Key Points:
- In situ fish foraging affects the microtopography, grain size, structure, and mobility of fluvial gravels
- Benthic foraging by fish disturbed, on average, 26.1% of riffle area in a 24 h period
- Foraging across broad spatial and temporal scales could have significant implications for gravel-bed stability and bedload transport

Foraging Fish as Zoogeomorphic Agents: An Assessment of Fish Impacts at Patch, Barform, and Reach Scales

A. G. Pledger[1], S. P. Rice[1], and J. Millett[1]

[1]Loughborough University, Loughborough, Leicestershire, UK

Abstract Flume studies have demonstrated that foraging by fish can modify the structure and topography of gravel substrates, thereby increasing particle entrainment probabilities and the amount of sediment mobilized during subsequent experimental high flows. However, the zoogeomorphic impact of benthic foraging has not previously been investigated in the field. This paper reports field experiments that examined the nature and extent of disturbance of riverbed gravels by foraging fish, predominately Cyprinids, at patch, riffle, and reach scales and complementary ex situ experiments of the impacts on bed stability. At patch scale, benthic feeding fish displaced particle sizes ≤90 mm in diameter, increased bed surface microtopography and grain protrusion, and loosened surface structures. Although enhanced mobility was expected from these structural changes, foraging also caused localized coarsening of sediments, and the ex situ experiments recorded significantly reduced grain entrainment, bedload flux, and total transported mass from foraged patches. Foraging disturbed bed materials at all 12 riffles in the study reach and, on average, disturbed 26.1% of riffle area per 24 h feeding period. These findings demonstrate for the first time that foraging fish, which are widespread and feed perennially, can act as zoogeomorphic agents in rivers, affecting grain-size distributions and bed material structure, with potential implications for bed stability and bedload transport at reach and river scales. Whether fish increase or reduce bed mobility is probably dependent on a host of factors, including the net effects of both structural disturbance and biogenic particle sorting, as these affect entrainment stresses under subsequent competent flows.

1. Introduction

Fish and aquatic macroinvertebrates are geomorphological agents that can modify the character and, therefore, stability of river bed sediments (Albertson & Allen, 2015; Rice et al., 2012; Statzner, 2012). Previous work has mostly used ex situ experimentation in flumes, mesocosms, and other artificial channels to demonstrate the ability of stream fauna to alter sediment transport by changing bed material grain-size distributions, microtopography, and fabrics (Johnson et al., 2011; Pledger et al., 2014; Statzner, Peltret, et al., 2003; Stazner & Peltret, 2006) or by increasing sediment cohesion through the addition of biogenic materials, including trichopteran silk (Albertson et al., 2014; Cardinale et al., 2004; Johnson et al., 2009; Statzner et al., 1999). With the exception of investigations of salmonid redd building effects on gravel transport (Field-Dodgson, 1987; Hassan et al., 2008; Kondolf et al., 1993; Montgomery et al., 1996) and crayfish effects on suspended sediment loads (Rice et al., 2014, 2016), in situ experiments and field assessments of fluvial zoogeomorphic impacts are rare. Field studies focused on ecological questions have, however, revealed faunal impacts on the accrual and suspension of riverine sediments by macroinvertebrates (Creed et al., 2003; Moulton et al., 2004; Pringle et al., 1993; Visoni & Moulton, 2003; Wallace et al., 1993; Zanetell & Peckarsky, 1996) and foraging fish (Bowen, 1983; Bowen et al., 1984; Cross et al., 2008; Flecker, 1992, 1996, 1997; Flecker & Taylor, 2004; Gido & Matthews, 2001; Power, 1990; Pringle & Hamazaki, 1998; Shirakawa et al., 2013) but have not explicitly considered the implications for sediment transport mechanisms and fluxes.

In this study, we measured the impact of benthic foraging, mainly by European Barbel *Barbus barbus* (hereafter Barbel) and Chub *Squalius cephalus*, on bed material characteristics and entrainment in an English gravel-bed river. To date, investigations of the geomorphological implications of foraging have exclusively involved ex situ experiments. Using small (0.2 m wide) outdoor artificial channels, Statzner, Sagnes, et al. (2003) observed that Barbel foraging altered the structuring of water-worked surface particles, loosened bed materials, and increased the mean bed elevation by moving gravel into piles and increasing particle elevations. In a flume experiment using juvenile Barbel, Pledger et al. (2014) showed that foraging modified the structure developed in gravelly sediments by water working, reducing the extent of imbrication, increasing

microtopographic roughness, and increasing the mobility of bed material particles when exposed to a subsequent high flow. In an additional flume experiment, Pledger et al. (2016) found that fish size and species were important controls of foraged depth and area, changes in microtopographic roughness and sediment structure, and consequent increases in sediment mobility. In particular, larger fish and Barbel (a benthic foraging specialist) had greater impacts than juvenile specimens and Chub (an opportunistic forager), respectively. Lentic microcosm experiments by Canal et al. (2015) have shown that environmental factors, in this case water temperature, can also affect the spatial extent of substrate disturbance by foraging with Chub, Stone Loach *Barbatula barbatula*, and Sofie *Parachondostoma toxostoma* disturbing two to three times larger areas at 20°C than 10°C.

This ex situ work demonstrates the clear potential for foraging fish to affect bed material transport in gravel-bed rivers. It also suggests that the geomorphic impact of foraging is likely to vary between locations and over time as a function of the composition and demography of the fish community as well as abiotic factors, including bed material size composition. Moreover, natural river settings contain Barbel and Chub that are larger in terms of body size than those used in published ex situ experiments, they contain shoals of fish, and they contain other fauna that may themselves forage or interact with foragers to affect zoogeomorphic impacts (Statzner & Sagnes, 2008). It is therefore reasonable to assume that in situ fish impacts, such as modifications of the size distribution and structure of fluvial substrates, might be qualitatively and quantitatively different to those identified in ex situ experiments.

In order to extend previous ex situ experimentation and begin to develop an understanding of the impacts of foraging in river settings, we assessed the geomorphic role of foraging fish in the River Idle, a gravel-bed river in the UK, at patch, bedform, and reach scales. We used an in situ experiment to quantify patch-scale effects of foraging fish, predominantly Barbel and Chub, on bed sediment structures and surface grain-size distributions and used field-conditioned substrates in an ex situ entrainment test to evaluate the impacts on sediment mobility (Component 1). The experiment compared changes in bed sediment characteristics and transport between trays of sediment that were exposed to foraging fish and control trays that were not. Four hypotheses were derived from the results of earlier ex situ experiments (Pledger et al., 2014, 2016):

1. by foraging upstream into the flow, fish are more likely to reverse the inclination of imbricated structures;
2. fish foraging will alter bed surface topography and increase the standard deviation of bed elevations;
3. fish foraging will modify the grain-size distribution of bed surface material at the patch scale;
4. structural and compositional changes to the bed caused by foraging will significantly increase (a) grain entrainment, (b) bedload flux, and (c) total transported mass.

Component 2 investigated the nature and magnitude of foraging effects at bedform and reach scales at 12 sites (covering approximately 600 m^2) along a reach of the River Idle. In this investigation, we quantified the local rate of foraging impact on riffles and considered the nature and spatial distribution of the foraging disturbance. The aims were to quantify:

1. the spatial distribution and consistency of foraging disturbances at the riffle scale;
2. the spatial extent and variance of riffle disturbances.

2. Materials, Methods, and Data Analysis

2.1. Field Site

Fieldwork was conducted in a 1 km reach of the River Idle (Figure 1), a low-gradient (Downs & Thorne, 1998), rainfall-dominated, mixed sand and gravel-bed river in Nottinghamshire, England, which maintains a pool-riffle morphology and drains a catchment of 842 km^2. The catchment is generally of low relief; the upper catchment is underlain by Sherwood sandstones, coal measures and magnesium limestone while Keuper Marls, and alluvial sands and gravels dominate the geology of lower reaches (Downs & Thorne, 1998). Within the catchment, agriculture is the primary land use (Downs & Thorne, 1998), particularly arable farming in respect to the catchment area adjacent to the study reach. The study reach was selected for two reasons. First, it is representative of the Barbel zone as defined by Huet (1949) and is known to support a population of generalist and benthivorous feeders such as Roach *Rutilus rutilus* and Chub and Carp *Cyprinus carpio*, Bream *Abramis brama*, and Barbel, respectively. Differences in diets (Table 4 in Pledger et al., 2014) and feeding
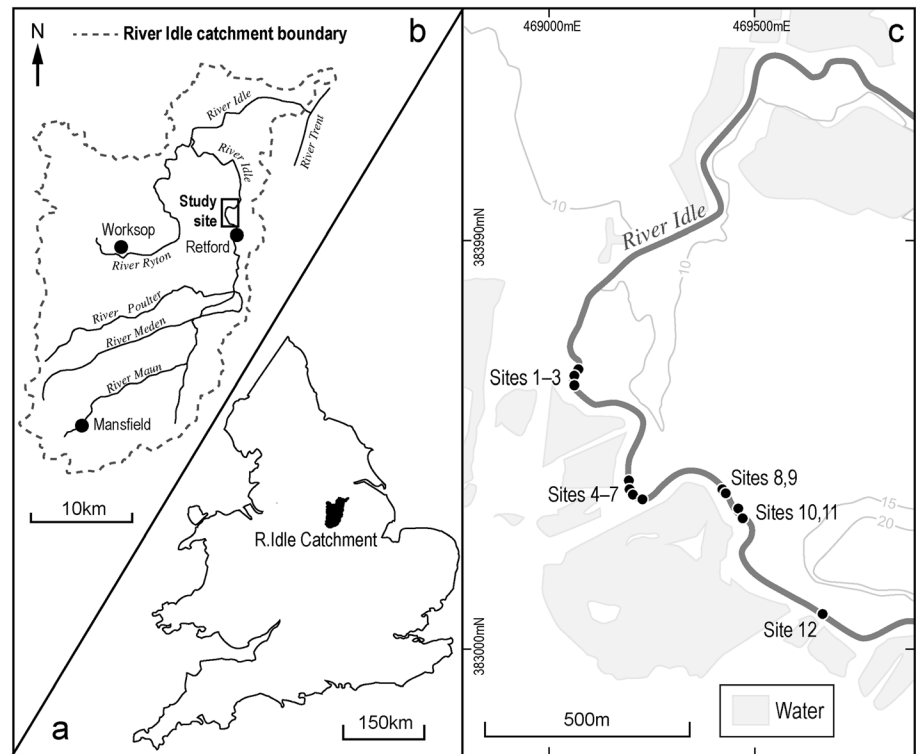
Figure 1. (a) Location and (b) catchment of the River Idle and (c) details of study sites on the Derbyshire County Angling Club stretch between Retford and Mattersey, at which sediment trays (site 1) and disturbance indicators (sites 1–12) were installed. The stretch of river, represented in Figure 1c is highlighted black in Figure 1b. Gray polygons identify lentic systems in Figure 1c.

preferences between functional groups will likely control the nature and magnitude of foraging effects, with benthic feeding specialists anticipated to have greater geomorphic impacts (Pledger et al., 2016). Second, the river was wadeable under baseflow conditions, allowing detailed measurements and observations of the bed surface to be made in situ.

Component 1 was conducted at site 1 (Figure 1), a 9.6 × 12.8 m riffle located beneath a large steel bridge. The bridge reduced in-channel light levels and so, macrophyte coverage, making the process of installing field equipment significantly easier. Furthermore, it allowed for safe, outdoors use of a laboratory laser scanner (section 2.2.2), even under inclement weather conditions, and easy site access, allowing safe and successful recovery of tray inserts from the field. Component 2 utilized 12 sites (Figure 1) that were similar in character and known natural foraging riffles of Cyprinid fishes.

2.2. Component 1: Patch-Scale Tray Experiments
2.2.1. Experimental Setup

Six steel sediment-tray holders (internal dimensions 0.6 × 0.6 × 0.1 m) were installed in the riffle at site 1 (Figure 1) so they were flush and level with the bed surface. Tray holders were installed in two parallel rows of three across the stream (Figure 2a) with an average streamwise spacing of 1.5 m and cross-stream spacing of 0.5 m. Experimental sediment trays (internal dimensions 0.5 × 0.5 × 0.1 m; Figure 2b) slotted into these holders. The trays were filled with gravels from the river bed that were mixed to provide a grain-size distribution approximating the average size distribution of riffle sediments at the site, as established from a ≈160 kg bulk sample of surficial sediment. The mixture included sediment from sand to cobble size, with $D_5 = 1.4$ mm, $D_{50} = 24.1$ mm, $D_{95} = 52.3$ mm, $D_{100} = 90.5$ mm, and sorting = 0.58 (Trask, 1932) ($\sqrt{\frac{D_{25}}{D_{75}}}$), where Dx is the grain size for which x% of the cumulative distribution is finer. The a, b, and c axes of 100 randomly selected grains were measured using digital calipers to assess grain shape. Clasts were predominantly bladed (Sneed & Folk, 1958) and well rounded (Krumbein, 1941). Topographic measurements of sediment in these trays (section 2.2.3) were used to address Hypotheses 1 and 2. A smaller container ("insert" hereafter;
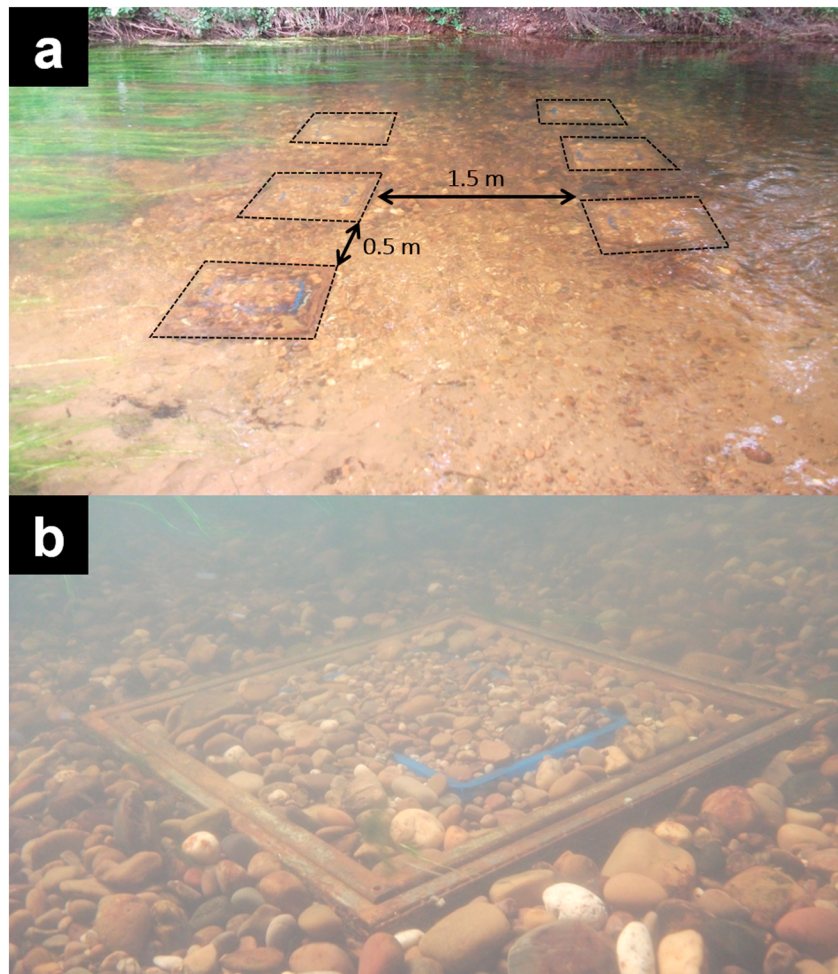
Figure 2. Photographs of (a) the configuration of experimental tray holders and corresponding trays at study site 1 and (b) an experimental sediment tray with tray insert (in blue), within the River Idle. Note: Both tray holders and sediment trays were 0.1 m deep and buried flush with the bed surface. In Figure 2a, flow direction is from left to right.

$0.35 \times 0.22 \times 0.1$ m) was placed in the middle of each tray before sediment was added (Figure 2b). These inserts and their sediment were recovered intact from the field and used to determine the effect of foraging on bed material size composition and stability using an ex situ entrainment test (Hypotheses 3 and 4, respectively).

2.2.2. Experimental Procedure

The patch-scale experiment was repeated on three occasions (3–9, 10–16, and 18–24 August 2012). In each experimental run, three control trays were covered to exclude fish, and three trays were left open for fish to forage. This resulted in nine replicates of the treatment (open trays) and control (closed trays). Each experimental run consisted of two sequential elements: a water-working phase and a treatment phase.

Trays and their inserts were filled to a 10 cm depth with the sediment mixture and screeded flat, level with the tray lip. Eye bolts were attached to each corner of the trays, and four chains, connected to a ratchet lever hoist mounted on a tripod, were attached. Before trays were lowered into the water, the flow directly upstream of each holder was retarded using a large baffle board (1.5×1.5 m; 0.5″ plywood sheet). Trays were slowly lowered through the water column and located within their holders, with care taken to avoid sediment disturbance. The eye bolts were then removed. Fish exclusion cages ($0.6 \times 0.6 \times 0.15$ m) constructed of 0.025×0.025 m grid weldmesh were then placed over each substrate tray to prevent fish from foraging tray sediments during the water-working phase, which lasted 5 days under baseflow conditions. After water-working, which served to stabilize and structure randomly arranged tray sediments, the trays were carefully winched from the bed and carried to the river bank where a laser scanner (Konica-Minolta Noncontact 3D
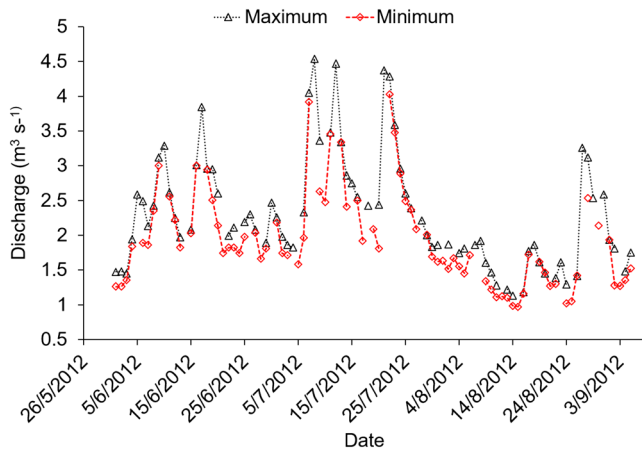
Figure 3. Daily maximum and minimum gauged flow ($m^3 s^{-1}$) at Mattersey in summer 2012 (Environment Agency, 2012).

Digitizer Vivid 910) was used to obtain elevation data for characterizing microtopography and bed structure (details in section 2.2.3). Baseflow water-working is not expected to have caused substantial transport (winnowing of fines) and alteration of grain-size distributions in the sediment trays.

Three treatment sediment trays were then seeded with 887 grains of boiled, untreated hempseed *Cannabis sativa* (used as fish food) in an even distribution over the sediment surface, at the average prey density (3,548 m^{-2}; Pledger et al., 2014) measured in the River Idle. The three control trays were left without food. Selection of an appropriate feed treatment was achieved through a preparatory set of in situ experiments that examined fish feeding behaviors across a range of feed types and densities (Pledger, 2015). These preliminary experiments found that hempseed administered at the River Idle average prey density (3,548 m^{-2}) was associated with natural feeding behaviors, and this food type and seeding density were therefore adopted here. Following seeding, all six trays were again slowly lowered into their holders, ensuring fish food remained in the bed, and cages were placed over the control trays. Fish always moved in the upstream direction when feeding, so control trays were placed upstream of the treatment trays to prevent the exclusion cages from influencing fish foraging behaviors. Lowering the treatment trays through the flow gently washed the hempseeds into interstitial gaps between grains, where prey would be found in the river bed.

In summer, Barbel (Baras, 1995; Lucas & Batley, 1996) and other fish species in UK rivers (e.g., Perch (Anthouard & Fontaine, 1998; Huusko et al., 1996) and Bream (Lyons & Lucas, 2002) tend to feed at dusk and dawn. Therefore, the treatment phase began 4 h before sunset and ended 12 h later so each experimental run included a dusk and dawn period.

Feeding behaviors were monitored and recorded during the treatment phase using two downstream-facing underwater video cameras. Each camera was installed upstream of a randomly selected treatment tray and positioned as to avoid disturbance of experimental substrates and fish foraging, as fish swam upstream to feed. With regard to camera impacts on flows and tray sediments, substrates were coarse, camera mounts were held within their mounts close to the bed, and we observed no particle movement during their installation. Video footage was recorded during the first 4 h of the treatment phase with recording limited to daylight hours, and behaviors were quantified using the classification scheme described in Pledger et al. (2014). Additional records were kept, including approximate sizes and species of foraging fish, shoal composition, and the duration of each feed event. Further details and results can be found in Pledger (2015), but key observations are included here to provide context regarding fish–sediment interactions.

Water quality parameters were measured three times daily during each experimental period. Monitoring utilized Hanna Instruments pH and conductivity meters (pH = 8.5 ± 0.04; conductivity = 1167.7 ± 1.1 μS/L; mean ± SD) and a Hanna Instruments HI-9142 dissolved oxygen meter (mg/L and %; dissolved oxygen = 10.0 ± 0.5 mg/L; dissolved oxygen = 100 ± 3.1%; means ± SD). Two Tinytag PLUS 2 temperature sensors sampling every minute were used to collect time series of water (19.3 ± 0.001°C) and air temperature (17.4 ± 0.008°C; means ± SD). A continuous record of flow depth was measured using a Van Walt Mini-Diver and corresponding Baro-Diver, required for barometric compensation (0.56 ± 0.21 m; mean ± SD). The three runs were performed during a period of baseflow, when variations in discharge were small (Figure 3). Flow conditions were therefore similar between replicates, and small differences between runs were not observed to affect fish behavior, sediment mobility, or environmental variables. This was to ensure that the flow did not significantly affect sediment structuring during the experiment or the composition of the fish community and foraging behaviors during the treatment phase.

At the end of each treatment phase, flows were baffled and the trays carefully removed to the river bank where they were scanned a second time. Scans of the control trays provided data for establishing minimum discernible differences in surface elevation, required for subsequent digital elevation model (DEM hereafter) analysis (section 2.2.3). Tray inserts were then carefully removed and transported to the laboratory for determination of grain-size changes and foraging impacts on bed stability.

2.2.3. Characterizing and Analyzing Differences in Bed Surface Microtopography and Surface Structures

To address Hypotheses 1 and 2, microtopographic parameters and structural information were extracted from DEMs constructed using the laser scans made before and after the treatment phase. Four scans were obtained on each occasion by rotating trays through 90° after each scan. Scans were collected in this manner to reduce errors associated with the scanning procedure (e.g., grain hiding effects Hodge, 2010). The scans consisted of approximately 14,000 irregularly spaced x, y, and z coordinates with an average $x–y$ spacing of 1 mm. Painted reference marks on the trays provided elevation control for rectification and scaling the point clouds in Polygon Editing Tool. The point clouds were then merged in ArcGIS© v.9.2 [Environmental Systems Research Institute, Redlands, CA, USA] and converted into elevation data using Rapidform and then into raster DEMs using a kriging interpolation algorithm. The trays were rigid and scanned on a mostly flat surface, and any slope was removed by detrending DEM surfaces with a simple planar model.

Topographic changes (Δz) to the granular surfaces through foraging were quantified by creating digital elevation models of difference (DoDs hereafter) from the surface DEMs of the treatment trays before and after exposure to fish. To quantify the minimum discernible difference, DoDs were also calculated from DEMs obtained in the equivalent pairs of scans from control trays. Differences between these scans accounted for both experimental errors associated with the extraction, insertion, water-working, and transportation of trays and processing errors associated with the capture, rectification, and interpolation of DEMs from the point clouds. The maximum calculated elevation difference for the control trays was 5.56 mm. An error factor of ±6 mm was therefore applied as a liberal estimate of the minimum discernible difference in surface elevation.

Differences in bed surface topography on the treatment trays that exceeded ±6 mm were considered to be the result of fish foraging. Foraging disturbance was partitioned into four discrete categories: surface rearrangement (positive and negative, i.e., surface elevation increases and reductions, respectively) was defined as a topographic change greater than the minimum discernible difference (±6 mm) but less than ±24 mm, the median diameter of the bed material. Topographic changes greater than ±24 mm may reflect displacement of individual grains from the tray rather than their in situ rearrangement and were categorized as surface gain if the elevation difference was positive or as surface retreat if the difference was negative.

The standard deviation of surface elevations was used as a measure of microtopographic roughness (Aberle & Smart, 2003) and was compared before and after the treatment period for control trays and treatment trays. Measurements from all trays across the three experimental runs were combined to obtain means for the before and after groups. These means were tested for statistical differences using paired t tests after confirming normality with Shapiro–Wilk tests (Shapiro & Wilk, 1965). We expected to find no significant change in microtopographic roughness in control trays but a significant increase in the treatment trays.

The degree of particle structuring or imbrication in the streamwise direction was quantified and compared using Smart et al. (2004) inclination index. This index compares the proportion of positive and negative sloping DEM cells at a specified lag distance, $l = 2$ mm in this case:

$$I_l = \frac{p_l - n_l}{p_l + n_l + z_l} \tag{1}$$

where I is the inclination and p_l, n_l, and z_l are the number of positive, negative, and zero slopes, respectively. Water-worked surfaces typically maintain a positive index value that ranges between 0 (unstructured) and 1 (heavily structured). Comparisons were made for both control and treatment trays of mean I_l, before and after foraging using paired t tests.

2.2.4. Characterizing and Analyzing Differences in Bed Material Grain-Size Distributions

Sieve analysis of sediments recovered from the inserts in control and treatment trays was used to quantify the effect of foraging on the surface grain-size distribution (Hypothesis 3). This was achieved after the ex situ entrainment tests by sieving the recombination of the lag in the tray insert with the material caught in the bedload trap during the flume experiments described in section 2.2.5. Collected sediments were dried and sieved into half-phi fractions (phi $=\log_2 D$, where D is the diameter of the particle and D_0 a reference diameter, equal to 1 mm). The amount of material (by mass) below 2 mm was determined but not differentiated. Comparisons of the D_{10}, D_{50}, D_{90}, and sorting parameter (Trask, 1932) (hereafter grain-size

distribution (GSD) metrics) for control and treatment trays were used to investigate fish impacts on surface grain-size distributions and tails of the distributions.

GSD metrics for the sediment mixture that went into each insert at the beginning of the experiment were known. After the treatment phase, GSD metrics were recalculated for control and treatment tray inserts. The distributions of each metric in each of the resulting four groups (control and treatment, before and after) were tested for normality using Shapiro–Wilk tests. As appropriate, a paired *t* test or a Wilcoxon Signed-Rank test was used to compare mean GSD metrics before and after the treatment for (1) control and (2) treatment tray sediments. The first comparison between control tray sediments provides a test of whether the period of water working combined with subsequent hydraulic conditions had any impact on GSD metrics, with the expectation that no difference would be detected. The second comparison provides an assessment of the impact of foraging plus the combined effects of water working and subsequent hydraulic conditions. We assumed that if the control trays did not reveal a significant effect, then any significant effect in the treatment trays must be due to foraging.

To supplement these results, the impact of foraging on the total mass of sediment and the mass within each half-phi size class was assessed. This was achieved ex situ by comparing dry masses from control and treatment tray inserts. As above, this involved combining the coarse lag left within tray inserts after entrainment with bed material captured during entrainment in the flume (section 2.2.5). Data were tested for normality (Shapiro–Wilk test) and analyzed using two-tail *t* tests or Mann–Whitney *U* tests as appropriate. Results from these analyses were used to address Hypothesis 3.

2.2.5. Characterizing and Analyzing Differences in Particle Entrainment and Bedload Flux

A modified version of the experimental setup described in Pledger et al. (2014) was used to quantify the mobility of sediments in the tray inserts returned to the laboratory. Tray inserts were located in a false bed of sheet steel and epoxied roughness gravels, constructed within a 10 m long, 0.3 m wide tilting flume. The trays sat flush with the surrounding bed immediately upstream of a bedload trap (0.275 × 0.125 × 0.10 m) with an attached "entrainment plate" along its upstream edge (0.275 × 0.12 × 0.003 m) that facilitated videography of mobile grains. Tray inserts effectively replaced the test bed described by Pledger et al. (2014), but the experimental setup was otherwise the same and did not replicate conditions in a field setting. After careful filling of the flume, slope, flow rate, and tailgate height were adjusted to a bed shear stress that exceeded the critical level for entrainment of the gravel mixture used in the trays, such that moderate rates of transport developed. No subsequent adjustments to the flume were made, and the bed was allowed to stabilize under the constant entrainment flow.

Flow velocity profiles for calculating basal shear stress during the entrainment test were obtained using a Nixon Streamflo Velocity meter V1.3 with a high-speed probe, averaging over 60 s. Profiles were collected almost immediately after establishment of the constant entrainment flow and above the center of the test bed, with point measurements every 2.5 mm throughout the bottom 20% of the flow and at increasing vertical increments above. The velocity probe was not observed to impede sediment movement, and profiles consisted of 23 points. Six profiles were collected outside of the main experimental program to quantify hydraulic conditions under entrainment. Velocity profiles were used to estimate near-bed shear stresses (τ_0) using the law of the wall (Biron et al., 1998), corrected for sidewall drag using Williams's (1970) empirical approach. Dimensionless Shields parameters (θ) were calculated as described in Pledger et al. (2014), using the median grain size $D_{50} = 24.1$ mm. Reynolds number Re was calculated using

$$Re = UR/v \tag{2}$$

where U, R, and v are mean flow velocity (measured at 0.6 of the flow depth; average = 0.62 m s^{-1}), hydraulic radius (0.043 m), and kinematic viscosity (0.000001 m^2 s^{-1}), respectively. Pertinent hydraulic data are presented in Table 1.

An Inspektor 1 Video Inspection Camera positioned downstream of the pit, facing upstream at the bare steel entrainment plate, provided a constant record of mobile grains leaving the observation area. Sediments remaining within the tray insert at the end of this period were retained for grain-size analysis. Particle entrainment was quantified by counting the number of grains that left the tray inserts during the 1 h entrainment test. Counting was based on a 30% subsample of the entire video record using 36 regularly spaced 1 min counts separated by 66 s intervals. During entrainment, bedload measurements were made every 5 min

Table 1
Flow Characteristics in Flume During Entrainment Tests

Flow parameters	Entrainment flow
Slope, %	1.75
Average velocity (0.6 depth), m s^{-1}	0.62
Local bed shear stress,[a] N m^{-2}	5.8
Bed shear stress corrected for sidewall, N m^{-2}	4.84
Shields' dimensionless shear stress parameter	0.012
Reynolds number	26,592

[a]Local bed shear stress was corrected using Williams (1970) empirical function, and the corrected value was used to estimate Shields parameter values.

by emptying the bedload trap and weighing the trapped sediment. Bedload samples were dried, sieved into half-phi size fractions, and weighed. Sediment flux and cumulative mass over time were obtained from bedload measurements. Sediment transport data were used to address Hypothesis 4.

Direct comparisons were made between treatment and control trays to quantify the effects of foraging on sediment transport. The impact of foraging immediately after the treatment period (i.e., using the first bedload measurement between 0 and 300 s) was a particularly important test because as the entrainment period progressed, the bed adjusted to the flow by stabilizing, so that there was a decline in transport with time. Analyses were performed on data pertaining to total flux and flux by size fraction. All data were tested for normality (Shapiro–Wilk test) and analyzed using unpaired, two-tail *t* tests or Mann–Whitney *U* tests (Shaw et al., 2010), as appropriate. These analyses were also performed to assess the impact of foraging on the total transported mass, mass by size fraction, and the total number of transported grains during the 3,600 s entrainment period.

The temporal persistence of any fish effect (to 3,600 s) was evaluated using a linear mixed model (McCulloch et al., 2008). Within the model, each "replicate" was a subject, and time was the repeated measure. Time and treatment (treatment or control) were specified as fixed factors. Autocorrelation between time points was modeled using a compound symmetry covariance structure. Data analysis was carried out using IBM SPSS Statistics v21.0 (IBM Corp, 2012).

2.3. Component 2: Barform and Reach Scale Disturbance Study
2.3.1. Disturbance Indicator Deployment and Displacement
The spatial extent and nature of fish foraging were quantified at each of 12 riffles along the River Idle study reach by installing disturbance indicators in the riverbed and assessing their displacement over a 24 h period. Each indicator consisted of a spray-painted steel washer (38 × 2 mm) inserted vertically between bed particles until it was flush with the grain tops between which the washers were inserted, with diameter oriented approximately parallel to the flow to minimize drag. Disturbance during deployment was indicated by a change in the attitude of the washer. This method has previously been used for documenting bed material dilation, contraction, and entrainment in gravel-bed rivers (e.g., Konrad et al., 2002; Marquis & Roy, 2012).

At each riffle, washers were installed in a grid pattern across the entire channel width. Due to the overloose nature of riverbed sediments, trampling had negligible impact on the structure of fluvial gravels and, therefore, stability of installed washers. Depending on riffle size, 41–160 washers were installed, with a mean of 126 per riffle and a total of 1,392 washers across the 12 sites (Figure 1c; Table 2). Washers were installed for 24 h on one or more occasions at different locations in the study reach in the period between 24 August and 5 September 2012, although a high flow event between 27 August and 1 September (Figure 3) precluded any deployments on those days. Gauge data (Figure 3) indicated negligible differences in daily stream flow on days when washer data were recorded. It was not possible to equip and monitor every riffle in 1 day so different sites were monitored with washers on different days. Easily accessible sites were monitored more than once. In total, foraging disturbance was monitored for twenty-five 24 h periods with washers at the 12 sites. One site provided 5 days of observations; three sites, 3 days each; three sites provided 2 days each, and the remaining five sites provided 1 day of data each (Table 2).

Given that component 2 was conducted under base flow conditions, likely insufficient to mobilize coarse surface materials, washers should record instances of nonhydraulic disturbance, including those caused by foraging fish. To evaluate this assumption, constant observations of disturbance indicators were initially made over a 7 h period (12:00–19:00) at a single site (site 1; Figure 1; Table 2) on 23 August 2012, by looking down through the water column from a bridge spanning the river. During this period no washers were knocked over by the flow or drifting debris (mainly aquatic macrophytes), and the only washer displacements observed were those caused by foraging fish (predominately Barbel).

No feed treatment was applied on monitored riffles, so the magnitude of disturbance reflected natural foraging. After 24 h had passed, washers were inspected to determine if they had been disturbed. A washer was

Table 2
Details of Washers Placed in River Idle to Monitor Bed Disturbance by Benthic Feeding Fish

Site number	Number of replicates	Number of transects		Washers installed	Area covered (m^2)
		Parallel to the flow	Adjacent to the flow		
*1	1	7	18	126	70.0
1	5	7	18	126	70.0
2	1	7	18	126	60.0
3	1	7	20	140	60.0
4	3	7	20	140	70.0
5	3	6	14	74	31.1
6	3	8	20	93	42.2
7	1	7	20	140	55.0
8	2	9	8	72	30.0
9	2	8	20	160	30.0
10	1	7	20	140	60.0
11	1	7	20	140	12.7
12	2	4	11	41	24.0

Note. Presented are details of replication (number of different days), spatial extent, and spatial arrangement of washers. The first replicate at site 1 (indicated with an asterisk) was an initial test to identify whether washers were disturbed by flow or drifting debris, rather than fish.

considered disturbed if it had been (1) dislodged from its original location and was lying flat on the bed or (2) buried by foraging activity. If a washer had been disturbed, its location within the site (planar x–y coordinates) was recorded. At sites that were monitored with washers more than once (Table 2), disturbed washers were reset in original locations using the installation method described above and were left for another 24 h.

2.3.2. Analysis of Disturbance Indicator Displacements at Barform and Reach Scales

To address Aim 1, the spatial distribution of foraging was quantified as uniform, clumped, or random using the Clark–Evans nearest neighbor (R) method (Clark & Evans, 1954), wherein

$$R = \frac{\bar{r}}{0.5\sqrt{\rho}} \tag{3}$$

where $\bar{r}$ is the mean distance between nearest neighbors (defining neighbors as adjacent disturbed washers in each case) and ρ is the number of disturbed washers per unit bed area. One-sample t tests (Shaw et al., 2010) were performed using data from the four sites with three or more sets of observations, to identify the significance of the relationship between R and 1. If $R = 1$, the population is randomly dispersed. If R is statistically significantly greater than or less than 1, the population is either uniform or clumped, respectively.

Summary statistics were used to investigate the number of washers and area of the river bed disturbed by foraging during each 24 h period. Results from these analyses were used to address Aim 2. To assess whether the local magnitude of disturbance was consistent between sites, proportional data (% of riffle foraged per 24 h) were analyzed with a linear mixed model (LMM) using data from the four sites where three or more days of observations were made. Data were angular transformed before analysis to meet the assumption of homoscedasticity (Pollard, 1977). The potential for autocorrelation between observations at each site was accounted for by using a model with a first-order autoregression (AR(1)) covariance structure where preceding values in a series are used to predict values at subsequent time points. A compound symmetry structure was also tested, but the model using an AR(1) structure was more appropriate, as determined by Akaike's information criterion. Within the model, site numbers were subjects and observation numbers the repeated measure. Site numbers were specified as fixed factors. This test identified whether the impact of foraging was consistent between sites or whether fish foraged particular riffles more than others. In all the above analyses, IBM SPSS Statistics v21.0 (IBM Corp, 2012) was used.

3. Results

3.1. Component 1: Patch-Scale Effects

After the first run of the field experiments, large amounts of fine sediment were deposited across one pair of trays (one control, one treatment) in the lee of a tree that became submerged upstream of the trays. The
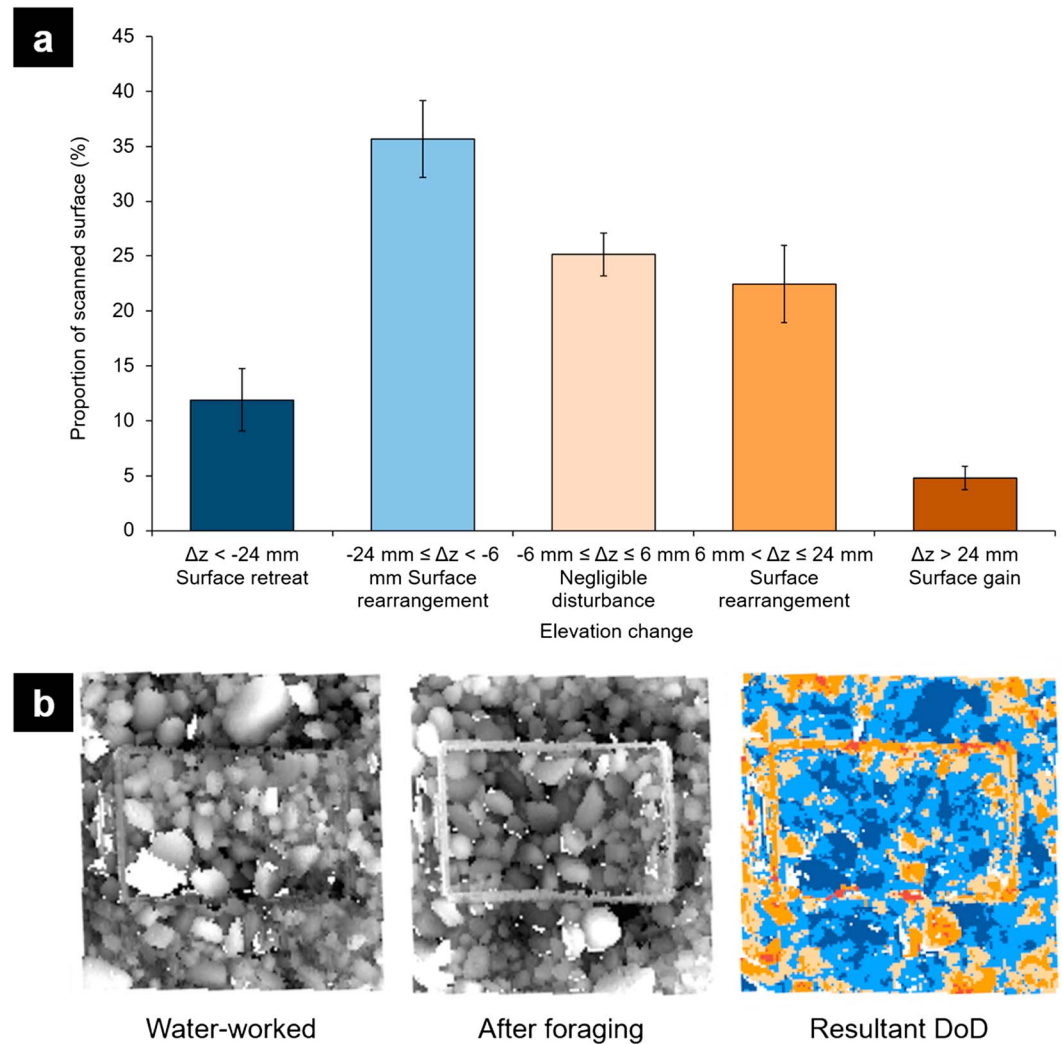
Figure 4. (a) Mean surface elevation change as a percentage of the DEM surface area (3.9 μm–90 mm gravel surfaces, 0.5 × 0.5 m) before and after 12 h of fish activity under baseflow conditions in the River Idle. Values represent means (n = 6, ±SE). (b) Examples of a treatment tray at the end of the water-working phase and after the foraging phase, and the resultant DoDs (digital elevation models of difference) are also presented. Note: Bar colors correspond to those within the resultant DoD image.

effect of this deposition was only understood once the grain-size data from the trays was analyzed. Due to the exploratory nature of the study and the small sample size, we chose to remove these compromised data from all subsequent analyses, so that six pairs of control and foraged trays are used throughout.

3.1.1. The Effect of Foraging on River Bed Microtopography and Surface Structures

On average, 75% of the surface area of treatment trays was modified (i.e., elevation change > ±6 mm) by fish during the 12 h study period (Figure 4). Within the modified area, the majority of the disturbance (58%) was in

Table 3

Microtopographic Roughness (SD of Surface Elevations), Inclination Index, and the P Value for the Difference Between Substrates Within Water Worked Trays, Before and After Foraging

		Before foraging	After foraging	d.f.	Test result	P value
Treatment trays	SD of surface elevations (mm)	9.40 ± 0.89	15.51 ± 1.45	5	−7.01	<0.001
	Inclination index	0.059 ± 0.012	0.056 ± 0.015	5	0.36	0.73
Control trays	SD of surface elevations (mm)	8.56 ± 1.00	8.54 ± 1.01	5	0.30	0.78
	Inclination index	0.058 ± 0.026	0.058 ± 0.021	5	0.15	0.89

Note. Values represent means ± SE (n = 6). Test statistics are for paired *t* tests (α = 0.05).

Table 4

D_{10}, D_{50}, D_{90}, and Sorting Metrics From Control and Treatment Trays, for Initial and Post-Foraging Conditions

	Control trays					Treatment trays				
	Initial	After foraging	d.f.	Test result	P value	Initial	After foraging	d.f.	Test result	P value
D_{10}	4.46 ± 0	5.44 ± 0.81	10	−1.21	0.28	4.46 ± 0	7.60 ± 0.99	10	−3.16	0.025
D_{50}	24.07 ± 0	23.14 ± 1.30	10	0.71	0.51	24.07 ± 0	27.73 ± 1.47	10	−2.48	0.056
D_{90}	43.74 ± 0	46.47 ± 2.23	10	−1.22	0.28	43.74 ± 0	53.42 ± 3.00	10	−3.22	0.023
Sorting; Trask (1932)	0.58 ± 0	0.59 ± 0.01	10	−0.66	0.53	0.58 ± 0	0.65 ± 0.02	10	−3.83	0.01

Note. Values represent means ±SE ($n = 6$). Test statistics are for paired *t* tests ($\alpha = 0.05$).

the surface rearrangement category (±24 mm to ±6 mm). DoDs revealed that fish within the River Idle foraged to depths of 98 mm while the maximum increase in surface elevation as a result of feeding was 92 mm.

Foraging occurred on treatment trays in all experimental runs. There was a statistically significant increase in microtopography in the treatment trays during treatment periods (Table 3; paired *t* test, $t_5 = -7.01$, $P < 0.001$), confirming that foraging significantly affected bed microtopography (Hypothesis 2). Furthermore, there was no statistically significant change in microtopography for control trays over the treatment period, which confirmed that only foraging affected grain structures. The water-working phase generated weakly imbricated surface textures (treatment mean = 0.059) with an asymmetric distribution of inclinations at the lower end of those observed in natural, gravel-bed rivers, where values of *I* typically range between 0.03 and 0.18 (Millane et al., 2006). Foraging by fish did not have a statistically significant impact on the inclination index (Table 3; paired *t* test, $t_5 = 0.36$, $P = 0.73$), with only a small change in the mean value from 0.059 to 0.056 before and after foraging.

3.1.2. The Effect of Foraging on Grain-Size Distributions

Control trays did not record statistically significant changes in any GSD before and after foraging, but the treatment trays experienced significant increases in sorting, D_{10} and D_{90} (paired *t* tests; $\alpha = 0.05$) and in D_{50} (paired *t* test; $\alpha = 0.10$) (Table 4). After the foraging period, there were also statistically significant differences in the mass of sediment between control and treatment trays with lower masses in the treatment trays for all size classes within the 4–22.6 mm range (Table 5; Figure 5). During the experiment, the mass of material smaller than 2 mm was not differentiated, which almost certainly led to an underestimation of the fish effect for grains <2 mm. Changes in the amount of sediment within each size fraction led to a statistically significant, 2.8 kg (33%) decrease in the total mass of sediment remaining in treatment trays, relative to control trays after the foraging period (*t* test: $t_{10} = -7.89$, $P \leq 0.001$). Post-foraging, total masses within treatment trays were similar (mean = 11.2 kg; standard deviation = 0.5), indicating relatively consistent foraging disturbance between trays.

3.1.3. The Effect of Foraging on Particle Entrainment and Bedload Flux

Comparing bedload flux estimates from treatment and control tray inserts indicates that foraging fish had a statistically significant impact, increasing bed stability and reducing sediment flux. When considering the full

Table 5

Mass of Sediment Remaining in Tray Inserts Within Each Size Class After Foraging for Control Trays and Treatment Trays

				Test statistics		
Grain size (mm)	Control (kg)	Treatment (kg)	Statistical test	d.f.	Test result	P value
<2	0.74 ± 0.13	0.48 ± 0.097	*t* test	10	−1.66	0.13
4	0.11 ± 0.025	0.045 ± 0.0046	Mann–Whitney	10	<0.001	0.004
8	0.79 ± 0.12	0.43 ± 0.049	*t* test	10	−2.88	0.016
11.31	0.81 ± 0.054	0.43 ± 0.023	*t* test	10	−6.43	<0.001
16	1.14 ± 0.12	0.72 ± 0.078	*t* test	10	−2.91	0.016
22.63	1.64 ± 0.13	1.11 ± 0.16	*t* test	10	−2.58	0.027
32	2.48 ± 0.058	2.032 ± 0.23	*t* test	10	−1.92	0.084
45	2.16 ± 0.32	2.12 ± 0.27	Mann–Whitney	10	15.00	0.63
64	1.27 ± 0.30	0.88 ± 0.15	*t* test	10	−1.17	0.27
90	0 ± 0	0.11 ± 0.11	Mann–Whitney	10	15.00	0.32

Note. Values represent means ± SE ($n = 6$). $\alpha = 0.05$.
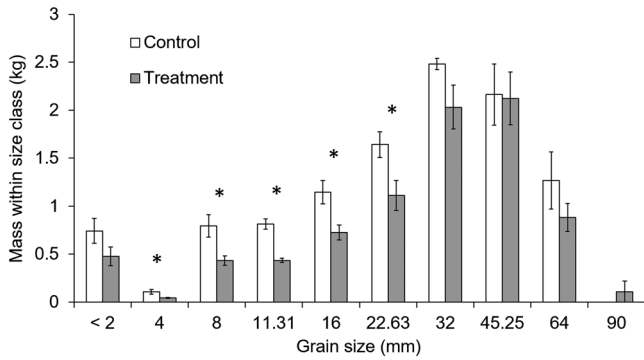
Figure 5. Mass of sediment remaining in tray inserts within each size class (mm) after foraging for control trays ($n = 6$) and treatment trays ($n = 6$). An asterisk above a pair of bars indicates a significant difference at $\alpha = 0.05$. Values represent means ($\pm$SE).

time-series, the impact was persistent (Figure 6). There was a statistically significant effect of time (LMM: $F_{11} = 17.48$, $P = 0.002$) and treatment (LMM: $F_1 = 11.56$, $P = 0.007$), with a significant interaction between the two (LMM: $F_{11} = 10.93$, $P < 0.001$). Over the 1 h entrainment period, mean bedload transport rates declined from 0.0013 to 0 kg m^{-1} s^{-1} for treatment tray inserts and from 0.012 to 0.000017 kg m^{-1} s^{-1} for control tray inserts (Figure 6). This pattern of decline was expected as less stable particles were quickly entrained and the bed became increasingly structured under the entrainment flow. Importantly, the initial bedload flux between 0 and 300 s was significantly greater for control than treatment tray inserts (Mann–Whitney U test: $U_{10} = 1.00$, $P = 0.006$; Figure 6), confirming the impact of foraging on bed stability and grain entrainment.

At $t = 300$ s, mass fluxes of bedload were statistically significantly lower ($\alpha = 0.05$) in treatment trays than control trays for grains <2 mm and for grain sizes in half-phi increments from 2 to 32 mm (Figure 7; Table 6).

Over the 1 h entrainment period, foraged trays were associated with a statistically significant decrease in the cumulative mass of transported bedload (Figure 8a) and total number of entrained clasts (Figure 8b), by factors of 12 and 36, respectively (total bedload: Mann–Whitney U test; $U_{10} < 0.001$, $P = 0.002$; number of grains moved: unpaired t test; $t_{10} = -3.65$, $P = 0.004$).

For the transported sediment, the mass of grains transported within each size class (<2 to 32 mm) was statistically significantly lower in treatment inserts than control inserts (Mann–Whitney U test, $U_{10} = 3.00$, 1.00, 3.00, 3.00, 1.00, <0.001, <0.001; $P = 0.015$, 0.005, 0.16, 0.014, 0.006, 0.004, and 0.003, respectively; Figure 9).

3.2. Component 2: Barform and Reach-Scale Disturbance
3.2.1. The Pattern of Foraging at Barform Scale
At the four sites where washer disturbance was monitored for three or more 24 h periods, one-sample t tests confirmed that Clark–Evans R values were significantly greater than 1.0 in all cases ($P < 0.05$; Figure 10), and all values were >2. This indicates that disturbance by foraging was evenly distributed across the riffles rather than being clumped or random (Aim 1).
### 3.2.2. The Magnitude of Disturbance at Reach Scale, Between Riffles
On average, washers indicated that 26.1% or 13.6 m^2 of each surveyed riffle area were disturbed by foraging fish during the 24 h periods (Table 7; Aim 2). However, different riffles experienced different amounts of foraging (Figure 11), and the magnitude of disturbance varied significantly between sites where multiple observations ($n \geq 3$) made comparisons possible (Figure 12; LMM: $F_3 = 11.05$, $P = 0.03$). In particular, site 1 was disturbed more heavily than the other three sites, which could imply that fish showed a preference for this location within the study reach.

4. Discussion
4.1. Foraging Impacts at the Patch Scale
Foraging by fish in the River Idle caused significant changes to the microtopography and size composition of water-worked gravel substrates. Specifically, foraging increased microtopographic roughness, coarsened the substrate, and reduced the total mass of sediment, especially the finer fractions (4–22.6 mm), in treatment trays, which confirms Hypotheses 2 and 3. These disturbances were consistent with findings from ex situ experiments (Pledger et al., 2014, 2016) in that the majority of microtopographic alterations involved particle rearrangement rather than digging holes and creating mounds of grains with a depth/height that exceeded the diameter of the D_{50}. Fish predominantly foraged the bed surface layer, where the attitude and position of individual clasts
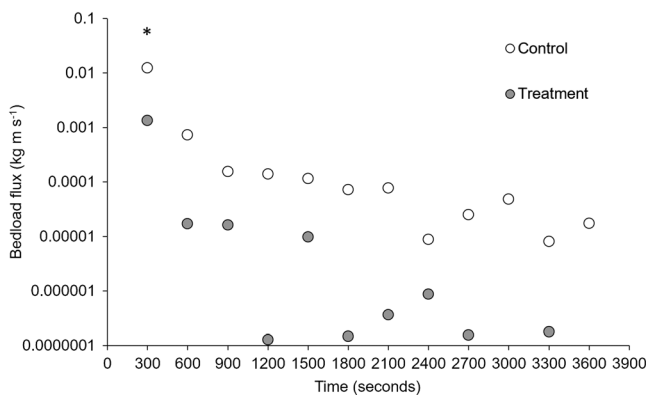
Figure 6. Bedload flux (measured averages for 300 s periods) during the entrainment test. Means for treatment (gray symbols and solid line, $n = 6$) and control (open symbols and dashed line, $n = 6$) replicates. An asterisk above a pair of points indicates that the difference between treatment and control values is significant ($\alpha = 0.05$).
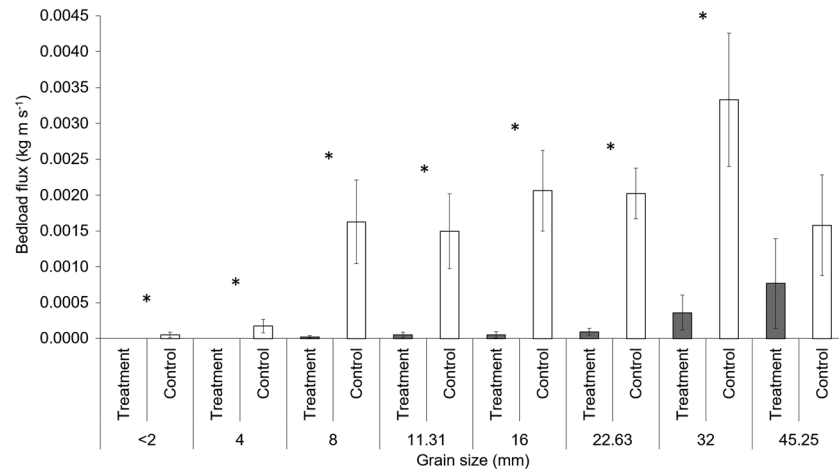
Figure 7. Fractional bedload flux after 300 s during the entrainment test. Means ± SE for treatment ($n = 6$) and control ($n = 6$) replicates. An asterisk above a pair of points indicates that the difference between treatment and control values is significant ($\alpha = 0.05$).

were altered. Disturbance by foraging fish did not extend below the active layer or involve the creation of sediment mounds that result from nest construction by Pacific Salmon *Oncorhynchus* spp., for example, Burner (1951).

Significant increases in the standard deviation of surface elevations imply that foraging increased the protrusion of individual particles. As in previous ex situ experiments (Pledger et al., 2014, 2016), grain reversal was also observed (Figure 13) and reflects the propensity of fish to *always* feed in the upstream direction, pushing grains over as they bulldoze the bed facing into the flow. These structural changes did not manifest as a significant change in inclination index values, or a shift from positive to negative values, so Hypothesis 1 was not upheld. The likely reason for this is that imbrication was weak to begin with—the large size and relatively rounded shape of bed material in the River Idle mean that they are not prone to developing strongly imbricated structures—and foraging simply produced a different random arrangement of grains rather than reversing imbrication. The overloose structure could also result from the sediment size distribution available to the stream and the foraging that causes a lack of fines for filling interstitial spaces and packing grains in resting pockets. Furthermore, bed structure is influenced by the frequency, longevity, and magnitude of flood events (e.g., Paphitis & Collins, 2005; Reid et al., 1985), with flow characteristics and regime therefore potentially responsible in part for the overloose and weakly imbricated nature of bed materials.

Foraging tended to reduce the elevation of the bed surface. On average, 63% of all significant elevation changes (i.e., changes $> \pm 6$ mm) were negative compared with 37% that were positive (Figure 4). Foraging therefore reduced the sediment surface to a level below the lip of the experimental trays

Table 6
Fractional Flux Statistics for the Difference Between Control and Treatment Conditions After 300 s During the Entrainment Period

Grain size (mm)	Control (kg m^{-1} s^{-1})	Treatment (kg m^{-1} s^{-1})	Statistical test	Test statistics d.f.	Test result	*P* value
<2	0.000051 ± 0.000041	0 ± 0	Mann–Whitney	10	6.00	0.022
4	0.00017 ± 0.000096	0 ± 0	Mann–Whitney	10	<0.001	0.002
8	0.0016 ± 0.00058	0.000023 ± 0.000019	Mann–Whitney	10	3.00	0.016
11.31	0.0015 ± 0.0052	0.000052 ± 0.000038	Mann–Whitney	10	3.00	0.014
16	0.0020 ± 0.000056	0.000051 ± 0.000043	Mann–Whitney	10	1.00	0.004
22.63	0.0020 ± 0.00035	0.000095 ± 0.000047	*t* test	10	5.39	<0.001
32	0.0033 ± 0.00092	0.00036 ± 0.00024	Mann–Whitney	10	2.00	0.009
45	0.0016 ± 0.00070	0.00077 ± 0.00063	Mann–Whitney	10	11.00	0.23

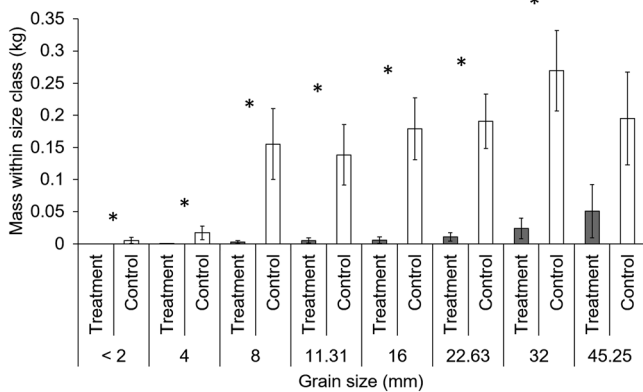*Note.* Values represent means ± SE. $\alpha = 0.05$.
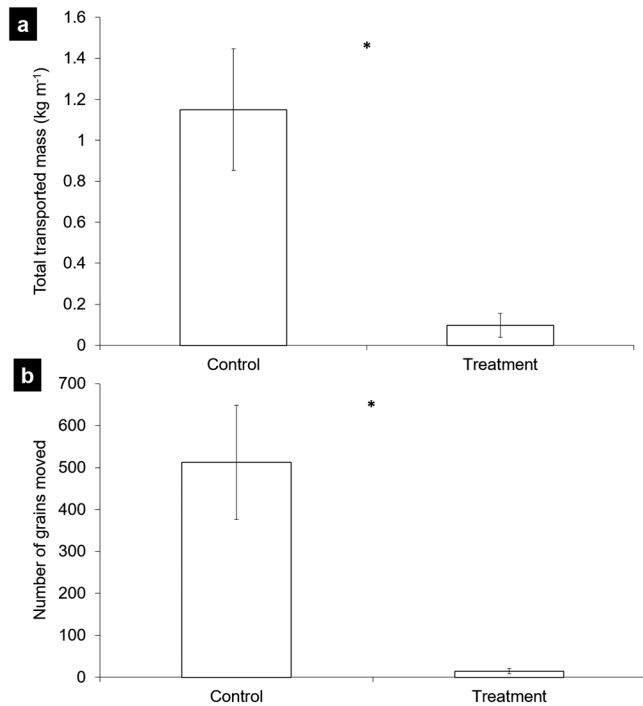
Figure 8. The impact of foraging fish on the stability of water-worked gravel-bed textures. (a) Total transported mass and (b) total number of transported grains at the end of the entrainment period, for treatment and control replicates. Points represent means ± SE (control $n = 6$; treatment $n = 6$). An asterisk above a pair of points indicates that the difference between treatment and control values is significant ($\alpha = 0.05$).

(Figure 13). This reduction in elevation was a response to whole-grain displacements and the removal of grains from sediment trays that also affected the size distribution of fluvial sediments left in the tray inserts. On average, 2.8 kg (33%) of sediment was ejected from the treatment tray inserts relative to control tray inserts, and significant losses of sediment were recorded for the 4 mm (−58%), 8 mm (−46%), 11.31 mm (−47%), 16 mm (−37%), and 22.6 mm (−32%) size classes (Figure 5). These data indicate that fish preferentially removed finer grain-size fractions, perhaps due to their small size and mass, which is consistent with the significant increases in D_{10} and D_{90} values.

Entrainment tests on the tray inserts found that foraged sediments were less mobile and so Hypothesis 4 was not upheld. This result disagrees with the results of earlier ex situ experiments (Pledger et al., 2014, 2016) where foraging caused reduced bed stability and consistent increases in bedload transport. Both sets of experiments documented similar changes in grain attitude and increases in microtopographic roughness in foraged beds, but the magnitude of fish impact during this in situ experiment was greater with significant substrate coarsening and large reductions in surface elevation that together reduced particle mobility. In this experiment, the overall reduction in bedload flux was also associated with a greater flux of coarse material (Figure 7). This occurred in both treatment and control runs and may reflect the grain size distribution of the mixture, in which finer grains were relatively less available (Figure 5). Winnowing of fine sediments by fish may have contributed to the reduced availability of fine sizes from the foraged trays (Figure 7 and 9). Also, because of removal of clasts by fish, sediment sat lower in foraged trays. Therefore, when trays were inserted into the flume bed for entrainment tests, entrained particles had to overcome the exposed lip of the tray. This was never more than 10 mm high, but it is possible that large clasts rolled over that lip more easily than small particles.
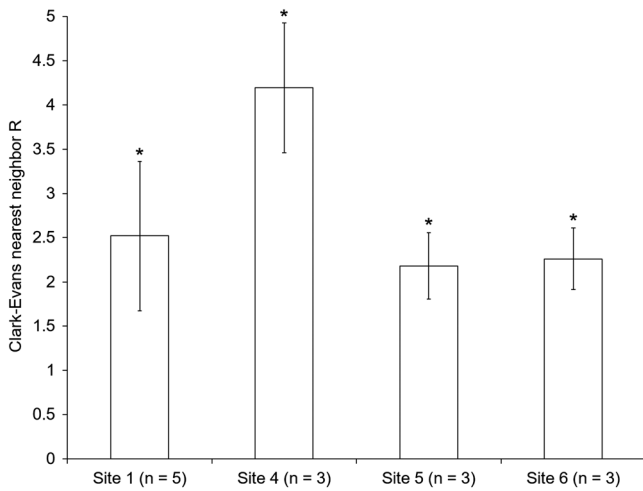
While the results from the entrainment tests suggest a link between foraging and a reduction in bed mobility, this is not the whole story. It is reasonable to assume that grains that moved out of the experimental trays by fish and deposited on the surrounding sediment surface, which were predominantly finer sizes, would be relatively more mobile than the coarse lag left behind. As such, the net effect of foraging on the bed surface was not captured by focusing attention on the small inserts. The overall net effect of foraging on sediment transport processes within a natural setting requires measurements at larger spatial scales that encompass the disturbance, displacement, and local deposition of affected grains.

4.2. Observations of Fish–Sediment Interactions During Foraging

Analysis of the underwater video indicated that fish interacted with and processed different sediment sizes in different ways. The nature of this interaction was strongly influenced by fish size (relative to particle size) and species, which suggests that community and population structures might be important in determining zoogeomorphic impacts. Observations suggest that large clasts were consistently pushed upstream, because fish consistently oriented upstream against the flow. Barbel were particularly effective in this regard and regularly exhibited the push and gulping foraging behavior where fish selectively displaced grains upstream before capturing prey items exposed by particle displacement (Pledger et al., 2014, for classification scheme of foraging behaviors).

Figure 9. The impact of foraging fish on the size distribution of transported sediment at the end of the entrainment test, for control and treatment replicates. Points represent means ± SE ($n = 6$). An asterisk above a pair of points indicates that the difference between control and treatment values is significant ($\alpha = 0.05$).

Figure 10. Clark–Evans nearest neighbor statistics derived from sites where the number of replicates was greater than or equal to 3. Values represent site means (±SE). Replicate numbers are included as part of x axis labels. An asterisk above a bar indicates that the difference between Clark–Evans nearest neighbor statistics and the value 1 was significant ($\alpha = 0.05$).

Table 7

Percent (%) and Surface Area (m^2) of Riffle Disturbed by Foraging Fish Over a 24 h Period in the River Idle

Site number	Replicate	Percent of river bed disturbed (%)	Area of river bed disturbed (m^2)
1	1	51.66	36.16
1	2	30.24	21.17
1	3	30.24	21.17
1	4	42.84	29.99
1	5	56.70	39.69
2	1	17.64	10.58
3	1	36.40	21.84
4	1	21.00	14.70
4	2	22.40	15.68
4	3	25.20	17.64
5	1	7.40	2.30
5	2	14.06	4.37
5	3	12.58	3.91
6	1	20.46	8.64
6	2	26.97	11.39
6	3	19.53	8.25
7	1	37.80	20.79
8	1	12.96	3.89
8	2	13.68	4.10
9	1	35.20	10.56
9	2	28.80	8.64
10	1	28.00	16.80
11	1	53.20	6.77
12	1	3.28	0.79
12	2	4.51	1.08
	Mean	26.11	13.64

Note. Values represent discrete replicates.

Fine sediments were often displaced downstream of their original positions when mature Barbel and Chub utilized gulping and spit behavior, which involved the fish taking mixtures of food and substrate in their mouth cavity. While processing the mixture, fish consistently fell back in the flow, presumably to minimize energy expenditure. Fish were then observed spitting the inedible component out at a location downstream of its original position. Juvenile fish (predominately Chub and Roach *Rutilus rutilus*) rarely adopted this gulping and spit behavior, and it is reasonable to assume that small fish with small mouths were gape limited in the grain sizes they could process. It is therefore likely that small fish utilize this behavior on only smaller grain-size fractions, likely resulting in different geomorphic impacts when comparing different size classes of a single species of fish.

4.3. The Extent and Nature of Foraging Disturbances at Reach and Barform Scales

Fish disturbed all 12 riffles in the study reach, implying that fish foraged the entire study reach while feeding. The pattern of washer displacements indicated that feeding was distributed evenly across each riffle and not focused in particular spots or executed at random. This is consistent with our observations of structured foraging behavior in which fish systematically combed feeding riffles as they moved upstream. This possibly reflects an expectation that macroinvertebrate preys are available across entire riffles and/or that systematic searching is the most efficient form of prey capture.

4.4. The Magnitude of Foraging Disturbance at Barform and Reach Scales

On average 26.1% of each riffle surface was disturbed in each 24 h period that was monitored. If fish foraged undisturbed sections on successive days and foraged at this rate, the entire surface area of riffles could be completely disturbed in approximately 4 days. This represents a substantial zoogeomorphic effect, given the importance of bed surface structure, microtopography, and grain-size distribution for bed material entrainment and transport (Bathurst, 1987; Reid et al., 1992, 1997).

The percentage of the total area disturbed in a 24 h period by fish varied between riffles (Aim 2). For example, the largest amount of disturbance that occurred in a 24 h period was at site 1 (56.70% representing 39.69 m^2) while the smallest amount was recorded at site 12 (3.28% of the area representing 0.79 m^2). The reasons for between-site differences are unknown, but there are numerous biotic and abiotic factors that might influence the magnitude of local foraging effects. These include differences in flow characteristics, temperature, prey availability, predator abundance, and characteristics of the fish community (functional groups, abundance, and fish size). What is clear is that fish impacts are spatially heterogeneous, at least across riffles of this study, and so might contribute to overall within-stream habitat heterogeneity.

4.5. The Potential Importance of Benthic Foraging as a Zoogeomorphic Activity

Published studies of the role of fish as zoogeomorphic agents in streams have primarily focused on disturbance caused by salmonids during nest building. This is clearly an important mechanism by which fish can substantially alter sediment conditions, near-bed hydraulics, and sediment
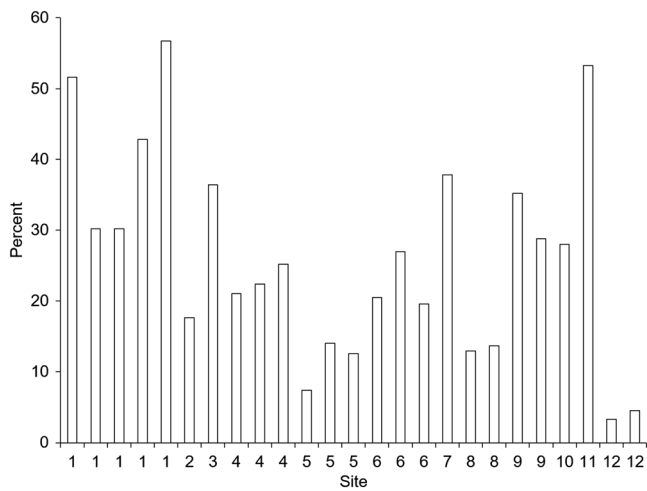
Figure 11. Percentages of riffles disturbed by foraging fish over 24 h periods. Bars represent site- and replicate-specific values.

transport (Albers & Petticrew, 2013; Buxton et al., 2015; Field-Dodgson, 1987; Gottesfeld et al., 2008; Hassan et al., 2008, 2015; Kondolf et al., 1993; Macdonald et al., 2010; Montgomery et al., 1996; Moore, 2006; Moore et al., 2004; Peterson & Foote, 2000). We speculate that foraging may be equally, if not more, important as a zoogeomorphic mechanism in UK rivers. First, in the majority of UK riverine systems, benthic feeders are more common than lithophilic spawners. For example, of the 21 most common fish species (excluding anadromous and catadromous fishes) in UK rivers, nine species (42%) are lithophilic spawners, but when classified by feeding behaviors, seven (33%) are obligate benthic foragers, 12 (57%) that are opportunistic foragers and only two (10%) do not purposefully interact with the bed during feeding. Second, lithophilic species require specific substrate characteristics to spawn successfully, so that the impacts of nest building are spatially restricted to specific river reaches, whereas foraging fish are mostly nomadic and will utilize a variety of habitat types to feed. Third, foraging fish must feed year-round, albeit at variable rates depending on water temperature and fish metabolism, which contrasts with the relatively restricted time window associated with spawning. It seems likely that benthic foraging is an important zoogeomorphic process within many river networks and therefore worthy of further investigation.

Entrainment tests of foraged trays found that bed materials were less mobile than in control trays, which contrasts with the results of previous ex situ experiments (Pledger et al., 2014, 2016) where foraging caused an increase in transport rates. This result suggests that foraging impacts on sediment flux are complex, involving several interacting processes with unknown net effects. We envisage a situation in which disturbance of bed structures that might generally increase mobility is mediated by local biogenic sediment sorting that renders some coarsened patches less mobile and other patches finer and more mobile.

Thus, it is reasonable to suppose that during competent flows, bed materials rendered less stable by foraging will move relatively more easily, at lower entrainment stresses than would be required in the absence of foraging. Specific foraging behaviors, including upstream bulldozing and gulping and spit feeding, also displace significant quantities of sediment; on the Idle, fish displaced an average of 2.8 kg of sediment from tray inserts during a 12 h period. Video observation of feeding behaviors suggests that this constituted upstream movement of relatively coarse material and downstream movement of relatively fine material (via push and gulping and gulping and spit feeding styles, respectively). This was confirmed by measured coarsening in the foraged trays, which rendered the bed material less mobile than that in control trays. We observed, but did not measure, that coincident downstream deposition of finer materials moved short distances by direct disturbance and by ejection from fishes' mouths as they drifted back downstream from foraged patches. Such downstream displacement of relatively fine sediment may produce finer patches of relatively more mobile materials, not least because particles dropped by fish are left in relatively exposed and therefore vulnerable positions.

The impact of benthic foraging may therefore reflect the net effects of both textural disturbance and biogenic particle sorting, as these affect entrainment stresses under subsequent competent flows. We did not consider this combination of processes here and in particular did not measure grain sizes and entrainment for patches downstream of foraged trays. This emerging view of how benthic feeding can affect bed conditioning and sediment flux might be extended further to consider the net effect of direct biogenic displacement of sediment and also the effects of feeding at flows close to the threshold of entrainment. Rheophilic species such as Barbel are capable of foraging under high flows, and the direct expenditure of biogenic energy may act as a surcharge sufficient to increase transport rates.
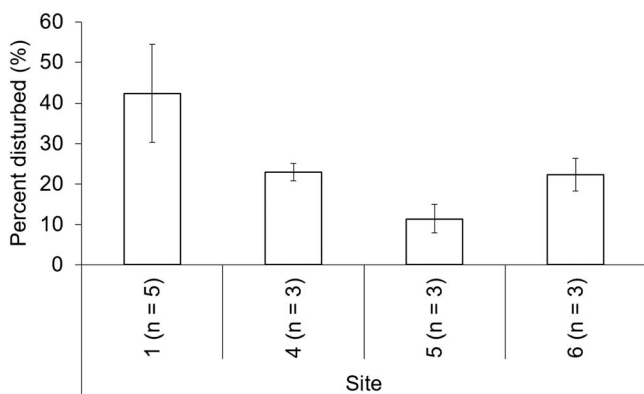
Figure 12. Percentages of the riffle disturbed by foraging fish over a 24 h period at sites where multiple replicates were recorded. Values represent means ± SD. Replicate numbers are presented as part of x axis labels.

Figure 13. Photograph of a treatment tray affected by foraging that shows (1) restructuring of grains and the reversal of inclinations (red circle) by foraging fish, (2) the effect of foraging on substrate depth, and (3) the effect of foraging on sediment composition (compare Figures 2b and 9). Note: The experimental tray was initially filled with gravels such that the sediment surface was level with the top of the blue tray inset. Flow direction is from right to left in image.

5. Conclusion

For the first time, a series of in situ experiments and observations have quantified patch-, riffle-, and reach-scale bed material disturbances caused by benthic-feeding fish. Benthic foraging was prolific along a 1 km study reach of the River Idle. Fish foraged in a systematic and meticulous manner, combing entire riffles in search of food. The average rate of disturbance (26.1% of each riffle representing 13.64 m^2) suggests that the surface layer of surveyed riffles could be turned over in as little as 4 days. Patch-scale experiments showed that benthic foraging increased bed surface microtopography and coarsened the grain-size distribution of bed materials. Building on initial observations by Statzner, Sagnes, et al. (2003) and Statzner and Sagnes (2008), ex situ experiments (Pledger et al., 2014, 2016) showed that such bed disturbance is associated with increased sediment flux under subsequent high flows. In the field, further work is needed to investigate the net effects of foraging on bedload transport at scales that encapsulate the disturbance, displacement, and deposition of affected bed materials. In this study, our measurements revealed reduced bed material transport from within coarse-grained lag patches where fish had fed and where residual grains were relatively heavy and stable. We expect that if measured at a larger scale, including the surrounding areas of the bed where fish deposited relatively finer sediments in exposed positions, measurements might reveal a different net effect on particle stability and flux. Additionally, the direct impact of feeding mechanisms (e.g., gulp and spit feeding) on local grain displacements and fish-induced sediment mobility during foraging at near-critical flows requires further investigation. These are potentially important zoogeomorphic processes with implications for understanding coarse sediment mobility in gravel-bed rivers.

Video analysis revealed that fish interacted with the riverbed sediments in different ways depending on their size and species. In addition, differences in the extent of bed disturbance were observed between riffles in the study reach. It is likely that the nature, magnitude, and spatial extent of fish-foraging impacts will be variable in space and in time as a function of community composition (species, fish size, and demographics) and local flow, substrate characteristics. Future work should investigate the spatial extent and temporal persistence of foraging effects at reach and river scales. This type of upscaling work is essential to evaluate the importance of zoogeomorphic impacts on river environments.

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