$ = 7.662, p = 0.001), with the rivers Teme and Great Ouse maintaining the coarsest (mean = 27.9 mm) and finest (mean = 19.3 mm) sediments, respectively (Figure 2). Post hoc tests revealed that the river Teme D_{50} was significantly larger than in the Great Ouse and Idle (p < 0.01 and p = 0.04, respectively), but that the Idle and Great Ouse values were similar (p = 0.22). The D_{95} also varied significantly between rivers (ANOVA; $F_{2,\,43}$ = 7.19, p < 0.01), with the Teme having the largest (76.6 mm) and the Idle having the smallest (53.0 mm) (Figure 2). As with the D_{50}, post hoc tests showed that the river Teme sediments were significantly coarser than the Great Ouse and Idle sediments (p = 0.01 and p < 0.01, respectively), but Great Ouse and Idle sediments were not significantly different (p = 0.98). Mean grain size also differed significantly between the three rivers (ANOVA; $F_{2,\,43}$ = 5.22, p < 0.01), with mean particle sizes largest in the Teme (29.9 mm) and smallest in the Great Ouse (21.4 mm) (Figure 2). There were no significant differences in mean grain sizes between the rivers Idle and the Great Ouse or the Teme (p = 0.42 and p = 0.08, respectively), but mean values were significantly higher between the river Teme and Great Ouse sediments (p < 0.01). There was no significant difference between the sorting ($F_{2,\,43}$ = 2.51, p = 0.09; Figure 2), skewness ($F_{2,\,43}$ = 2.18, p = 0.13, Figure 2) or kurtosis ($F_{2,\,43}$ = 1.70, p = 0.20; Figure 2) values of the three rivers. There was also no significant
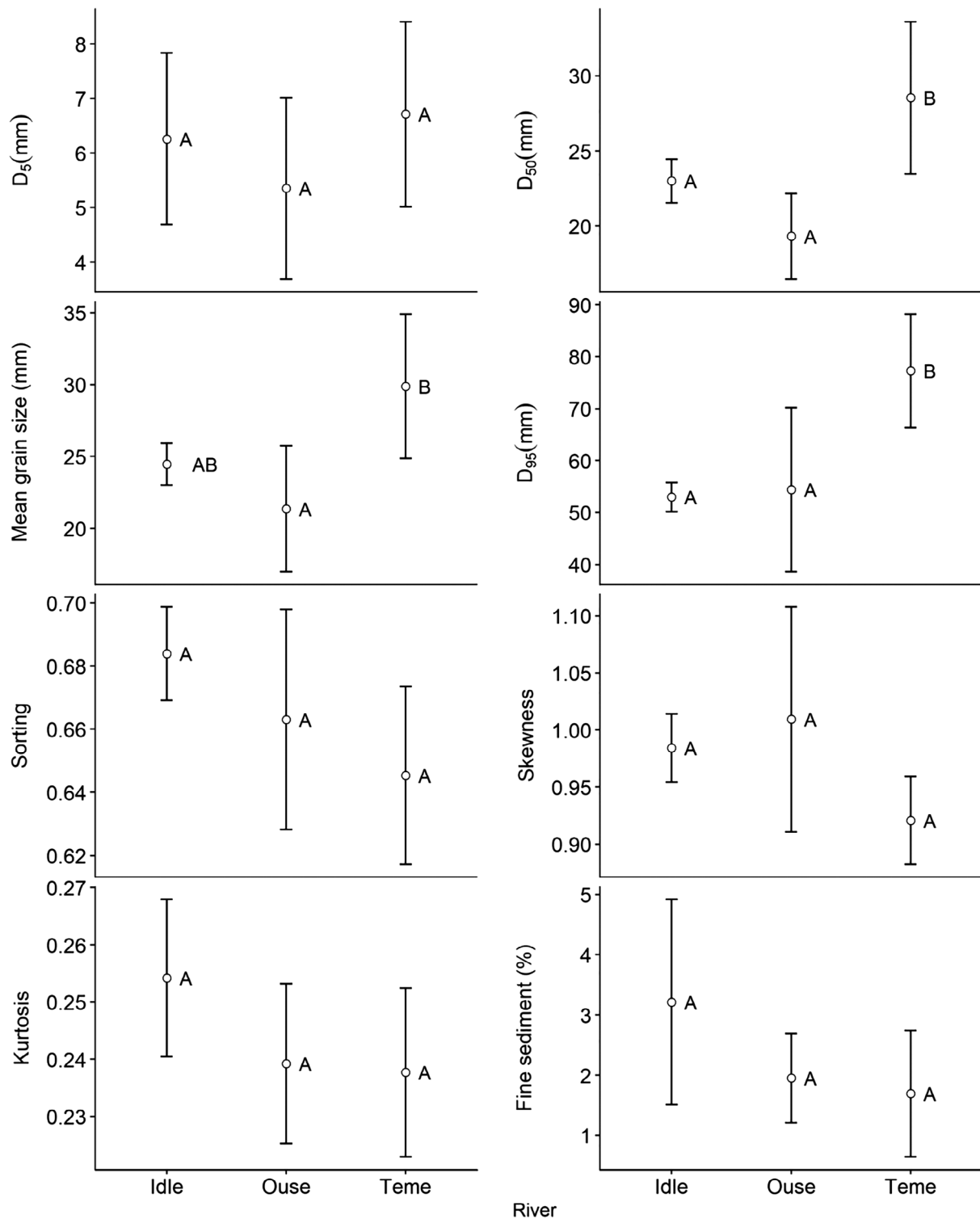
FIGURE 2 Characteristics of surface sediments within the rivers Idle (n = 20), Great Ouse (n = 13) and Teme (n = 13). Values represent means (±95% confidence interval) and letters right of bars indicate homogeneous groups

difference in the percentage of surface fine sediment between the three rivers ($F_{2, 43}$ = 1.35, p = 0.27, Figure 2).

Subsurface sediments from the rivers Great Ouse and Teme were relatively coarse (D_{50} = 12.24 ± 1.15 mm), well sorted (0.38 ± <0.01) and characterized by positively skewed (0.62 ± <0.01) and leptokurtic

(0.29 ± <0.01) distributions. D_5, D_{50}, D_{95}, mean grain size, sorting, skewness and kurtosis values were similar between the two rivers (Table 3). Subsurface sediments were comprised of 20.30 ± 2.85% fines, of which the majority (19.99 ± 3.14%) was sand and only a small proportion was silt (0.32 ± 0.29%). Organic content across the two

	Teme	Great Ouse	Significance	F value
D_5 (mm)	0.47 ± 0.14	0.48 ± 0.08	0.94	0.006
D_{50} (mm)	12.83 ± 2.95	11.66 ± 2.60	0.52	0.435
D_{95} (mm)	50.07 ± 7.44	48.35 ± 7.97	0.74	0.115
Mean grain size (mm)	15.21 ± 3.02	13.51 ± 2.13	0.30	1.112
Sorting	0.38 ± 0.04	0.39 ± 0.05	0.76	0.098
Skewness	0.62 ± 0.06	0.62 ± 0.08	0.92	0.012
Kurtosis	0.29 ± 0.01	0.29 ± 0.04	0.94	0.007
Fine sediment (<2 mm, %)	18.85 ± 4.88	21.76 ± 4.53	0.35	0.923
Sand (%)	18.38 ± 4.83	21.59 ± 4.46	0.30	1.147
Silt (%)	0.47 ± 0.10	0.17 ± 0.09	>0.001	23.780
Organic matter (%)	2.19 ± 0.64	2.36 ± 0.60	0.68	0.182

TABLE 3 Subsurface sediment metric means (±95% confidence intervals) for the river Teme ($n = 10$) and river Great Ouse ($n = 13$) and the statistical significance (P) and F values from ANOVAs (df = 21), apart from organic matter where Teme ($n = 10$) and Great Ouse ($n = 7$)
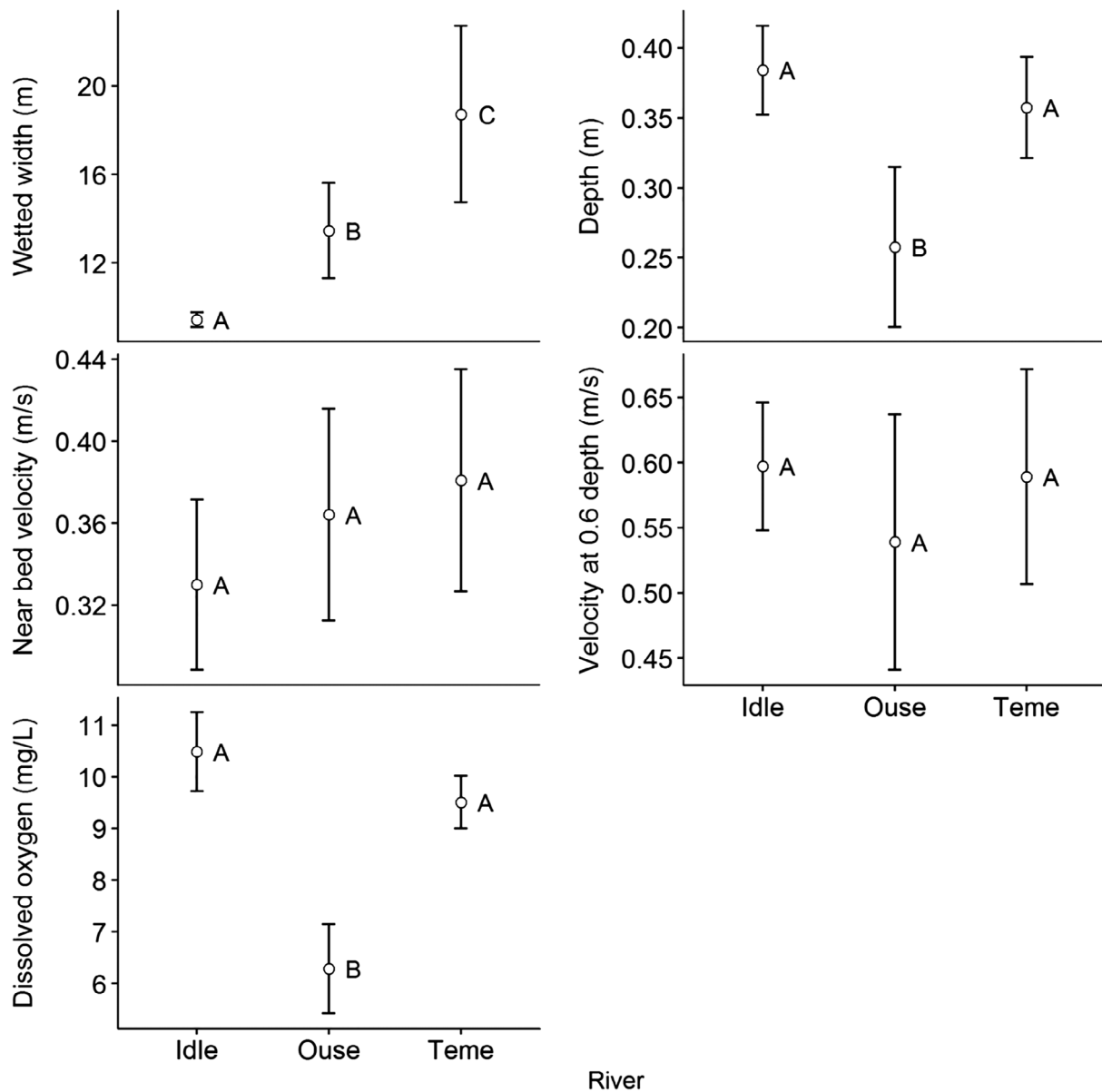

FIGURE 3 Flow characteristics and dissolved oxygen across three rivers: Idle ($n = 20$), Great Ouse ($n = 13$, four for oxygen only) and Teme ($n = 10$, five for oxygen only); wetted width (m), depth (m), near-bed velocity (m s^{-1}), velocity at 0.6 depth (m/s) and amount of dissolved oxygen (mgL^{-1}). Values represent means (±95% confidence interval) and letters right of bars indicate homogeneous groups

rivers was 2.13 ± 0.45%. There was no significant difference between rivers in terms of the proportion of subsurface fines (ANOVA; $F_{1,21}$ = 0.92, p = 0.35) or sand (ANOVA; $F_{1, 21}$ = 1.15, p = 0.30, Table 3). There was, however, a significant difference in silt content (ANOVA; $F_{1,21}$ = 23.78, p < 0.01, Table 3) between rivers, with river Teme subsurface sediments (0.47 ± 0.09%) containing higher proportions of silt than river Great Ouse subsurface sediments (0.17 ± 0.08%). Subsurface sediments at four sites in the river Teme contained >0.5% silt and these were located between Ashford Carbonel (site 2) and Powick (site 11), whereas subsurface sediments at only one river Great Ouse site (2) contained >0.5% silt (Figure 4). There was no significant difference between rivers in terms of the organic content of fines (ANOVA; $F_{1, 15}$ = 0.18, p = 0.68, Table 3). Both the Teme and the Ouse displayed armoured beds, with the ratio of surface-to-subsurface D_{50} maintaining values of 2.2 (± 0.4) and 1.8 (± 0.4), respectively.

Wetted width (m) was significantly different between the three rivers (ANOVA: $F_{2, 38}$ = 18.64, p < 0.001), with post-hoc analyses showing that each river differed significantly from each other (p < 0.02). The river Teme was the widest river (18.72 ± 4.60 m) and the river Idle was the narrowest (9.44 ± 0.35 m, Figure 3). Depth (m) differed significantly between the three rivers ($F_{2, 40}$ = 9.85, p < 0.001, Figure 3), with post-hoc analyses indicating that the Teme and Idle were not significantly different (p = 0.68), but that the Ouse was significantly different to both the Teme and Idle (p = 0.02 and p < 0.001, respectively). Near-bed and 0.6-depth velocities (m/s) were not significantly different between the rivers ($F_{2, 40}$ = 1.14, p = 0.33 and $F_{2, 40}$ = 0.72, p = 0.49, respectively; Figure 3). Dissolved oxygen levels differed significantly between the three rivers ($F_{2, 26}$ = 12.53, p < 0.001, Figure 3); however, the post hoc tests showed that the Teme and Idle were not significantly different (p = 0.42) but that the Ouse had significantly lower dissolved oxygen than the Teme and Idle (p = 0.01 and p < 0.01, respectively).

3.2 | Barbel redd characteristics

In the six measured redds, the tailspill tended to be longer and wider than the pit, with a mean difference of 29 ± 22 and 19 ± 17 cm, respectively (Table 3). Mean tailspill height was 14 ± 5 cm and pit depth ranged between 4 and 11 cm, with a mean difference in height of the tailspill and depth of the pit of 20.0 ± 8.8 cm. Total redd area ranged from 1.37 to 9.11 m² at sites 10–12, and 2.23–2.58 m² at site 4. The mean total redd area was 3.47 ± 0.42 m². The area of the tailspill was larger than that of the pit for five of the six redds. Pit volumes ranged from 1,900 to 34,819 cm³ (14,390 ± 5,338 cm³; mean ± 95% CI) and the tailspill volume ranged from 0 to 234,834 cm³ (74,754 ± 43,284 cm³; mean ± 95% CI). Pit volume was larger than tailspill volume for two of the redds, and for four of the redds, the opposite relationship was found. The largest grain diameter found in barbel tailspills was 110 mm, providing a barbel-specific estimate of the threshold grain size (D_T).

Sediments within the pit and tailspill were coarse (mean grain size = 22.2 ± 9.5 and 28.2 ± 3.7 mm, respectively) and moderately

TABLE 4 Site-averaged values for redd pit and tailspill dimensions and surface sediment parameters (mean ± 95% confidence intervals) at Powick (n = 4) and Stanford Bridge (n = 2) on the river Teme

Parameter	Redd pit	Redd tailspill
Length (cm)	60 ± 20	89 ± 28
Width (cm)	63 ± 20	82 ± 24
Depth/height (cm)	−7 ± 1	14 ± 5
Area (m²)	1.19 ± 0.15	2.28 ± 0.26
Volume (cm³)	14,390 ± 5,338	74,754 ± 43,284
D_5 (mm)	4.4 ± 3.3	4.4 ± 1.5
D_{50} (mm)	21.6 ± 14.3	25.1 ± 5.4
D_{84} (mm)	36.4 ± 18.6	51.1 ± 11.2
D_{95} (mm)	54.5 ± 29.7	71.5 ± 16.7
Mean grain size (mm)	22.2 ± 13.1	28.2 ± 5.1
Sorting	0.58 ± 0.01	0.62 ± 0.01
Skewness	0.90 ± 0.01	1.01 ± 0.01
Kurtosis	0.25 ± 0.01	0.25 ± 0.01
Fine sediment (<2 mm, %)	3.2 ± 1.4	0.7 ± 0.6

well sorted (sorting = 0.58 ± 0.07 and 0.62 ± 0.05 mm, respectively) (Table 4). While fine sediments appeared more prevalent at the surface of the pit than at the surface of the tailspill (Table 4), the difference was not significant (p > 0.05; Table 5). Surface grain-size parameters of the pit and tailspill sediments were similar (t tests, p > 0.05 in all cases; Table 5). Generally, levels of fine sediment found on the redd surfaces were low, but surficial sediments of the pit at site 10 were fines-rich (26.7% fines by area) and finer than the surrounding bed (6.4% fines by area). There were no significant differences between the surface grain-size characteristics of the pit and tailspill areas compared with their surrounding riffle for D_5, D_{50}, D_{95}, mean, sorting, skewness, kurtotsis and percentage of fine sediment (Table 5).

3.3 | Barbel reproductive potential and geomorphological controls

As mean barbel FLs were 464, 616 and 651 mm for the rivers Idle, Great Ouse and Teme respectively, the maximum particle size that barbel could move (D_T, Equation 8) was estimated to be 98, 117 and 121 mm, respectively (Table 6). This salmon-derived estimate suggested an 11 mm overestimation for the Teme, relative to the largest recorded particle size displaced by spawning barbel (110 mm at Powick). Median grain size was significantly different between rivers (Subsection 3.1), as was D_{84} (mm; ANOVA: $F_{2, 43}$ = 5.07, p = 0.01), with post hoc tests showing the Ouse and Idle were not significantly different (p = 0.86), but that the Teme was significantly different to the Ouse and the Idle (p = 0.02 and p = 0.03, respectively). Mean (95% CI) D_{84} for the Teme was 51 (±8) mm compared to 37 (±10) mm in the Ouse and 39 (±2) mm in the Idle. The fraction of moveable particles, as calculated from salmon-derived models, was not significantly

TABLE 5 Paired *t* test comparisons between pit and tailspill surface characteristics of barbel redds and the adjacent riffle surface characteristics

	Pit vs. tailspill		Pit vs. riffle		Tailspill vs. riffle	
	t	*P*	*t*	*P*	*t*	*P*
D_5	−0.01	0.99	−0.48	0.65	−0.88	0.42
D_{50}	−0.55	0.61	−0.37	0.73	0.08	0.94
D_{95}	−1.63	0.16	−1.90	0.12	−1.27	0.26
Mean grain size	−0.99	0.37	−0.67	0.53	0.28	0.79
Sorting	−0.59	0.58	−0.34	0.75	0.35	0.74
Skewness	−1.28	0.26	−0.92	0.40	0.58	0.59
Kurtosis	−0.21	0.84	0.12	0.91	0.47	0.66
Fines	1.78	0.14	2.48	0.06	0.18	0.87

Note: Degrees of freedom for all tests was 5.

TABLE 6 Predicted reproductive potential for barbel using salmonid equations with salmonid- vs. barbel-specific input parameters, where N/A is not applicable

River	Idle	Great Ouse	Teme	Teme (site-specific)	Teme (site-specific)	Meuse (single site)
Mean barbel length (mm)	480 ± 71	616 ± 46	651 ± 37	651 ± 37	651 ± 37	437 ± 2
Parameters	**Salmon-specific input**				**Barbel-specific input**	
D_T (mm)	100 ± 9	116 ± 6	121 ± 4	121 ± 4	110	N/A
F_M	0.99 ± <0.01	0.99 ± 0.02	0.98 ± >0.01	0.98 ± 0.01	0.97 ± 0.07	100[a]
A_{REDD} (m^2)	2.08 ± 0.73	3.71 ± 0.48	4.01 ± 0.52	4.01 ± 0.52	3.47 ± 0.42	2.11
N_{REDDS} (redds m^{-2})	0.49 ± <0.01	0.27 ± <0.01	0.25 ± <0.01	0.24 ± <0.01	0.28 ± <0.01	0.47
Fecundity (eggs)	2,436 ± 575	3,539 ± 370	3,821 ± 301	3,821 ± 301	40,510 ± 8,510	8,648
Reproductive potential (N_{EGGS} m^{-2})	1,194 ± 2	942 ± 16	937 ± 7	930 ± 8	11,321 ± 108	4,093

Note: Mean barbel length (mm ± 95% confidence intervals) was measured at each study site, threshold particle size (D_T, mm; largest grain that can be moved by spawning fish) was predicted (8) for salmonid-specific parameters and measured for barbel-specific parameters, the fraction of moveable surface particles (F_M) was predicted (9), redd area (A_{REDD}, m^2) was predicted for salmonid specific parameters and measured for barbel-specific parameters, spawning capacity (number of redds m^{-2}, N_{REDDS}) was predicted (11), fecundity was predicted (13a [salmonid], 13b [barbel]), and reproductive potential (N_{EGGS}, eggs m^{-2}) was predicted (12). Teme (site-specific) refers to the four sites where redds were measured. N/A; not applicable. [a]Assumed whole site to be moveable due to high coverage of redds, no sediment data available.

different between rivers ($F_{2, 43}$ = 0.57, *p* = 0.57), with barbel in each river being able to move over 97% of surface sediments, by area, during spawning (Table 6).

The mean redd area predicted for the river Teme (3.98 m^2) was 0.51 m^2 larger than that observed at the four sites where redds were measured (3.47 m^2) (Table 6), but the difference was not significant (ANOVA: $F_{1, 12}$ = 0.03, *p* = 0.87). The river Teme had the overall highest estimated reproductive potential due to a higher calculated fecundity resulting from the larger sizes of the female fish, despite having the lowest number of redds m^{-2} (Table 2). Using the barbel redd measurements, threshold grain size and fecundity across the specific sites on the Teme compared to the salmonid-specific values gave a mean reproductive potential difference of 10,391 eggs m^{-2} per site, where the salmonid model significantly under-estimated the potential (paired *t* test; t_3 = 187.22, *p* < 0.001). Data extracted from the river Meuse estimated a barbel redd area of 2.11 m^2, a 1.36 m^2 difference in area to the observed Teme redds, which was likely to be due to the

female barbel in the Meuse being 214 mm smaller than in the Teme. Extracting data from the Meuse gave a barbel-specific value for N_{REDDS} of 0.47 redds m^{-2}, which was higher than predicted values across the rivers Teme and Ouse, but lower than the Idle predicted value (Table 6), but as the redds were predicted to be smaller in the Meuse, this could account for the difference, especially as fish sizes in the Meuse and Idle were most similar.

Barbel eggs display a higher tolerance to sand than salmon, with barbel eggs remaining unaffected by SI levels as high as 3.5, which would cause 100% mortality of salmon eggs (Figure 4). Egg survival rates for the Teme, calculated using the salmon-specific model from the silt and sand content (Equations 14 and 15), varied between 7.7 and 63.4% (42.1 ± 9.6%; mean ± 95% CI). Calculated survival rates decreased from upstream to downstream until site 10 (downstream of Powick weir), but then increased again in the three sites farther downstream (Figure 5a). The river Great Ouse had mean calculated survival rates of 39.3 ± 5.8%, with three sites (sites 2–4) having survival

FIGURE 4 Sand index (SI) effects on egg survival (%) for European barbel (● Bašić et al., 2018) and Atlantic salmon (◆ Lapointe et al., 2004). Atlantic salmon egg survival calculated from the sand index (SI, Equation 14) from Lapointe et al., 2004, for sand index values comparable to those calculated from Bašić et al., 2018. Trendlines for: salmon (solid line), $y = -29x + 83$ and barbel (dotted), $y = 0.18x + 76$
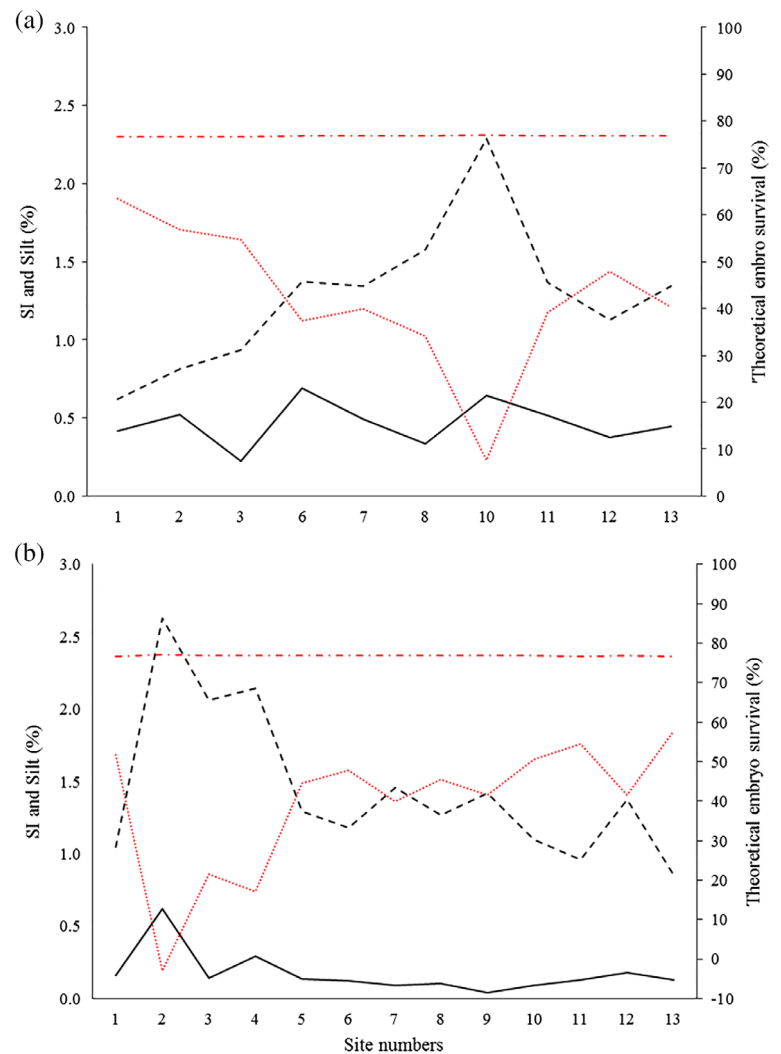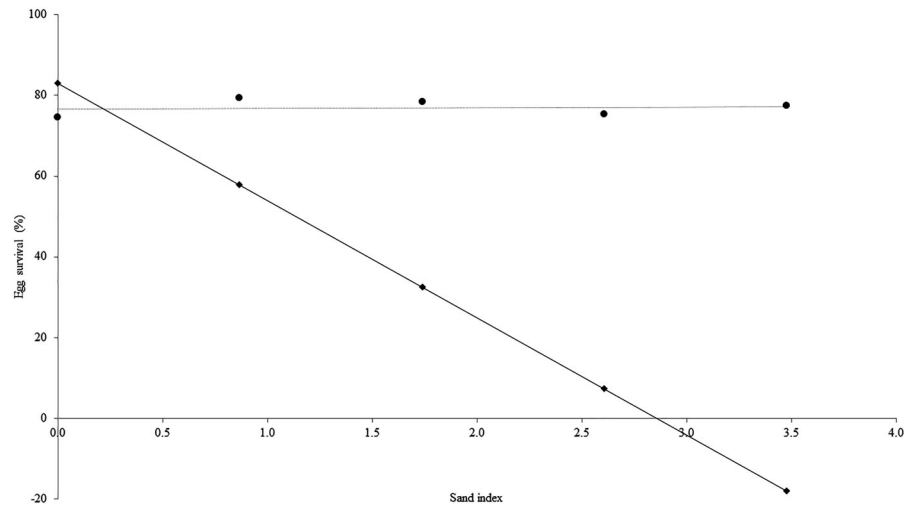

FIGURE 5 Calculated sand index (SI, dashed line, Equation 14) and observed silt (%, solid line) on the primary axis, with the theoretical survival of embryos (%, dotted line from the salmonid model, Equation 15, and dot and dash line from barbel derived equation determined from Bašić et al. (2018)) across 10 sites on the river Teme (a) and 13 sites on the river Great Ouse (b), ordered from upstream to downstream [Color figure can be viewed at wileyonlinelibrary.com]

between 0 and 22% (Figure 5b). Despite the significant difference in silt (%) between the two rivers, when both the percentage of silt and the sand index (SI) were taken into account, the theoretical calculated survival did not differ between rivers (ANOVA; $F_{1, 21} = 0.17$, $p = 0.69$), with both rivers having large variations in egg survival rates. When survival to emergence was calculated via the salmonid model (Equation 16) and successful incubation was defined as 50% of eggs and larvae surviving to emergence (Kondolf, 2000), 30% of the sites

had predicted successful incubation in the Teme and 31% in the Great Ouse. Using the salmonid model, the levels of silt in the river had a significant impact on egg survival in comparison to the assumption of 0% silt at all sites (paired t test; t_{22} = 4.98, p < 0.001), where silt reduced egg survival by 4% in the Teme and 2% in the Great Ouse. When not accounting for silt, one more site in the Teme showed survival above 50% leading to 40% of sites indicating "successful" survival to emergence, but the number of sites did not change for the Great Ouse. The barbel predictions derived from the equation from Figure 4 (survival = [0.18*SI] + 76) resulted in significantly different egg survival compared to salmonid models, when both models discounted silt (paired t test; t_{22} = 11.22, p < 0.001). The barbel-specific values predicted higher survival (Figure 4), with a mean difference of 33.65 (±6.22) %. Barbel-derived values predicted successful incubation conditions across both rivers at all sites.

4 | DISCUSSION

Research concerning lithophilic fish spawning habitat has focused primarily on salmonids, while the biotic and abiotic characteristics of non-salmonid spawning habitats remain poorly understood (Collins et al., 2011). For barbel in their indigenous range in Eastern England, this has been a major impediment to restoring populations, where strategies rely on a combination of gravel cleaning and stocking that have been largely unsuccessful in producing sustainable populations (Bašić et al., 2017; Bašić & Britton, 2016). Here, comparisons of spawning habitats in three rivers in England revealed barbel surficial spawning sediments were principally composed of gravels (D_{50} = 19.32–27.90 mm; Figure 2). At the sediment depth where barbel eggs incubate, the particles were generally coarse, well sorted and positively skewed. Spawning sites varied in mean width (9.4–18.7 m) and depth (0.26–0.38 m) but had similar velocities (0.6 depth; 0.54–0.60 m/s; Figure 3). While data from other studies reveal considerable inter-river differences in barbel spawning success (e.g., high in the Teme; Gutmann Roberts & Britton, 2018, negligible in the Great Ouse; Bašić & Britton, 2016), the majority of sediment and water velocity parameters did not vary between the study rivers, with relatively similar predictions of habitat suitability for barbel spawning and egg incubation success.

Across the rivers, surface sediments were relatively coarse and well-sorted gravels, with most substratum metrics similar between the Great Ouse and the Idle, but with coarser sediments in the Teme. Despite this, the fraction of particles estimated to be moveable by barbel was high (minimum 97%; Table 6) and similar across all three rivers; this was due to the length of barbel relative to the size of gravels. Thus, the presence of large clasts is not expected to be a limitation to barbel redd construction in these three rivers, either when using the maximum grain size estimated by the salmonid model or the largest grain from the tailspill. This has implications for relatively high potential for displacement by barbel, given that the three rivers generally had low D_{50} values, all below 35 mm. By comparison, in South Prairie Creek (North America), pink salmon (*Oncorhynchus gorbuscha*)

were capable of displacing grains ≤95 mm, yet the D_{50} sizes were 39 to 118 mm (Riebe et al., 2014). Consequently, at spawning sites, pink salmon were only able to move 59% of the bed (Riebe et al., 2014). Nevertheless, coarser sediments can be associated with larger egg sizes within and between populations (Quinn, Hendry, & Wetzel, 1995), which might have positive implications for post-emergence and overwinter survival. For example, larger eggs tend to produce larger larvae that are less vulnerable to predation and displacement, with higher lipid reserves and greater competitive abilities (Nunn, Harvey, & Cowx, 2007). Thus, the benefits of the majority of spawning gravels being made up of particles barbel can move, might be offset by surviving eggs being smaller and potentially leading to increased risk of egg and/or larval entrainment.

To our knowledge this is the first documentation of barbel redd dimensions. It is reasonable to assume the characteristics and persistence of redds will vary between and potentially within systems, as they are functions of spawning barbel lengths, surface sediment conditions, flow characteristics and bed mobility. No significant difference was detected when comparing measured and modelled Teme barbel redd areas, despite a mean 0.54 m^2 overestimation by the salmonid model (Table 4). This suggests that the length to redd relationship between salmonids and barbel is comparable, based on available evidence. The reproductive potential across the specific sites on the river Teme was, however, significantly different when using barbel values compared to using salmon-derived redd area, threshold grain size that a fish could move and fecundity. These led to an underestimate of over 10,391 eggs m^{-2} site^{-1}. This was largely due to the barbel-specific fecundity values that are over 10 times higher than the salmon-derived values because of, for example, smaller egg sizes (Table 6). Using published data (Baras, 1994), we were able to determine the number of barbel redds by area as 0.47 redds m^{-2} in the river Meuse, Belgium. We could not readily compare the Meuse barbel redds by area to the salmon-specific estimates from these study rivers, because barbel from Baras (1994) study were substantially smaller and thus predicted redd size was also smaller. The redd size estimated from the smaller fish in the river Meuse was 2.11 m^2 but this area should be used with caution as it assumed redds were not overlapping, yet Melcher and Schmutz (2010) found that at high-density spawning sites, barbel redd superimposition was common, as with salmonids (van den Berghe & Gross, 1984). As well as redd superimposition, it is common for salmonids to lay multiple egg clutches within one redd (Tonina & Buffington, 2009a), although the spawning description from Baras (1994) suggests that is not the case with barbel. The data from Baras (1994) was also based on field observations of spawning, yet experimental work from Gougnard, Poncin, Ruwet, and Philippart (1987) showed that not all female redd digging involved the release of ovules. Therefore, spawning observations could lead to an overestimation of successful spawning attempts. Spawning abandonment can be higher when there are large numbers of males present (Gougnard et al., 1987; Hancock et al., 1976), as in Baras (1994), which is believed to be an evolutionary response that protects eggs from abrasion-related mortality, caused when males mechanically aggravate the redd (Hancock et al., 1976). These high

spawning densities were generally not observed across the three study sites here. Barbel inter-spawning periods can be 8 days long, so it would be difficult to establish if all redds constructed by a given female had eggs without disturbing spawning gravels.

Regarding subsurface fines, there was little variation in sand and organic matter content between the rivers Great Ouse and Teme, but Teme sediments contained higher concentrations of silts (Table 3). Mean silt and clay concentrations were below 0.5%, which is low compared with other lowland English rivers (4–45%; Clarke & Wharton, 2001) and Lapointe et al. (2004) classification of "low fines content" (1.5%). However, presence of silt and clays in spawning gravels at levels as low as 0.03–0.41% can adversely impact Atlantic salmon, *S. salar* egg incubation and embryo survival (Julien & Bergeron, 2006), with maximum silt levels reaching 0.62 and 0.69% in the Great Ouse and Teme, respectively. The mean sand concentrations of the Teme and Great Ouse (22 and 18%, respectively) were higher than the tolerance threshold of salmonids (14%; Bryce et al., 2010). However, experimental work on barbel suggests survival to emergence is not affected by sand concentrations up to 40%, even though emergence timing can be accelerated by 8 days (Bašić et al., 2018). These early emerging fish were smaller, blind and had larger yolk sacs, suggesting their post-emergence survival could be low relative to more developed later-emerging larvae (Bašić et al., 2018), given their reduced ability to navigate flows and increased predation risk (Krupka, 1988; Vilizzi et al., 2013).

The tolerances of larvae to silt and sand cannot, however, be considered in isolation, as the salmonid literature suggests it is the interactions of the different fine sediment size fractions that can be more important for egg and embryo development (e.g., Lapointe et al., 2004). Indeed, Levasseur, Bergeron, Lapointe, and Bérubé (2006) revealed that it was the proportion of subsurface bed material <0.125 mm in *S. salar* redds that explained 83% of annual variation in embryo survival; in their study, there was a threshold of 0.2% concentration below which embryo survival dropped sharply below 50%. We found that different size fractions of fines in the rivers Teme and Great Ouse did not result in differences in the mean predicted egg and embryo survival between the rivers. However, there was an inverse relationship between predicted survival and the sand index for the salmonid model (Figure 5), with the levels of silt reducing survival by 2 and 4% in the rivers Great Ouse and Teme, respectively. Only 30 and 31% of sites were predicted to have egg survival rates over 50% in the Teme and Great Ouse, respectively. Here, we revealed that barbel have a much higher tolerance to sands than *S. salar* when using the sand index (Figure 4). This leads the salmonid model to overestimate mortality by a mean of 34% across the sites in the two rivers when silt is not accounted for (Figure 5b). Furthermore, the ex-situ data from Bašić et al. (2018) suggested 77% survival to emergence regardless of sand content (at least for values of SI ≤3.5; Figures 4 and 5), indicating successful incubation at all sites relative to Kondolf's (2000) 50% threshold. Fines vary spatially in rivers (Julien & Bergeron, 2006), due to fluctuations in sediment supply, flow velocity, channel profile, erosion, deposition and lithology (Middelkoop & Asselman, 1998). Spatial variation across sites in

barbel egg survival rates were not predicted from the barbel-derived calculations, despite salmonid egg survival rates varying from 0 to 63% and in-situ survival in studies showing 0 to 100% (Malcolm, Youngson, & Soulsby, 2003).

The barbel egg survival estimates from the parameterised salmonid models should be used cautiously, given the divergence in the egg survival rates from the salmonid model and the ex-situ egg survival rates of Bašić et al. (2018). Reasons for this are likely to include the higher oxygen requirements of salmonid eggs, although there is a paucity of information on the oxygen requirements of cyprinid eggs (Elshout, Dionisio Pires, Leuven, Wendelaar Bonga, & Hendriks, 2013). This is important, because the detrimental impacts of fine sediments on salmonid eggs and larvae relate to how they inhibit oxygen delivery to eggs and embryos by entombment (Sear et al., 2016) and by decomposition of organic matter (Collins et al., 2013; Sear et al., 2017). Compared to organic content found in other UK lowland rivers (2–21%; Clarke & Wharton, 2001), the organic matter found in these rivers was low (2%), although the implications of this are not clear given the knowledge gap in how organic materials influence cyprinid development (Collins et al., 2013). Our predictions of barbel egg survival did not consider the effect of pore water velocity in redds, although near-bed water velocities were high (Teme: 0.36 ms^{-1}, Great Ouse: 0.38 ms^{-1}). These near-bed water velocities might have facilitated increased oxygen delivery and metabolite removal at depth, increasing egg survival (Lapointe et al., 2004). Also, differences in burial depths might influence egg survival rates between species. For example, barbel eggs in this study tend to be in the top 5 cm of sediment, whereas similar sized salmonid eggs tend to be buried at greater depths (e.g., 15–30 cm for *S. salar*; Moir et al., 2002). Thus, relative to salmonids, barbel eggs may be exposed to greater hyporheic flows, higher oxygen exchange and increased flushing of metabolic waste, especially where redd topography is similar (Tonina and Buffington, 2009a & b).

The differences in incubation duration and egg size between barbel and salmonids also have implications for their survival (Springate & Bromage, 1985). Longer incubations of salmonid eggs might increase risk of exposure to suboptimal conditions within the egg pocket, such as reductions of oxygen concentrations to critical levels (Sear et al., 2017), especially as salmonid eggs are comparatively large and likely to have higher metabolic rates and oxygen requirements than barbel eggs (Rombough, 2007). Thus, the relatively small barbel eggs that are incubated for relatively short periods are likely to have lower oxygen requirements than salmonids, with a greater capacity for tolerating reduced oxygen levels. However, a recent study on a similar rheophilic cyprinid, nase *Chondrostoma nasus*, shows that even fine sediment (<0.085 mm) of 10 and 20% content can cause mortality and physically block larvae from emerging (Nagel, Pander, Mueller, & Geist, 2020). No sites were found to have the levels of sand above those that have been experimentally tested (40%) to impact barbel mortality (Bašić et al., 2018).

Spawning barbel altered the topography of the riverbed by displacing volumes of sediment during redd construction. However, the surface grain-size distributions between the pit and tailspill were not

different (Table 5), as has been found for other redd-building species (Chapman, 1988; Everest et al., 1987; Kondolf, Sale, & Wolman, 1993; Young, Hubert, & Wesche, 1989). A potential explanation for this is that the sediment excavated from the pit into the tailspill was not limited by grain size for barbel as it has been for some salmonid studies, where unmoveable coarse grains are left in the pit (Kondolf et al., 1993). Tailspill amplitude measured for barbel is comparable to those for Chinook, chum and sockeye salmon (13 and 15 cm; Buxton, 2018) This suggests shear stresses applied to the tailspills of barbel redds may be elevated, as has been found for salmonids. Spawning salmon have been found to change the surface sediment characteristics, although there have been contrasting effects, with sockeye salmon *Oncorhynchus nerka* reducing the coarseness and sorting of sediments in the redd compared to the surrounding riffles (Hassan et al., 2015), whereas chum salmon *Oncorhynchus keta* increase coarseness and sorting (Montgomery et al., 1996). However, altered surface sediment characteristics were not evident from barbel redds in comparison to surrounding riffles. Spawning salmon have also been shown to alter the composition of subsurface sediments, reducing fines content of the egg pocket (Young et al., 1989). Although not tested here, observations of plumes of fine sediment from barbel spawning were made. The surface sediment showed elevated fines in the pit compared with the tailspill, which could be due to the topography of the pit causing flow recirculation and fine sediment deposition (Buxton, Buffington, Yager, et al., 2015). Barbel eggs were detected 50 mm below the sediment surface in the tailspill, where previous sampling has found eggs within depths of 200 mm (Pinder et al., 2009). In cyprinid species such as nase, egg burial depths can vary between 0 and 300 mm, with those deposited at the surface (less than 5%) being most susceptible to mortality (Duerregger et al., 2018). Barbel eggs that are not retained in the bed can be consumed by other fish, such as grayling, *Thymallus thymallus* (Perks, 2019), suggesting higher egg mortality for shallowly deposited eggs or in highly mobile sediments. By comparison, salmonids deposit eggs between 0 and 500 mm (Table 1) from the sediment surface within the tailspill, where the top of the egg pocket is 110 mm (mean). Thus, barbel can be considered shallow spawners, with the majority of their bed disturbance resulting from redd construction occurring within the surface layers, which could leave eggs vulnerable to predation and entrainment. Further research should explore alternative and non-invasive methods of measuring in-situ changes in the structure, composition and/or topography of fluvial surfaces through spawning and indeed, other animal behaviours.

The impact of redd construction on river habitats transcends changes in channel morphology and substrata condition. In line with the geomorphic capabilities of some fishes, it is reasonable to assume bed disturbance by spawning barbel may also influence near-bed hydraulics and/or sediment transport processes in at least three ways. First, and as with barbel foraging (Pledger et al., 2014, 2016, 2017), it is reasonable to assume particles displaced during spawning, particularly those deposited in elevated positions as part of the tailspill, may sit proud on the sediment surface and in positions of relative instability. Thus, displaced grains may be more susceptible to entrainment, particularly during subsequent high flows. Second, bioturbation of surficial sediments might result in the loss of bed sediment structure and adjustments in packing (Buxton, 2018; Montgomery et al., 1996). Reworking of sediments in this manner, generating structureless or loosely packed fabrics, may promote bed load transport by reducing critical shear values required for particle entrainment (Buxton, 2018). Third, redd creation has a significant and varied impact on bed topography, which can influence near-bed hydraulics (Montgomery et al., 1996) and so, potential for particle entrainment. For example, topographic change through barbel redd construction may reduce basal shear stresses (Hassan et al., 2015) by increasing bed form drag, which may be mitigated by increased shear stresses on tailspill structures (Buxton, 2018; Buxton, Buffington, Tonina, et al., 2015), loss of stabilizing surface structures and/or substrate loosening, increasing particle entrainment probabilities. Further work is required to investigate the impacts of barbel and other cyprinid redd construction on near-bed hydraulics and sediment transport processes.

The spawning riffles studied here were not utilized by high densities of barbel, whereas in the river Ourthe (Belgium), up to 600 barbel utilize riffles of 150 m^2 to spawn (Baras, 1994). Most will be male, but up to 19 females can use the same riffle in a month (Baras, 1994). A single female can have up to 17 successful spawnings in a year, with less than 4 successful attempts being more typical (Baras, 1994). Thus, not all eggs will be deposited in a single redd, as per most salmonid species (Elliott, 1989). Multiple redd creation by barbel thus complicates the estimates of reproductive potential when salmonid model parameters are used. This is also compounded by the high density of female barbel during the spawning season compared to some salmonids, such as *S. trutta* (e.g., barbel: 0.16 females/m^2, Baras, 1994; *S. trutta*: 0.03 females/m^2, Elliott, 1989). Where spawning habitats are limited, salmonids may utilize suboptimal habitats, and this can facilitate future successful spawning here, the adaptability of barbel to use suboptimal habitats is unknown, but Baras (1994) showed that limited spawning success happened when there was not sufficient spawning habitat, such as specific depth and flow velocity. Barbel spawn in much greater densities than salmonids (salmonids = 0.01 to 0.43; Riebe et al., 2014); barbel = 0.24–0.49 redds m^{-2} (Table 6) which could lead to more intensive bed disturbance. Consequently, these differences between barbel and salmonids suggest that future work predicting barbel spawning success, such as egg production and survival, is needed to develop more specific models based on their spawning biology (e.g., multiple redd creation).

5 | CONCLUSION

The present study has started to fill the considerable knowledge gap in the two-way interactions between non-salmonid redd builders and their spawning environment, using barbel as a model species. Barbel were not limited by the size distribution of sediment available for redd construction on riffles in the study rivers, but recruitment may be impacted by fine sediment concentrations within spawning gravels. The study also indicates a need for further research to determine the optimal conditions for cyprinid egg and larval development and

therefore, survival, and how these early-life survival rates influence subsequent recruitment success of cohorts. The influence of these conditions can be tested empirically using both in- and ex-situ scenarios as has been done with salmonids (Cocchiglia, Curran, Hannigan, Purcell, & Kelly-Quinn, 2012), coupled with standardized monitoring of river sediment, water velocity and oxygen conditions. Until this knowledge is developed, the ability of river managers to enhance the spawning success of non-salmonid fishes, such as barbel, will remain highly constrained. Moreover, these studies may enable investigation of how anthropogenically altered rivers are impacting non-salmonid fish communities, and how restoration efforts can ensure sustainable populations in the face of continued environmental change.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in [BORDAR] at https://eur02.safelinks.protection.outlook.com/?url= http%3A%2F%2Fbordar.bournemouth.ac.uk%2F45%2F&data=02% 7C01%7Ccgutmannroberts%40bournemouth.ac.uk% 7C4ffbeb4ad4e249137ea308d772c3f535% 7Cede29655d09742e4bbb5f38d427fbfb8%7C0%7C0% 7C637104058265888818&sdata= wbJKeom2w4nnz1l86t7ifqF0MNtYd9TcmsZayzc%2Bn%2B4%3D& reserved=0.

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