ESPL State of the Science paper

Zoogeomorphological behaviours in fish and the potential impact of benthic feeding on bed material mobility in fluvial landscapes

Stephen Rice[1*], Andrew Pledger[1], Julia Toone[2], Kate Mathers[3]

* Corresponding author

1. Loughborough University, Department of Geography, Loughborough, UK, LE11 3TU
2. Environment Agency, Trentside, Nottingham, UK, NG2 5FA
3. Eawag, Department of Surface Waters Research and Management, 6047 Kastanienbaum, Switzerland

ABSTRACT

Foraging by benthivorous fish can affect bed material mobility and sediment flux. This paper collates evidence of benthic feeding effects at local scales and evaluates the possibility that large numbers of foraging fish, each of which accomplishes a small amount of geomorphic work when feeding, may have a cumulative effect across river systems. A first synthesis of research from several disciplines provides a deeper understanding of how fish disturb and condition bed materials with implications for sediment mobility. To evaluate the spatial extent of benthic feeding and therefore the potential for it to have a large-scale effect, the distribution of benthivorous fish is established across a large river network. After quality control, the dataset yields a comprehensive set of fish community information based on over 61,000 individuals and 30 species at 176 sites. The factors that are likely to mediate foraging and its geomorphological effectiveness are considered. A novel scoring system that incorporates three key controls (fish feeding behaviour, fish abundance and fish body size) is then applied across the river network to provide the first prediction of where geomorphologically effective benthic feeding is feasible and its possible relative magnitude. Our results demonstrate that the potential for zoogeomorphic impacts is widespread but variable in space as a function of community composition and the abundance of key benthivores. A preliminary calibration against measured field impacts suggests that benthic feeding may cause measurable geomorphological disturbance at more than 90% of sites. Together, previous work and this unique analysis suggest that benthic feeding is sufficiently effective and extensive to warrant additional research. Investigating the role of benthivorous fish in fluvial geomorphology is important because it may yield results that challenge the assumption that biota are irrelevant sources of energy in geomorphological systems. Key research questions and a roadmap to facilitate progress are identified.

KEYWORDS: fish, zoogeomorphology, sediment transport, foraging, biogeomorphology

BACKGROUND AND PURPOSE

Along with microbial life and vegetation (biogeomorphology: Viles, 1988), animals can affect sediment fluxes and moderate landform development, a process regime referred to as zoogeomorphology (Butler, 1995; Hall and Lamont, 2003; Butler and Sawyer, 2012; Holtmeier, 2015). Intricate ecogeomorphological feedbacks can affect the responsible organism or wider community (Naiman *et al.*, 2000; Wheaton *et al.*, 2011; Beschta and Ripple, 2012), in which case the geomorphological effect is a form of ecosystem engineering (Jones *et al.*, 1994; Wright and Jones, 2006; Moore, 2006; Jones, 2012). Zoogeomorphological contributions to ecosystem engineering are therefore part of the *evolutionary* process that entwines the biotic and abiotic elements of the Earth’s surface in the co-development of life and landscape (Meysman *et al.*, 2006, Corenblit *et al.*, 2007; Steiger and Corenblit 2012). In addition, zoogeomorphological processes can present significant socio-economic risks. For example, burrowing of levees on the Secchia River in Italy, possibly by den-building porcupines, contributed to a single structural failure that caused flood damage estimated to be greater than $500 million (Orlandini *et al.*, 2015).

Zoogeomorphological investigations in rivers have predominantly focused on iconic species that have impressive visual impacts; for example, on beaver (*Castor spp.*) where impacts on sediment transfer, hydromorphology and floodplain formation through dam building and meadow construction are plain to see and widely acknowledged (Butler & Malanson, 1995; Gurnell, 1998; Polvi and Wohl, 2012; Giriat *et al.* 2016). There has also been some focus on the geomorphological impact of prolific invasive species (Butler, 2006) because they have the potential to disturb landscapes that have not evolved to be resilient to them; for example, non-native crayfish that affect bank stability, sediment recruitment and the mobility of coarse and fine sediment particles (Statzner *et al.*, 2000, 2003; Harvey *et al.*, 2011; Johnson, 2011; Harvey *et al.*, 2014; Rice *et al.*, 2016; Faller *et al.*, 2016). Other research has considered the impact of less celebrated, somewhat hidden fluvial zoogeomorphic agents ("Cinderella" species, Rice *et al.*, 2012) where the impacts are not apparent to the casual observer but may nevertheless be important; for example, silk-spinning caddis fly larvae that increase bed particle stability (Statzner *et al.*, 1999; Cardinale *et al.*, 2004; Johnson *et al.* 2009; Albertson *et al.*, 2014).

Almost all this work has demonstrated the impact of river organisms on fluvial processes at small scales, often via relatively limited field observation programmes or in necessarily small *ex-situ* (and rarely, *in-situ*) experiments (see reviews in Statzner, 2012; Rice *et al.* 2012; Albertson and Allen, 2014; Atkinson *et al.*, 2017). There are only a few exceptions, including an estimation of beaver impacts on continental sediment yield (Butler and Malanson, 2005) and studies showing the importance, relative to flooding, of salmonid activity for coarse bedload movement (Hassan *et al.*, 2008) and of signal crayfish (*Pacifastacus leniusculus* (Dana)) activity for fine sediment entrainment (Rice *et al.*, 2016). In general, the results of small-scale experiments and local observations have not been scaled up. New technologies, including eDNA, are making it easier to establish the distribution of zoogeomorphic agents, and thence their potential to have impacts, over large scales, (Larsen *et al.*, 2017). However, in the absence of evidence demonstrating the impact of river organisms across larger spatial and temporal scales, a pervasive assumption remains that zoogeomorphic effects are inconsequential relative to geophysical forcing for fluvial sediment fluxes and landscape development.

However, biological energy expenditure by large numbers of individual organisms, each of which accomplishes a small amount of geomorphic work, may yield significant cumulative impacts at larger scales (Philips, 2009; Rice *et al.*, 2016). This idea is not new. Supported by measurements made over several decades, Darwin (1881) quantified the impact of casting by earthworms on downslope soil displacement and estimated that the activity could move as much as 0.057 kg m^{-1} a^{-1} (5.7 tonnes km^{-1} in 100 years) across gentle valley slopes in southern England, smoothing topography and contributing to continental denudation. Different species of earthworm in contrasting environments may have different effects, for example reducing soil erosion in some tropical highlands (Jouquet *et al.*, 2008). In fluvial geomorphology the likelihood of an effect equivalent to that of earthworms has not been demonstrated even though there may be many capable zoogeomorphic agents in river ecosystems (Statzner, 2012; Rice *et al.*, 2012).

In this paper we examine a common fish behaviour, foraging in coarse fluvial substrates for food (benthic feeding), and ask whether it could have a large-scale geomorphological impact in rivers, in much the same way that earthworms have an imperceptible but significant impact on terrestrial sediment fluxes and morphology (Darwin, 1881, *et seq.*). Fish utilise fluvial sediments in several ways. Most fish research has focused on redd construction by salmonids (DeVries, 2012) demonstrating that salmon (*Salmo spp.)* spawning can affect bed material characteristics (Kondolf *et al.*, 1993; Montgomery *et al.*, 1996), bed permeability and hyporheic exchange (Buxton *et al.*, 2015a), topographic drag (Montgomery *et al.*, 1996), bed material stability (Gottesfeld *et al.*, 2004; Buxton *et al.*, 2015b; Hassan *et al.*, 2015), bed load flux (Hassan *et al.*, 2008) and bedform generation (Field-Dodgson, 1987, Gottesfeld *et al.*, 2008). A welcome extension to this focus on local effects is found in Fremier *et al.*'s (2018) attempt to understand the impact of salmonid dispersal and bed destabilisation on long-term fluvial erosion and landscape evolution using a numerical modelling approach. The physical impacts of nest building by species other than salmonids have also been investigated. Although most of this work has an ecological focus without explicit geomorphological aims, the ecological literature includes the description of nests that are constructed from, or in, river bed sediment by fish including Arctic lamprey (*Lethenteron camtschaticum*), smallmouth bass (*Micropterus dolomi* (Lacepède)), three-spined sticklebacks (*Gasterosteus aculeatus* (L.)), stoneroller *(Campostoma anomalum* (Rafinesque)) and chub (*Nocomis spp.*), with *N. micropogin* (Cope) building spectacular dome-shaped nests that might comprise 10000 individual gravel particles (Lachner, 1952; Winemiller and Taylor, 1982; Thorpe, 1988; Sabaj *et al.*, 2000; Rushbrook and Barber, 2008; Shirakawa *et al.*, 2013; Peoples *et al.* 2016).

In comparison to spawning and nesting behaviours, the zoogeomorphic relevance of fish feeding from river bed sediments has not been widely studied (Statzner *et al.*, 2003; Stazner and Sagnes 2008; Fortino, 2006). One strand of ecological research has investigated how foraging of fine organic and mineral sediments on river beds affect benthic resource availability (Power, 1990; Flecker, 1996; 1997; Pringle and Hamazaki, 1998; Gido and Matthews, 2001; Flecker and Taylor, 2004; Cross *et al.*, 2008), but the primary motivation has been to understand the implications for ecological community structure and functioning, not sediment dynamics.

Foraging is an interesting behaviour to consider because of this lack of attention by geomorphologists, but also because a small body of work has demonstrated that benthic feeding can be an effective local zoogeomorphic process. If, in addition, foraging is widespread and persistent across river networks, then it is possible that foraging is an important, large-scale influence in fluvial geomorphology. This supposition is investigated in three steps. First, we review research on benthic foraging and its geomorphological impact, including discussion of those factors that might mediate the presence of foraging behaviours and geomorphological effectiveness at individual sites (e.g. fish community composition, fish body size, fish abundance). Second, based on a classification of UK freshwater fish by feeding behaviour, we examine the distribution of benthic feeding fish across a large river network in the UK. Finally, we use a simple modelling tool that incorporates these factors to provide a first-order prediction of the likelihood that foraging has geomorphological impacts across the same UK river network.

2. BENTHIC FORAGING, GEOMORPHIC IMPACTS AND FORAGING CONTROLS

Foraging by fish in coarse-grained river beds

Foraging involves the acquisition of food through searching and represents a key determinant of fitness, survival and reproduction in animals (Danchin *et al.*, 2008). Benthic foragers interact with bed sediments in a variety of ways determined by fish size, species, and the environmental setting (Pledger *et al.*, 2014; 2016; 2017). For example, small fish with small mouths may be restricted to feeding within the surface layer, adjusting grain orientations or flipping clasts, whereas large-bodied or highly adapted foragers, may cause whole-grain displacements by digging holes or bulldozing sediments. Fish with large mouths relative to the size of sediment, may also suck in and process particles before depositing them in new positions on the bed. Videos of some of these activities for a selection of UK freshwater fish are included in supplementary material (Supp. 1). Regardless of feeding habitat, foraging fish tend to orientate upstream against the flow (Pledger *et al.* 2014; 2017), offering hydrodynamic benefits and increased locomotive control. Flow therefore regulates the nature of foraging behaviour in rivers, meaning the geomorphic impact of lotic vs lentic fishes are likely to be different.

Most behavioural studies (e.g. Janssen, 1976, 1978; Sibbing, 1991) consider the food capture, processing and ingestion mechanisms of fish, with little regard for their geomorphic implications. Pledger *et al.* (2014) therefore developed a classification scheme to describe the manner in which barbel (*Barbus barbus* (L)*)* and other *cyprinid* fishes interact with bed sediments and the specific feeding modes utilised whilst foraging (Figure 1). Behaviours include swim + gulping, gulping, push + gulping and bite + spit (see Pledger *et al.* (2014) for behaviour descriptions). In a laboratory flume, juvenile barbel foraged water-worked river gravels for chirononomid larvae, a natural prey, using push + gulping, gulping and swim + gulping feeding styles, spending 62, 37 and 1% percent of their time, respectively, utilising each behaviour (Pledger *et al.*, 2014; Figure 2a). In the River Idle, underwater video of juvenile chub (*Leuciscus cephalus* (L)) foraging 0.5 x 0.5 m patches of river gravels for natural prey recorded the feeding preferences of an unconstrained wild fish community. Analysis was based on a 30% subsample of five, 4-hour-long underwater video recordings. Twenty-four discrete feed events were observed; 6 and 18 corresponded to the swim + gulping and gulping feeding styles, respectively (Figure 2b). The fish were too small to utilise push + gulping and bite + spit feeding styles. Feed events were short-lived, lasting only 1 second on average, and there were four such events per hour, on average.

Little is known about the scale of bed disturbance caused by individual feeding events. An *ex-situ* laboratory flume experiment (Pledger *et al.* 2014) quantified the spatial extent of foraging by juvenile barbel (0.0195 ± 0.009 m long), when feeding across 0.138 m^2 beds composed of 5.6 – 1.6 mm gravels. On average, individual fish searching for bloodworm (chironomidae) fed six times per hour and disturbed 0.05 m^2

(36.9%) of the bed in each 4-hour observation period. This corresponds to a mean disturbance rate of 0.002 m^2 per feed event, equivalent to the hourly disturbance of a circular patch of substrate 50.4 mm in diameter, which is approximately ten times the maximum experimental particle diameter. In the field, observations of foraged bed surfaces in the River Idle, UK, revealed distinctive scars (Figure 3) created by fish, predominately adult barbel. The size of individual scars varied, but lengths ranged between 87 and 168 mm, and widths between 52 and 140 mm. Further field observations demonstrated that mature fish displaced 64-90 mm clasts during these events. These data provide some evidence that the spatial extent of individual feeding events is relatively small and scales with fish size. This implies that cumulative foraging extent is at least partly controlled by the size and number of foraging fish in an area, as the latter affects number of feeding events.

Foraging and coarse sediment dynamics

Foraging has the potential to indirectly affect coarse sediment transport in several ways (Figure 4). First foraging can compromise water-worked structures, dismantling grain-scale fabrics like imbrication, that develop during the waning stages of flood flows and subsequent sub-critical flows, and that stabilise bed materials (Komar and Li, 1986; Clifford *et al.*, 1992; Church *et al.*, 1998; Church, 2010). After foraging, grains are left in less mechanically stable positions with greater degrees of protrusion, more random fabrics and reduced imbrication, all of which have the potential to increase drag, reduce critical entrainment stresses and therefore promote the movement of individual particles under subsequent high flows.

In small (0.2 m-wide) outdoor channels, Stazner *et al.* (2003) quantified the impact of juvenile barbel on the topography and mobility of randomly arranged, fine gravel beds. Foraging had a significant impact on bed surface topography and the authors observed fish pushing gravel into piles, which they supposed resulted in looser bed sediments with more grains resting in elevated positions, projecting above the surrounding bed. As the number of fish was increased from zero to eight, Statzner *et al.* (2003) observed a decrease in the critical shear stress for gravel entrainment of ~45%. Pledger *et al.* (2014) extended this work by considering water-worked gravelly sediments. In a 0.3 x 10 m laboratory flume, they quantified the effects of feeding juvenile barbel on particle displacements, bed sediment structures and surface topography. For foraged and unforaged substrates, gravel entrainment and transport fluxes were measured under a moderate transport regime. On average, barbel modified approximately 37% of the bed area during a four-hour period. Whole-grain displacements and adjustments of grain orientations resulted in increased microtopographic roughness, reduced structure and so, increased sediment mobility. Specifically, grain disturbance increased bedload flux and the number of entrained grains by 60% and 82%, respectively, when comparing transport data from foraged and unforaged beds.

Laboratory experiments were extended to a field situation (River Idle, UK) where the effects of foraging fish, primarily rheophilic *cyprinids*, on gravel structures, surface topography, grain-size distributions and bedload transport, were assessed (Pledger *et al.*, 2017). Large (0.5 x 0.5 x 0.1 m) trays of gravel, water-worked under ambient flows and seeded with food (hempseed, *cannabis sativa*), were either exposed to foraging fish or not by deploying exclusionary cages. Sections of experimental trays were retrieved from the field and exposed to an entrainment flow in a laboratory flume to quantify changes in sediment mobility after foraging. Benthic feeding fish disturbed, on average, 74 % of the substrate during a twelve-hour period, displacing particle sizes up to and including 90 mm clasts, increasing bed surface microtopography and grain protrusion, coarsening substrates and loosening surface structures (Pledger *et al.*, 2017). These changes caused significant reductions in sediment mobility from the experimental trays, with declines in sediment flux and total transported mass detected from foraged substrates. This result contrasts with ex-situ experiments (cf. Pledger *et al.* 2014, 2016) where foraging increased sediment transport and reflects displacement of finer grains by fish to leave a coarser lag within the experimental trays. It is likely that entrainment from the surrounding bed, where fine grains were deposited by fish and left in relatively unstable positions, would be enhanced.

In addition to changing clast arrangements and undoing stabilising structures, foraging can affect local grain size characteristics with potential consequences for sediment transport. During the *in-situ* experiment, Pledger *et al.* (2017) detected significant changes in the size distribution of experimental tray substrates with foraging resulting in better sorted and coarser sediments, as indicated by increases in all grain-size percentiles. Benthic foragers preferentially displaced finer particle sizes from experimental trays which caused a statistically significant, 2.8 kg (33%) decrease in the total mass of sediment remaining in foraged trays. Observations of grain displacements showed that large clasts were consistently pushed upstream, typically by barbel utilising the push + gulping behaviour. However, fine sediments tended to be deposited downstream of their original locations because fish feeding using the gulp + spit behaviour, collected and processed sediments then drifted downstream to conserve energy, before ejecting particles from their mouths onto the bed surface. These behaviours, which sort sediment locally, are important because they may increase sediment patchiness, which is known to affect sediment mobility and transport (Wiberg and Smith, 1987; Kirchner *et al.*, 1990; Buffington and Montgomery, 1997; Ferguson, 2003). Furthermore, finer grains deposited on the sediment surface downstream of their origin, in relatively exposed positions without the structural stability of water-worked counterparts, are likely to be relatively more susceptible to entrainment.

A third way in which foraging may affect bedload mobility is via near bed hydraulics. This has not been assessed, but in the same way that Montgomery *et al.* (1996) suggest that redd construction might affect topographic drag, foraging probably affects grain drag. In particular, increases in surface protrusion, rugosity and the microtopography associated with grain rearrangement and feeding scars may increase grain roughness resulting in increased drag and lower near-bed velocities and shear. Such an affect would reduce grain mobility by lowering bed shear stress.

Figure 4 also highlights the potential for impacts on bed material transport to feed back to the environmental, predator and prey factors that determine foraging intensity and extent. For example, transport might affect bed material grain size distribution and so the ease with which prey can be found and habitat suitability for prey.

Field observations of foraging at reach scales

At 12 sites (covering approximately 600 m^2) along a reach of the River Idle, Pledger *et al.* (2017) quantified the local rate of foraging impact on riffles and considered the nature and spatial distribution of the foraging disturbance. This was achieved by installing disturbance indicators (spray-painted steel washers; 38 x 2 mm) across feeding riffles, at an approximate density of one per square meter, and assessing their displacement over a 24-hour period in the absence of any hydraulic changes. Each riffle recorded some disturbance, implying the impact of foraging was widespread, but the number of washers disturbed varied between riffles, ranging between 3.3 and 56.7% (representing between 0.8 and 39.7 m^2 of bed area). During each 24-hour period, an average of 26.1% of washers were disturbed, equivalent to 13.6 m^2 per riffle. Disturbance was not patchy, but evenly distributed across riffles, reflecting the way in which fish foraged systematically, combing entire riffles for prey. These findings highlight the potential importance of benthic foraging as a widespread and temporally persistent geomorphic activity in some rivers.

Controls of foraging intensity

Published studies of the controls of foraging have focused on species, species interactions, temperature and fish size. The joint impacts of barbel, gudgeon (*Gobio gobio* (L)) and the spinycheek crayfish (*Faxonius limosus* (Rafinesque)), in two-species parings, on the condition and mobility of fine-grained sediments were investigated by Stazner and Sagnes (2008). Exposure to each species resulted in greater sediment mobility, but their net effects when paired were generally less than the sum of the individual impacts. This suggests that interactions between the species in a local community are an important control on foraging behaviour. Canal *et al.* (2015) demonstrated that disturbance rates amongst species including stone loach (*Barbatula barbatula* (L)) and the South-west European nase (*Parachondrostoma toxostoma* (Vallot)) are partly controlled by ambient water temperature. Surface sediment disturbance by these species increased by 200-300% for an increase in water temperature from 10 to 20°C. Fish are ectothermic and are unable to regulate corporal temperature with metabolic heat, so they rely on ambient water temperature to drive metabolism. The result of lower water temperatures is therefore reduced activity, including reduced feeding (Lemons and Crawshaw, 1985). It is likely that as energy requirements and foraging activity vary through the year as a function of temperature, so zoogeomorphic activity may vary seasonally.

In *ex-situ* flume experiments, Pledger *et al.* (2016) examined the role of fish size and species as controls of sediment disturbance using four size classes of barbel (4-5”, 5-6”, 6-8”, 8-10” in length) and one of chub (8-10”). The area of disturbed substrate, foraging depth, microtopographic roughness, bedload flux and total transported bedload all increased with fish size, whereas sediment structure (measured by imbrication) decreased. With regard to species effects, 8-10” barbel foraged a larger area of the riverbed than chub and had a greater impact on microtopographic roughness and sediment structure. Structural and topographic changes by both species were associated with increased sediment mobility, but the bed load flux and total transported mass after foraging by barbel was 150% and 98% greater, respectively, than that after foraging by chub.

In addition to these factors, foraging extent and intensity, and therefore the cumulative zoogeomorphic impact of foraging, is likely to be influenced by a broader set of biotic and abiotic factors that moderate the relationship between energy gains and costs during foraging. These factors are neither fully defined nor understood. Flow and bed material characteristics are likely to be important as these affect the energy expenditure required to move between sites and manipulate clasts to expose and consume prey. Meteorological factors including barometric air pressure and air temperature have been shown to influence catch rates (which are indicative of feeding rates) in recreational fisheries (Margenau *et al.*, 2003; Stoner *et al.*, 2004). The ratio of prey availability to predator abundance is also likely to be important as this affects the intensity with which individuals must forage to successfully gain sustenance in competition with other individuals. Characteristics of the fish community, including some species traits are also likely to be important. For example, research has found that shoal-feeding fish are less timid, will spend less time exhibiting vigilant behaviour and will forage for longer when feeding (Pitcher & Parrish, 1993). Shoaling behaviour may therefore increase the zoogeomorphic impact of gregarious fish species such as *B. barbus*. Finally, there may be anthropogenic controls on foraging, including the role of anglers in encouraging benthic foraging by deploying ground baits. Pledger (2015) completed a field experiment that examined how bait density and type (hemp seed, fishmeal pellets) affected foraging behaviour. Feeding styles were different when fish foraged for natural prey versus bait, suggesting that heavily fished river reaches may experience different degrees of bed disturbance.

THE EXTENT AND POTENTIAL ZOOGEOMORPHIC IMPACT OF BENTHIC FORAGING AT CATCHMENT SCALES

Given the small-scale impact of individual fish, any large-scale cumulative impacts must be dependent on the distribution of benthivorous fish across river networks and the moderation of individual geomorphic efficacy by biotic and abiotic controls on foraging intensity. It is therefore reasonable to suppose that the potential for a large-scale zoogeomorphic impact increases with the spatial distribution of benthivorous fish and, based on the evidence presented above, with intensity factors including the abundance and size of those fish.

To evaluate the potential for large-scale geomorphological effects we use fisheries data from a large UK river network as a case study, to investigate the distribution of benthic feeding fish in space and determine how widespread they are. In turn, we use a simple modelling tool that incorporates measures of feeding behaviour, fish size and abundance, which are the three key biotic controls of ecosystem engineering potential (Moore, 2006), to provide a first-order prediction of the likelihood that benthic feeding has geomorphological impacts across that UK river network.

Study Area and Methods

The River Trent (10,452 km^2) rises in the Pennines and the low hills of the western Midland Plain around Birmingham and flows east and north through the English Midlands and ultimately into the Humber estuary (Figure 5a). Millstone Grit and Carboniferous Limestone sequences in the Pennines give way to Triassic Mercian Mudstones and sandstones through the majority of the catchment, with local anomalies including the Charnwood Precambrian volcanics in Leicestershire and Jurassic limestones in Lincolnshire. Annual rainfall varies between approximately 2000 mm in the northern uplands, at elevations around 630m a.s.l., to 550 mm in the distal eastern areas. At North Muskham, where the catchment area is 8,231 km^2 (79%) mean daily discharge is 89.5 $m^3 s^{-1}$, the mean annual flood (2-year return period) is 434.3 $m^3 s^{-1}$ and the largest flood on record (since 1961) is 1000.2 $m^3 s^{-1}$. Land-use is predominantly agricultural (42% grassland, 30% arable) with 18% urban cover, 7% woodland and 3% mountain heath and bog. The Trent provides a useful case study because of its scale and environmental diversity, which encompasses a range of river types including rain- and groundwater-fed gravel-bed rivers in the dramatic valleys of the Peak District (e.g. R. Dove), lower gradient gravel-bed rivers draining north across the Midland Plain (e.g. R. Mease) and the Trent itself, which flows in a broad low-gradient valley through finer alluvium as it approaches the Humber.

Between 2013 and 2015, the Environment Agency of England surveyed fish populations at 238 sites across the Trent catchment and we used this data in our analysis. At some sites, samples were collected in multiple years and in these cases the most recent data were selected. Samples were collected using several different methods. To ensure data consistency and quality, we retained only electrofishing samples collected in wadable watercourses where stop nets were deployed at both ends of the sampled reach (n=176). Some samples were collected by electrofishing the survey reach once (n=111), and others included 2 (n=49) or 3 (n=16) passes. The different number of passes might have introduced differences in the quality of individual samples, because more passes may have caught more fish or sampled more species. However, there is no relation between fish catch or species richness and the number of electrofishing passes in the dataset and we therefore assume that, for our purposes, all samples are of equivalent quality. The final dataset provided reasonable spatial coverage of the river network, but excluded deeper channels including most of the mainstem Trent where standard fish sampling methods cannot routinely be deployed (Figure 5b).

The final dataset contained a total of 61,055 individual fish comprising 30 species (Table 1), caught in reaches that were on average 110.6 m long (SD = 25.0 m) and 5.9 m wide (SD = 3.4 m). Maitland (2004) lists 57 established fish species for Britain’s fresh waters, including introduced species and marine fish that are occasionally found inland. The 30 taxa recorded in the Trent samples therefore represent 53% of possible UK species.

To assess the potential for geomorphic work at any given survey site, a benthic impact score (BIS) was calculated for each species that was present as:

BIS = FBS x MS x (n/A)

where FBS is a feeding behaviour score for the species, mass score (MS) is a score for the average adult mass of the species, n is fish abundance at the site and A is survey area. BIS weights each of the component parts equally, in the absence of any evidence to suggest a more appropriate alternative weighting. Feeding behaviour scores differentiate between the dominant feeding mechanism of each fish species at the adult stage. It is recognised that feeding behaviour in fishes is complex and dependent on a range of variables, but for the purposes of assessing potential geomorphic impact a simple nominal classification establishes if species do or do not affect the bed when feeding. Taxa were assigned benthic feeding scores FBS, based on their dominant feeding mechanisms (Table 1): piscivorous and parasitic = 0; opportunistic = 1; benthic = 2. Opportunistic species feed from the bed some of the time (e.g. chub) and benthic species are obligate benthic feeders, evolved and physiologically adapted to benthic foraging (e.g. barbel). Atlantic Salmon were assigned a score of 0 because negligible feeding is expected amongst returning adults.

Fish size has been shown to influence geomorphic impact (e.g. Pledger *et al.*, 2016), and we incorporated that in BIS by assuming that the force a fish is able to exert on the bed when foraging is proportional to its mass. Length ranges for each adult species were taken from Maitland (2004) and an average length calculated. An average mass for each species was subsequently calculated using the Environment Agency’s in-house length-mass calculator (National Fish Population Database), which is routinely used to convert length observations for a species into mass because direct mass measurements in the field are time-consuming. Mass scores were then assigned based on natural breaks in the distribution when average adult masses for all taxa were sorted by magnitude: 0 – 13g = 0; 14 – 99g = 1; 100 – 499g = 2; 500 – 1499g =

3 and; 1500 – 4000g = 4 (Table 1). The decision to score fish lighter than 14g at zero may be conservative, because small fish can disturb sands and detritus, but it reflects what we know about impact on bed material mobility based on the smallest barbel used by Pledger *et al.*, (2014). In those experiments, the smallest group of barbel used had an average mass of 14 g and rearranged gravels between 5.6 and 16mm in diameter, with an impact on subsequent bedload transport.

Finally, BIS includes a measure of abundance because we assume that the number of feeding events increases with the number of individuals that are present (Statzner *et al.*, 2003). Abundance was normalised by sample area to account for differences in the length and width of the reaches that were electrofished at different sampling sites. BIS therefore includes the three key drivers identified by Moore (2006) as determinants of impactful ecosystem engineers in streams: behaviour, body size and density. At each site, the BIS scores for each species present were calculated, then added together to yield a single index of potential geomorphological impact for that site, $\sum \mathrm{BIS}_{\mathrm{site}}$. For each species, across all sites, the sum of BIS scores, $\sum \mathrm{BIS}_{\mathrm{species}}$, indicates the sum magnitude of that species potential geomorphic impact via foraging.

Distribution and abundance of benthivorous fish

Of 30 species recorded, 13 are benthic specialists and 12 are opportunistic benthic feeders (Table 1). The total number of individuals in these two groups accounted for 52.6% (32,118 fish) and 46.2% (28,185 fish) of the total catch, respectively. Benthic feeding fish therefore are abundant and dominated the overall sample (98.8%). This abundance is matched by broad spatial distribution, such that benthic feeding fish are ubiquitous in the Trent catchment (Figure 6). Of the 25 benthic and opportunistic species, six have small average adult body masses below 14 g. This group of small fish were abundant, comprising 29,704 individuals; notably with 20,557 minnows. Therefore, almost half of all benthivorous fish (49.3%) were assigned MS = 0 and so are not predicted to have any impact on sediment disturbance. In the absence of the necessary research to establish whether fish this small affect bed sediments, this is appropriate.

There were 19 species of benthivorous fish with an average adult mass more than 14 g, and therefore predicted to have an individual effect on bed materials (FBS x MS > 0; Table 2). The total abundance of these fish was 30,599 (50.1% of the total catch) and the number of sites where these 19 species were found increased approximately as the square root of their abundance (Figure 7). Notably, the most abundant and widespread species tended to have lower MS and FBS, and are therefore less likely to be effective *individual* geomorphic agents (Figure 7). For example, 21,800 bullhead (*Cottus gobio*) were found at 147 sites (Figure 8a). Although these are aggressive benthic feeders they are small fish (10-15cm long, 28g average adult weight) and so unlikely to disturb large particles, scoring FBS x MS = 2. In contrast, 23 barbel and 80 common bream (*Abramis brama*), which are large fish (average adult weights of 1451 g and 1231 g) that are known to disturb gravelly and silty substrates (FBS x MS = 6), were found at 14 sites (Figure 8b).

Benthic Impact Scores

Across the catchment, 174 of the 176 sites had $\Sigma BIS_{site} > 0$, suggesting that the potential for geomorphic foraging impact is widespread (Figure 9). The distribution of scores was strongly positively skewed: 86% of sites had scores between 0 and 1 and the mean score was 0.76, but the maximum score for a single site was 13.47. There are two sites in the database on the River Idle that fall within the study area used by Pledger *et al.* (2017). These two sites have $\Sigma \mathrm{BIS}_{\mathrm{site}}$ = 0.138 and 0.253, respectively, equivalent to the 3rd and 10th percentiles of all site scores; that is, between 90 and 97% of sites have higher $\Sigma \mathrm{BIS}_{\mathrm{site}}$ scores. Given that the fish communities at the Idle sites were effective in disturbing bed materials sufficiently to affect bed mobility (Pledger *et al.*, 2017), this comparison provides a limited qualitative calibration of the scoring system. It suggests, albeit very crudely, that the $\Sigma \mathrm{BIS}_{\mathrm{site}}$ scores recorded at 90% of sites could be associated with measurable geomorphic work.

High $\Sigma \mathrm{BIS}_{\mathrm{site}}$ scores tend to be in the northern and western parts of the catchment, specifically the upper Trent, River Sow, those tributaries (the Dove particularly) that drain the upland areas of the Peak District and the River Mease (Figure 9). The greater potential for zoogeomorphic work in these rivers reflects differences in the community composition. There is an unsurprising association between $\Sigma \mathrm{BIS}_{\mathrm{site}}$ and bullhead abundance, with large numbers of bullhead on the Sow, Mease and upper Trent (Figure 8a) responsible for higher scores on those rivers. High scores in the Dove and Derwent catchments are again associated with bullhead, but also with brown trout. Values of $\Sigma \mathrm{BIS}_{\mathrm{species}}$ show that bullhead and brown trout contribute most to the aggregate potential of all species to do geomorphic work (Figure 10), being responsible for 75.3% and 8.8%, respectively, of the total score across all species.

DISCUSSION AND ROUTE MAP

The purpose of this paper is to evaluate whether foraging by fish is a viable influence of bedload sediment flux across fluvial landscapes. The research reviewed above confirms that foraging fish can disturb coarse bed sediments, with implications for local sediment sorting, bed material fabric and structure, and bed load transport, but the body of evidence is small and there are many knowledge gaps. A key gateway question, affecting the perceived value of investigating these gaps, is whether benthic feeding is sufficiently common and widespread to have a potential cumulative impact on bed material condition and bedload fluxes at catchment scales.

Our analysis of benthivorous fish in the River Trent network provides a first ever attempt to address this question by establishing a scoring system that uses fish data to identify sites where the river bed is prone to be disturbed and conditioned by benthic feeding fish. It is important to emphasize that BIS scores indicate the potential for benthic foraging to accomplish geomorphic work; they are not a measure of that effect. BIS is based on Moore’s (2006) criteria for effective ecosystem engineering in rivers – organism abundance, size and behaviour. Although these three criteria are proven to be relevant at local scales by the work of Pledger *et al.* (2016, 2017) and others, the nature of the relations between these factors and geomorphic work is largely unknown. In addition, other biotic and abiotic factors that are likely to affect the geomorphic work done by benthivorous fish (Figure 4) are not included; for example, bed-material grain size distribution. Furthermore, although we have made some attempt to calibrate the scores against known zoogeomorphic impacts on the River Idle, we cannot easily translate the scores into meaningful geomorphological expression. Although the scoring system is relatively unsophisticated and untested, it is an appropriate, low-cost, high-level index for a first attempt to establish the extent of site and species potentials.

In this context, calculated BIS scores indicate that the potential for zoogeomorphic impacts is widespread (benthic feeding fish are widespread and abundant) and variable in space as a function of community composition and the abundance of key benthivorous species. We do not make any greater claims, but suggest that this analysis, alongside previous research reviewed above, provide sufficient evidence to warrant additional investigation of the role of benthivorous fish in fluvial geomorphology. The case for redd-building impacts has been established over a long period but is now yielding large-scale assessments of the impacts that salmonids might have on millennial timescales and orogenic spatial scales (Fremier *et al.*, 2018). The aim of investigating foraging impacts is similar; to establish the detailed understanding of processes necessary to develop local and basin scale transport models that incorporate foraging effects. There are three key elements of the problem that together define a roadmap for future research in this area.

(1) Quantify the impact of benthic feeding by common freshwater fishes, individually and in typical community structures, including an understanding of the role of key biotic and abiotic controls (Figure 4). This could be addressed using controlled flume experiments to establish which common, benthivorous, fish species are capable of conditioning river bed sediments (altering size characteristics and structural organisation). The same experiments could investigate the impact of this conditioning on transport mechanics and sediment fluxes, and establish general relations in which the mechanistic impact is parameterised using generalisable parameters. Key abiotic factors (e.g. flow rate, bed material characteristics) and biotic factors (fish size, prey characteristics, inter-species competition) should be manipulated to understand and quantify their effect on bed conditioning and particle mobility.

(2) Develop predictive models of this disturbance effect based on fish community characteristics and the spatiotemporal distribution of relevant foraging behaviours in rivers. Establish typical rates of benthic bed disturbance and the extent to which ecological factors (e.g. community composition, demography, abundance, life stage) and environmental factors (e.g. substrate type, flow regime) control the magnitude and spatiotemporal distribution of bed-conditioning activity. Simple devices like washer disturbance indicators would be valuable for gathering such information. In addition, field experiments (*sensu* Pledger *et al.*, 2017) could investigate the extent of substrate conditioning by wild fish communities.

(3) Estimate the cumulative impact of benthic feeding for river-scale sediment fluxes. With a fuller understanding of which species and fish communities disrupt bed materials and how abiotic and biotic factors mediate their effects, a feasible goal becomes the development of a generic model for predicting the impact of foraging on sediment flux. This could, for example, be built using a spatially-explicit numerical sediment routing model, applied with Shields' values that have been adjusted to reflect the change in bed stability caused by foraging disturbance.

Why is this important? Because, despite seminal work (Darwin, 1881), growing theoretical understanding (Steiger and Corenblit 2012), strong empirical evidence (Philips, 2009; Rice *et al.*, 2016), technological innovations (Larsen et al., 2017) and societal implications (Orlandini *et al.*, 2015), geomorphologists have not fully assessed or incorporated the role of biological energy in models of geomorphological processes. The relative exclusion of biological processes from geomorphological thinking may have happened for a complex mixture of reasons, including historic accident, lack of conceptual frameworks and the inertia of conventional thought (Johnson, 2002). Nevertheless, it is possible that the failure to assess the potential geomorphic impact of common river fauna is a constraint on our understanding of fluvial sediment dynamics and landscape change (National Research Council, 2010; Atkinson *et al.*, 2017) and is therefore an omission worthy of greater attention.

ACKNOWLEDGEMENT

We are very grateful to Matthew Johnson for drawing Figure 1 and to James Smith for useful discussions pertaining to the research. The videos in supplementary material were collected by co-author Pledger, except for the log perch sequence, which was shot by Noel Burkhead (formerly USGS) who has kindly given his permission for us to use this. The Environment Agency of England supplied the fish survey information under licence, but this does not mean that the analysis or arguments presented here have any official status or that the Environment Agency endorse the authors or our use of the information supplied. Contains Environment Agency information © Environment Agency and database right. We are grateful for two anonymous reviews that improved the manuscript.

REFERENCES

Albertson LK, Sklar LS, Pontau P, Dow M, BJ Cardinale. 2014. A mechanistic model linking insect (Hydropsychidae), silk nets to incipient sediment motion in gravel-bedded streams. *Journal of Geophysical Research: Earth Surface* **119**: 1833–1852. https://doi.org/:10.1002/2013JF003024

Atkinson CL, Allen DC, Davis L, Nickerson ZL. 2017. Incorporating ecogeomorphic feedbacks to better understand resiliency in streams: A review and directions forward. *Geomorphology* **305**: 123-140. https://doi.org/10.1016/j.geomorph.2017.07.016

Beschta RJ, Ripple WJ. 2012. The role of large predators in maintaining riparian plant communities and river morphology. *Geomorphology* **157**: 88-98. https://doi.org/10.1016/j.geomorph.2011.04.042

Buffington JM, Montgomery DR. 1997. A systematic analysis of eight decades of incipient motion studies, with special reference to gravel-bedded rivers. *Water Resources Research* **33**: 1993-2029. https://doi.org/10.1029/96WR03190

Butler DR, Malanson GP. 1995. Sedimentation rates and patterns in beaver ponds in a mountain environment. *Geomorphology* **13**: 255–269. https://doi.org/10.1016/0169-555X(95)00031-Y

Butler DR, Malanson GP. 2005. The geomorphic influences of beaver dams and failures of beaver dams. *Geomorphology* **71:** 48-60. https://doi.org/10.1016/j.geomorph.2004.08.016.

Butler DR, Sawyer CF. 2012. Introduction to the special issue — zoogeomorphology and ecosystem engineering. *Geomorphology* **157–158**: 1–5. https://doi.org/10.1016/j.geomorph.2012.02.027

Butler DR. 1995. Zoogeomorphology Animals as geomorphic agents. Cambridge University Press, UK

Butler DR. 2006. Human-induced changes in animal populations and distributions, and the subsequent effects on fluvial systems. *Geomorphology* **79**: 448–459. https://doi.org/10.1016/j.geomorph.2006.06.026

Buxton TH, Buffington JM, Tonina D, Fremier AK, Yager EM. 2015a. Modeling the influence of salmon spawning on hyporheic exchange of marine-derived nutrients in gravel stream beds. *Canadian Journal of Fisheries and Aquatic Sciences* **72**: 1146-1158, https://doi.org/10.1139/cjfas-2014-0413

Buxton TH, Buffington JM, Yager EM, Hassan MA, Fremier AK. 2015b. The relative stability of salmon redds and unspawned streambeds, *Water Resources Research* **51:** 6074-6092. https://doi.org/10.1002/2015WR016908

Canal J, Laffaille P, Gilbert F, Lauzeral C, Buisson L. 2015. Influence of temperature on surface sediment disturbance by freshwater fish: a microcosm experiment, *Annales de Limnologie* **51:** 179-188. https://doi.org/10.1051/limn/2015012

Cardinale BJ, Gelmann ER, Palmer MA. 2004. Net spinning caddisflies as stream ecosystem engineers: the influence of hydropsyche on benthic substrate stability. *Functional Ecology* **18**: 381-387.

Church M, Hassan MA, Wolcott JF.1998. Stabilizing self-organized structures in gravel-bed stream channels: Field and experimental observations. *Water Resources Research* **34**: 3169-3179. https://doi.org/10.1029/98WR00484

Church M. 2010. Gravel-bed rivers. In Burt TP and Allison RJ (Eds) *Sediment Cascades: An Integrated Approach*, John Wiley and Sons, Chichester, 241-269 https://doi.org/10.1002/9780470682876.ch9

Clifford NJ, Richards K. Robert A. 1992. The influence of microform bed roughness elements on flow and sediment transport in gravel bed rivers: comment on a paper by Marwan A Hassan and Ian Reid. Earth Surface Processes and Landforms 17: 529-534. https://doi.org/10.1002/esp.3290170511

Corenblit D, Steiger J, Gurnell A, Tabacchi E. 2007. Darwinian origin of landforms. *Earth Surface Processes and Landforms* **32**: 2070-2073. https://doi.org/10.1002/esp.1536

Cross WF, Ramirez A, Santana A, Santiago LS. 2008. Toward Quantifying the Relative Importance of Invertebrate Consumption and Bioturbation in Puerto Rican Streams. *Biotropica* **40**: 477–484. https://doi.org/10.1111/j.1744-7429.2007.00388.x

Danchin E, Giraldeau L Cezilly F. (2008). Behavioural Ecology. New York: Oxford University Press.

Darwin CR. 1881. The Formation of Vegetable Mould, through the action of worms, with observations on their habitat. John Murray, London.

DeVries P. 2012. Salmonid influences on rivers: A geomorphic fish tail. *Geomorphology* **157–158**: 66–74. https://doi.org/10.1016/j.geomorph.2011.04.040

Faller M, Harvey GL, Henshaw AJ, Bertoldi W, Bruno MC, England J. 2016. River bank burrowing by invasive crayfish: Spatial distribution, biophysical controls and biogeomorphic significance. Science of The Total Environment **569-570**: 1190-1200. https://doi.org/10.1016/j.scitotenv.2016.06.194

Ferguson RI. 2003. The missing dimension: Effects of lateral variation on 1-D calculations of fluvial bedload transport. *Geomorphology* **56:** 1-14. https://doi.org/10.1016/S0169 - 555X

Fremier AK, Yanites BJ, Yager EM. 2018. Sex that moves mountains: The influence of spawning fish on river profiles over geologic timescales. *Geomorphology* 305:163-172. https://doi.org/10.1016/j.geomorph.2017.09.033

Field-Dodgson MS. 1987. The effect of salmon redd excavation on stream substrate and benthic community of two salmon spawning streams in Canterbury, New Zealand. *Hydrobiologia* **154**: 3-11

Flecker AS, Taylor BW. 2004. Tropical fishes as biological bulldozers: density effects on resource heterogeneity and species diversity. *Ecology* **85**: 2267-2278. https://doi.org/10.1890/03-0194

Flecker AS. 1996. Ecosystem engineering by a dominant detritivore in a diverse tropical stream. *Ecology* ***77***: 1845-1854. https://doi.org/10.2307/2265788

Flecker AS. 1997. Habitat modification by tropical fishes: environmental heterogeneity and the variability of interaction strength, *Journal of the North American Benthological Society* **16**: 286-295. https://doi.org/10.2307/1468258

Fortino K. 2006. Effect of season on the impact of ecosystem engineers in the New River, NC, *Hydrobiologia* **559:** 463-466, https://doi.org/10.1007/s10750-005-5325-5

Gido KB, Matthews WJ. 2001. Ecosystem effects of water column minnows in experimental streams. *Oecologia* **126:** 247-253. https://doi.org/10.1007/s004420000505

Giriat D, Gorczyca E, Sobucki M. 2016. Beaver ponds' impact on fluvial processes (Beskid Niski Mts., SE Poland). *Science of the Total Environment* **544**: 339–353. https://doi.org/10.1016/j.scitotenv.2015.11.103

Gottesfeld AS, Hassan MA, Tunnicliffe JF, Poirier AW. 2004. Sediment dispersion in salmon spawning streams: The influence of floods and salmon redd construction. *Journal of the American Water Resources Association* **40**: 1071-1086. https://doi.org/10.1111/j.1752-1688.2004.tb01068.x

Gottesfeld AS, Hassan MA, Tunnicliffe JF. 2008. Salmon bioturbation and stream process. *American Fisheries Society Symposium* **65**: 175 – 193

Gurnell, A.M., 1998. The hydrogeomorphological effects of beaver dam-building activity. *Progress in Physical Geography* **22:** 167–189. https://doi.org/10.1177/030913339802200202

Hall K, Lamont N. 2003. Zoogeomorphology in the Alpine: some observations on abiotic-biotic interactions. *Geomorphology* **55:** 219-234. https://doi.org/10.1016/S0169-555X(03)00141-7

Harvey G, Henshaw A, Moorhouse TP, Clifford NJ, Holah H, Grey J, Macdonald D. 2014. Invasive crayfish as drivers of fine sediment dynamics in rivers: field and laboratory evidence. *Earth Surface Processes and Landforms* **39**: 259-271. https://doi.org/10.1002/esp.3486

Harvey G, Moorhouse TP, Clifford NJ, Henshaw A, Johnson MF, MacDonald DW, Reid I, Rice SP. 2011. Evaluating the role of invasive aquatic species as drivers of fine sediment-related river management problems: the case of the signal crayfish (Pacifastacus leniusculus). *Progress in Physical Geography* **35**: 517-533. https://doi.org/10.1177/0309133311409092

Hassan MA, Gottesfeld AS, Montgomery DR, Tunnicliffe JF, Clarke GKC, Wynn G, Jones-Cox H, Poirier R, MacIsaac E, Herunter H and Macdonald SJ. 2008. Salmon-driven bedload transport and bed morphology in mountain streams. *Geophysical Research Letters* **35**: L04405. https://doi.org/10.1029/2007GL032997

Hassan MW, Tonina D, Buxton TH. 2015. Does small-bodied salmon spawning activity enhance streambed mobility? *Water Resources Research* **51:** 7467-7484. https://doi.org/10.1002/2015WR017079

Holtmeier F-K. 2015. Animals' Influence on the Landscape and Ecological Importance: Natives, Newcomers, Homecomers. Springer, London. https://doi.org/10.1007/978-94-017-9294-3

Janssen J. 1976. Feeding modes and prey size selection in the alewife (*Alosa pseudoharengus*). *Journal of the Fisheries Research Board of Canada* **33**: 1972-1975. https://doi.org/10.1139/f76-251

Janssen J. 1978. Feeding-behavior repertoire of the alewife, *Alosa pseudoharengus*, and the ciscoes *Coregonus hoyi* and C. *artedii*. *Journal of the Fisheries Research Board of Canada* **35**: 249-253. https://doi.org/10.1139/f78-040

Johnson MF, Reid I, Rice SP, Wood J. 2009. Stabilisation of fine gravels by net-spinning caddisfly larvae. Earth Surface Processes and Landforms 34: 413-423. https://doi.org/10.1002/esp.1750

Johnson MF, Rice SP, Reid I. 2011. Increase in coarse sediment transport associated with disturbance of gravel river beds by signal crayfish (*Pacifastacus leniusculus*). *Earth Surfaces Processes and landforms* **36**: 1680-1692. https://doi.org/10.1002/esp.2192

Jones CG, Lawton JH, Shachak M. 1994. Organisms as ecosystem engineers. *Oikos* **69** 373-386. https://doi.org/10.2307/3545850

Jones CG. 2012. Ecosystem engineers and geomorphological signatures in landscapes. *Geomorphology* **157-158**: 75-87. https://doi.org/10.1016/j.geomorph.2011.04.039

Jouquet P, Henry-des-Tureaux T. Mathieu J., Thu TD, Duc TT, and Orange D. 2010. Utilization of near infrared reflectance spectroscopy (NIRS), to quantify the impact of earthworms on soil and carbon erosion in steep slope ecosystem: A study case in Northern Vietnam. *Catena* **81**: 113-116. https://doi.org/10.1016/j.catena.2010.01.010

Kirchner JW, Dietrich WE, Iseya F, Ikeda H. 1990. The variability of critical shear stress, friction angle, and grain protrusion in water ‐ worked sediments. Sedimentology **37**: 647-672. https://doi.org/10.1111/j.1365-3091.1990.tb00627.x

Komar PD, Li Z. 1986. Pivoting analyses of the selective entrainment of sediments by shape and size with application to gravel threshold. Sedimentology 33: 425-436. https://doi.org/10.1111/j.1365-3091.1986.tb00546.x

Kondolf GM, Sale MJ and Wolman MG. 1993. Modification of fluvial gravel size by spawning salmonids. Water Resources Research 20: 2265 – 2274. https://doi.org/10.1029/93WR00401

Lachner EA. 1952. Studies of the biology of the cyprinid fishes of the chub genus nocomis of northeastern United States. *American Midland Naturalist* **48**: 433-466

Larsen A, Alvarez N, Sperisen C, Lane SN. 2017. Biotic drivers of river and floodplain geomorphology – New molecular methods for assessing present-day and past biota. Earth Surface Processes and Landforms **43:** 333–338. https://doi.org/10.1002/esp.4238

Maitland PS. 2004. Keys to the freshwater fish of Britain and Ireland, with notes on their distribution and ecology. Freshwater Biological Association Scientific Publication 62. Freshwater Biological Association, Ambleside UK.

Margenau TL, Gilbert SJ, Hatzenbeler GR. 2003. Angler catch and harvest of northern pike in northern Wisconsin lakes. N. Am. J. Fish. Manage. 23, 307–312. https://doi.org/10.1577/1548-8675(2003)023<0307:ACAHON>2.0.CO;2

Meysman FJR, Middleburg JJ, Heip CHR. 2006. Bioturbation: a fresh look at Darwin's last idea. *Trends in Ecology and Evolution* **21**: 688-695. https://doi.org/10.1016/j.tree.2006.08.002

Montgomery DR, Buffington JM, Peterson NP, Schuett-Hames D, Quinn TP. 1996. Stream-bed scour, egg burial depths, and the influence of salmonid spawning on bed surface mobility and embryo survival. *Canadian Journal of Aquatics and Fisheries Science* **53**: 1061 – 1070. https://doi.org/10.1139/f96-028

Moore JW. 2006. Animal ecosystem engineers in streams. *Bioscience* **56**: 237-246. https://doi.org/10.1641/0006-3568(2006)056[0237:AEEIS]2.0.CO;2

Naiman, RJ, Elliott, SR, Hellfield, JM, O'Keefe, TC. 2000. Biophysical interactions and the structure and dynamics of riverine ecosystems: the importance of biotic feedbacks. *Hydrobiologia* 410: 79-86.

National Research Council. 2009. Landscapes on the edge: new horizons for research on Earth’s surface. National Academies Press, Washington, D.C., USA.

Orlandini S, Moretti G, Albertson JD. 2015. Evidence of an emerging levee failure mechanism causing disastrous floods in Italy. Water Resources Research 51, 7995–8011. https://doi.org/10.1002/2015WR017426.

Peoples BK, Floyd SP, Frimpong EA. 2016. Nesting microhabitat comparison of Central stoneroller and Bluehead chub: potential inference for host-switching by nest associates. *Journal of Freshwater Ecology*, **31**: 251-259, https://doi.org/10.1080/02705060.2015.1091390

Pflieger WL. 1966. Reproduction of the smallmouth bass (Micropterus dolomieui) in a small Ozark stream. *The American Midland Naturalist* **76:** 410-418

Phillips JD. 2009. Biological energy in landscape evolution. *American Journal of Science* **309**: 271-289. https://doi.org/10.2475/04.2009.01.

Pitcher TJ, Parrish JK. 1993. Functions of shoaling behaviour in teleosts. In *Behaviour of teleost fishes*, Pitcher TJ (ed), Chapman and Hall, 2-6 Boundary Row, London, UK.

Pledger, A.G. (2015), Foraging fish as zoogeomorphic agents: their effects on the structure and composition of gravel-bed river sediments with implications for bed material transport, Unpublished PhD thesis, Loughborough University. https://dspace.lboro.ac.uk/dspace-jspui/handle/2134/16680

Pledger AG, Rice SP, Millet J. 2014. Reduced bed material stability and increased bedload transport caused by foraging fish: a flume study with juvenile Barbel (Barbus barbus). *Earth Surface Processes and Landforms* **39:** 1500-1513, https://doi.org/10.1002/esp.3592

Pledger AG, Rice SP, Millet J. 2016. Bed disturbance via foraging fish increases bedload transport during subsequent high flows and is controlled by fish size and species. *Geomorphology* **253:** 83-93. https://doi.org/10.1016/j.geomorph.2015.09.021

Pledger AG, Rice SP, Millet J. 2017. Foraging fish as zoogeomorphic agents: an assessment of fish impacts at patch, barform, and reach scales. *Journal of Geophysical Research: Earth Surface* **122**: 2105-2123. https://doi.org/10.1002/2017JF004362

Polvi LE, Wohl E. 2012. The beaver meadow complex revisited – the role of beavers in post-glacial floodplain development. Earth Surface Processes and Landforms 36: 332–346. https://doi.org/10.1002/esp.2261

Power ME. 1990. Resource enhancement by indirect effects of grazers: armored catfish, algae and sediment. *Ecology* **71:** 897-904. https://doi.org/10.2307/1937361

Pringle CM, Hamazaki T. 1998. The role of omnivory in a neotropical stream: separating diurnal and nocturnal effects. Ecology **79**: 269-280, https://doi.org/10.1890/0012-9658(1998)079[0269:TROOIA]2.0.CO;2

Rice SP, Johnson MF, Reid I. 2012. Animals and the Geomorphology of Gravel-bed Rivers in Church M, Biron P and Roy AG (Eds), Gravel-bed rivers: processes, tools, environments, 225-241. John Wiley and Sons, Chichester.

Rice SP, Johnson MF, Mathers K, Reeds J, Extence C. 2016. The importance of biotic entrainment for base flow fluvial sediment transport. *Journal of Geophysical Research: Earth Surface* **121**: 890-906. https://doi.org/10.1002/2015JF003726

Rushbrook BJ, Barber I. 2008. A comparison of nest building by three-spined sticklebacks *Gasterosteus aculeatus* from still and flowing waters. *Journal of Fish Biology* **73**: 746–752. https://doi.org/10.1111/j.1095-8649.2008.01970.x

Sabaj MH, Maurakis EG, Woolcott WS. 2000. Spawning behaviors in the bluehead chub, Nocomis leptocephalus, river chub, Nocomis micropogon and central stoneroller, Campostoma anomalum. *American Midland Naturalist* **144**:187-201.

Shirakawa H, Yanai S, Goto A. 2013. Lamprey larvae as ecosystem engineers: physical and geochemical impact on the streambed by their burrowing behaviour. *Hydrobiologia* **701:** 313-322.

Sibbing FA. 1991. Food capture and oral processing. In: Winfield, IJ & Nelson, JS (Eds), Cyprinid Fishes Systematics, biology and exploitation. Chapman and Hall, Bury St. Edmunds, pp 377-412.

Statzner B, Arens BF, Champagne J-Y, Morel R. Herouin E. 1999. Silk producing stream insects and gravel erosion: significant biological effects on critical shear stress. *Water Resources Research* **35:** 3495-3506. https://doi.org/10.1029/1999WR900196

Statzner B, Fièvet E, Champagne J-Y, Morel R, Herouin, E. 2000. Crayfish as geomorphic agents and ecosystem engineers: biological behavior affects sand and gravel erosion in experimental streams. *Limnology and Oceanography* **45**: 1030–1040.

Statzner B, Sagnes P, Champagne J-Y, Viboud S. 2003. Contribution of benthic fish on the patch dynamics of gravel and sand transport in streams. *Water Resources Research* **39**: 1-17.

Statzner B. 2012. Geomorphological implications of engineering bed sediments by lotic animals. *Geomorphology* **157**: 49-65. https://doi.org/10.1016/j.geomorph.2011.03.022

Statzner B, Sagnes P. 2008. Crayfish and fish as bioturbators of streambed sediments: assessing joint effects of species with different mechanistic abilities. *Geomorphology* **3**: 267-287. https://doi.org/10.1016/j.geomorph.2007.02.019

Steiger J. Corenblit D. 2012. The emergence of an ‘evolutionary geomorphology’? *Central European Journal of Geoscience* **4**: 376-382. https://doi.org/10.2478/s13533-011-0075-6

Stoner, A.W., 2004. Effects of environmental variables of fish feeding ecology: implications for the performance of baited fishing gear and stock assessment. J. Fish Biol. 65, 1445–1471. https://doi.org/10.1111/j.0022-1112.2004.00593.x

Thorpe JH. 1988. Patches and the responses of lake benthos to sunfish nest-building. Oecologia **76**:168-174. https://doi.org/10.1007/BF00379949

Viles HA. 1988. Introduction. In Viles, HA (ed.) *Biogeomorphology*. Blackwell, New York.

Wheaton JM, Gibbins C, Wainright J, Larsen L, McElroy B. 2011. Preface: Multiscale Feedbacks in Ecogeomorphology. *Geomorphology* **126**: 265-268. https://doi.org/10.1016/j.geomorph.2011.01.002

Wiberg PL, Smith JD.1987. Calculations of the critical shear stress for motion of uniform and heterogeneous sediments. Water Resources Research **23:** 1471-1480. https://doi.org/10.1029/WR023i008p01471

Winemiller KO, Taylor DH. 1982. Smallmouth bass nesting behaviour and nest site selection in a small Ohio stream. Ohio Journal of Science **82**: 266-273.

Wright JP, Jones CG. 2006. The concept of organisms as ecosystem engineers ten years on: progress, limitations, and challenges. *Bioscience* **56:** 203 – 209. https://doi.org/10.1641/0006-3568(2006)056[0203:TCOOAE]2.0.CO;2

Table 1. Fish species recorded in the River Trent catchment and their respective behaviour, weight and benthic impact scores. See methods for details of how the scores were assigned. Feeding Behaviour score (FBS): piscivorous and parasitic = 0; opportunistic = 1; obligate benthic = 2. Mass score, MS: 0 – 15 g = 0; 16 – 99 g = 1; 100 – 499 g = 2; 500 – 1499 g = 3 and; 1500 – 4000 g = 4.

Latin name	**Common name**	**Feeding Behaviour score (FBS)**	**Mass score (MS)**	**FBS*MS**
Salmo salar	Atlantic salmon	0	4	0
Lampetra planeri	Brook lamprey	1	0	0
Phoxinus phoxinus	Minnow	1	0	0
Pungitius pungitius	Nine-spined stickleback	1	0	0
Perca fluviatilis	Perch	0	2	0
Esox lucius	Pike	0	4	0
Lampetra fluviatilis	River lamprey	0	1	0
Petromyzon marinus	Sea lamprey	0	2	0
Cobitis taenia	Spined loach	2	0	0
Barbatula barbatula	Stone loach	2	0	0
Gasterosteus aculeatus	Three-spined stickleback	1	0	0
Alburnus alburnus	Bleak	1	1	1
Salmo trutta	Brown / Sea trout	1	2	2
Cottus gobio	Bullhead	2	1	2
Leuciscus leuciscus	Dace	1	2	2
Carassius auratus	Goldfish	1	2	2
Thymallus thymallus	Grayling	1	2	2
Gobio gobio	Gudgeon	2	1	2
Oncorhynchus mykiss	Rainbow trout	1	2	2
Rutilus rutilus	Roach	1	2	2
Scardinius erythrophthalmus	Rudd	1	2	2
Gymnocephalus cernuus	Ruffe	2	1	2
Leuciscus cephalus	Chub	1	3	3
Anguilla anguilla	European eel	1	3	3
Platichthys flesus	European flounder	2	2	4
Blicca bjoerkna	Silver bream	2	2	4
Tinca tinca	Tench	2	2	4
Barbus barbus	Barbel	2	3	6
Abramis brama	Common bream	2	3	6
Cyprinus carpio	Common carp	2	4	8

Table 2. Abundance and extent of 19 fish species scoring FBS x MS > 0. Fish were sampled at 176 sites.

	FBS*MS	**Abundance**	**Percent of scoring fish**	**Number of sites**	**Percent of sites**
Bleak	1	26	0.085	2	1.1
Goldfish	2	1	0.003	1	0.6
Rudd	2	5	0.016	3	1.7
Ruffe	2	9	0.029	3	1.7
Rainbow Trout	2	123	0.402	6	3.4
Grayling	2	159	0.520	23	13.1
Dace	2	807	2.637	52	29.5
Gudgeon	2	1181	3.860	62	35.2
Roach	2	1976	6.458	64	36.4
Brown/Sea Trout	2	3059	9.997	91	51.7
Bullhead	2	21800	71.244	147	83.5
Eel	3	335	1.095	26	14.8
Chub	3	985	3.219	66	37.5
Flounder	4	3	0.010	3	1.7
Silver Bream	4	11	0.036	2	1.1
Tench	4	14	0.046	8	4.5
Barbel	6	23	0.075	7	4.0
Common Bream	6	80	0.261	8	4.5
Carp	8	2	0.007	1	0.6
Sum		*30599*			

List of Figures

Figure 1. Common cyprinid feeding behaviours and their impacts on riverbed sediment condition. Grey and black arrows indicate typical magnitudes and directions of fish movements and grain displacements, respectively. Flow direction from right to left. (Credit: Matt Johnson).

Figure 2. The prevalence of different foraging behaviours for a) juvenile Barbel during an ex-situ experiment (n = 5) (adapted from Pledger *et al.* (2014)). and b) juvenile Chub during an in-situ experiment in the River Idle (n = 4). Values represent means ± SE.

Figure 3. Examples of linear foraging scars (black dashed line) in the River Idle, Nottinghamshire, UK.

Figure 4. Factors that may affect foraging impacts on coarse bed material sediments and bed material transport. Note the potential feedbacks from bed material transport to local environmental, predator and prey factors that affect foraging (dashed line).

Figure 5 (a) Map of Trent catchment showing principal tributaries and (b) Sampling sites in the entire data set and those retained for analysis based on quality criteria.

Figure 6. Proportion of fish at each sampling location categorised as specialist benthic feeders, opportunistic benthic feeders or piscivorous. Circle size is proportional to log abundance.

Figure 7. Abundance across 176 sites within the Trent catchment and number of sites occupied by 19 fish species that have FBS x MS > 0. Circle diameter is proportional to FBS x MS such that larger circles indicate a greater likelihood that foraging by an individual will have a geomorphological impact.

Figure 8. Distribution and abundance of bullhead, barbel and bream, some key benthivorous fish, based on sampling at 176 sites across the Trent catchment. Circle size reflects three abundance categories based on natural breaks in the distribution of values.

Figure 9. Benthic Impact Scores for each site across the Trent catchment (ΣBIS_{site}).

Figure 10. Cumulative benthic impact score ($\Sigma BIS_{species}$) for all sites across the Trent catchment. Circle diameter is proportional to $\Sigma BIS_{species}$ and indicates the possible cumulative geomorphic impact of foraging by that species, taking into account site-by-site density (m^{-2}), feeding behaviour and average adult mass. Numbers beside the species labels are the percentage of the sum score for all species.

Figure 1

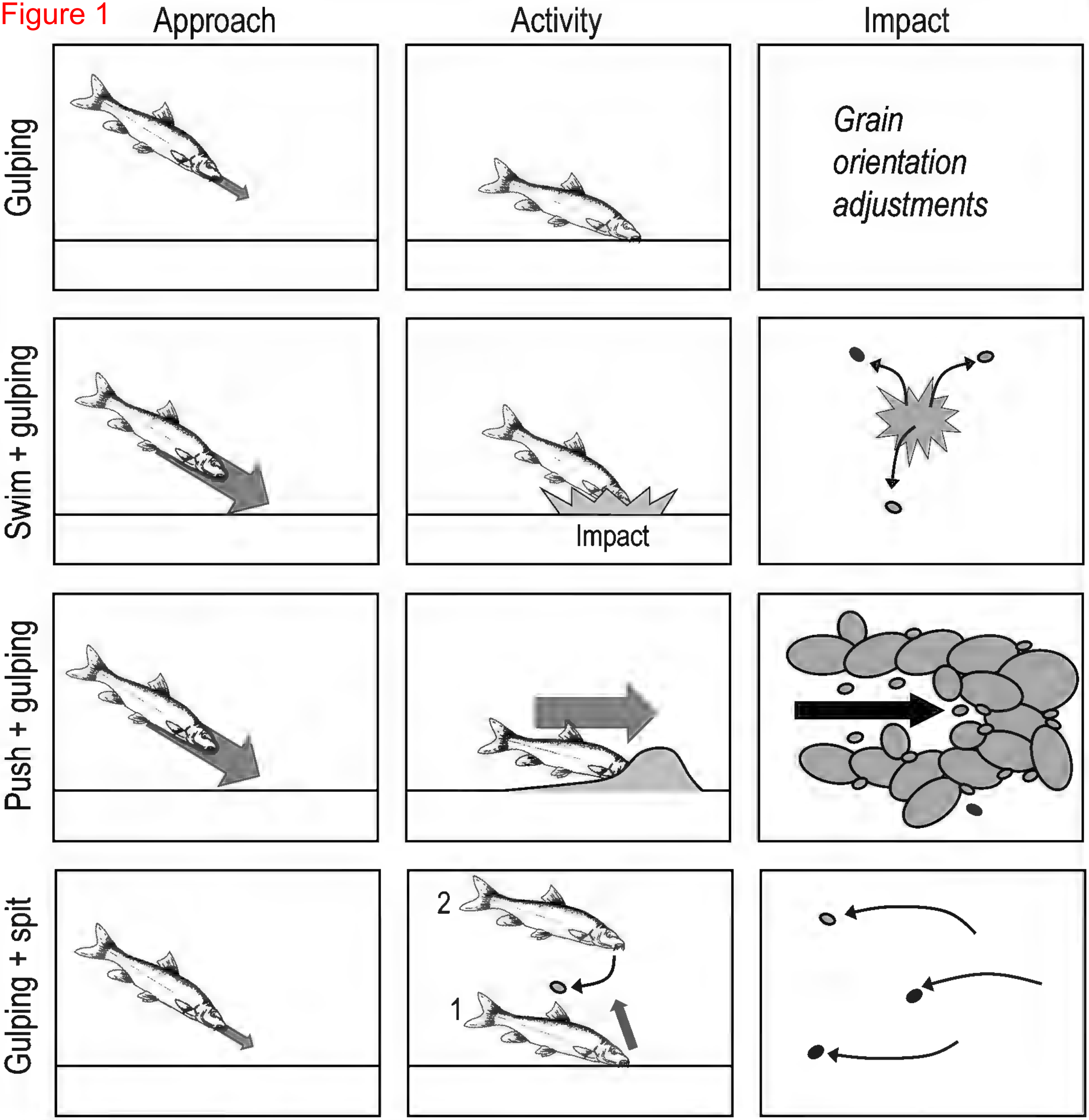

Approach
Activity
Impact
Gulping
Grain orientation adjustments
Swim + gulping
Impact
Push + gulping
Gulping + spit
2
1

Figure 2

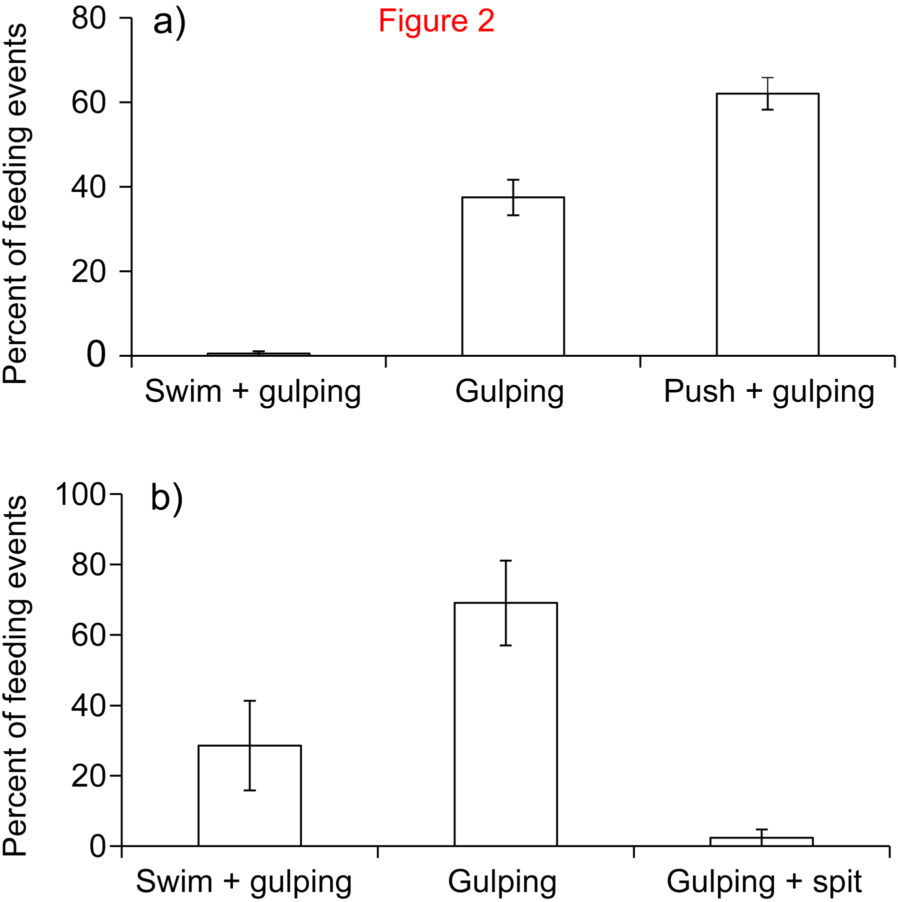

a)
Percent of feeding events
0
20
40
60
80
Swim + gulping
Gulping
Push + gulping
b)
Percent of feeding events
0
20
40
60
80
100
Swim + gulping
Gulping
Gulping + spit

Figure 3

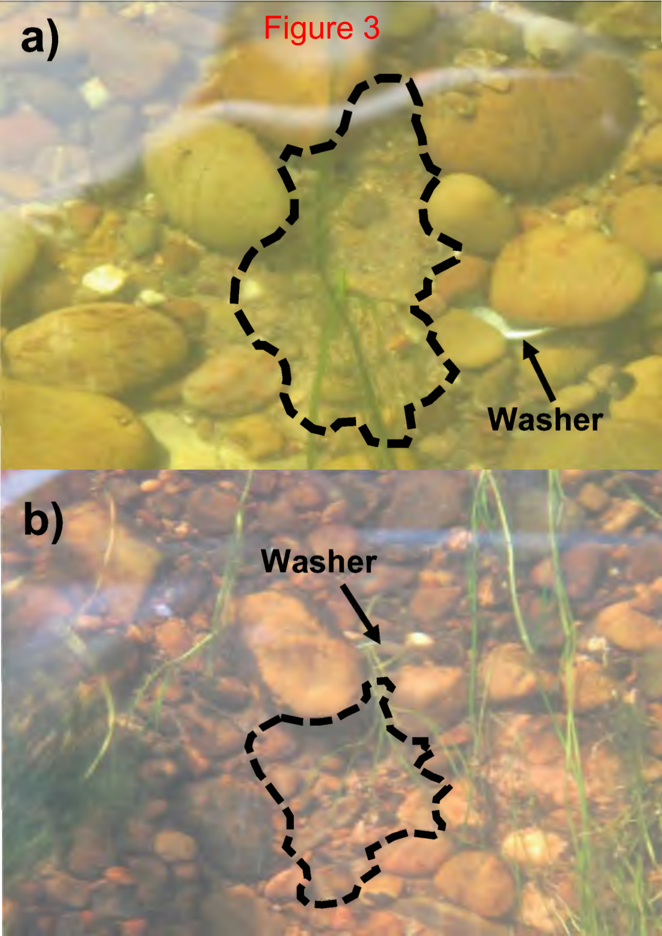


Figure 4

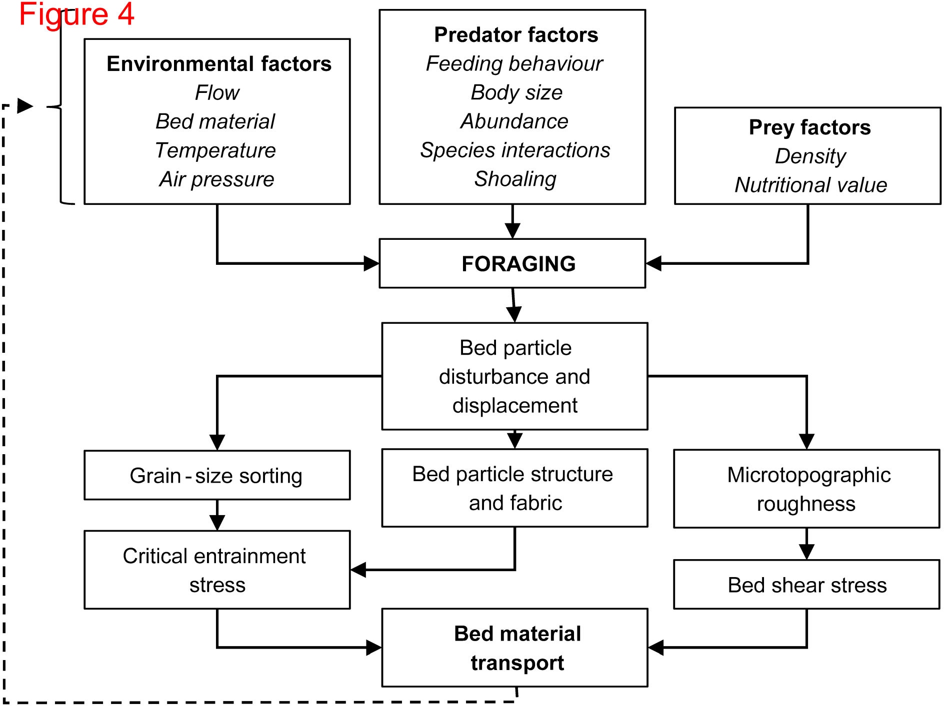
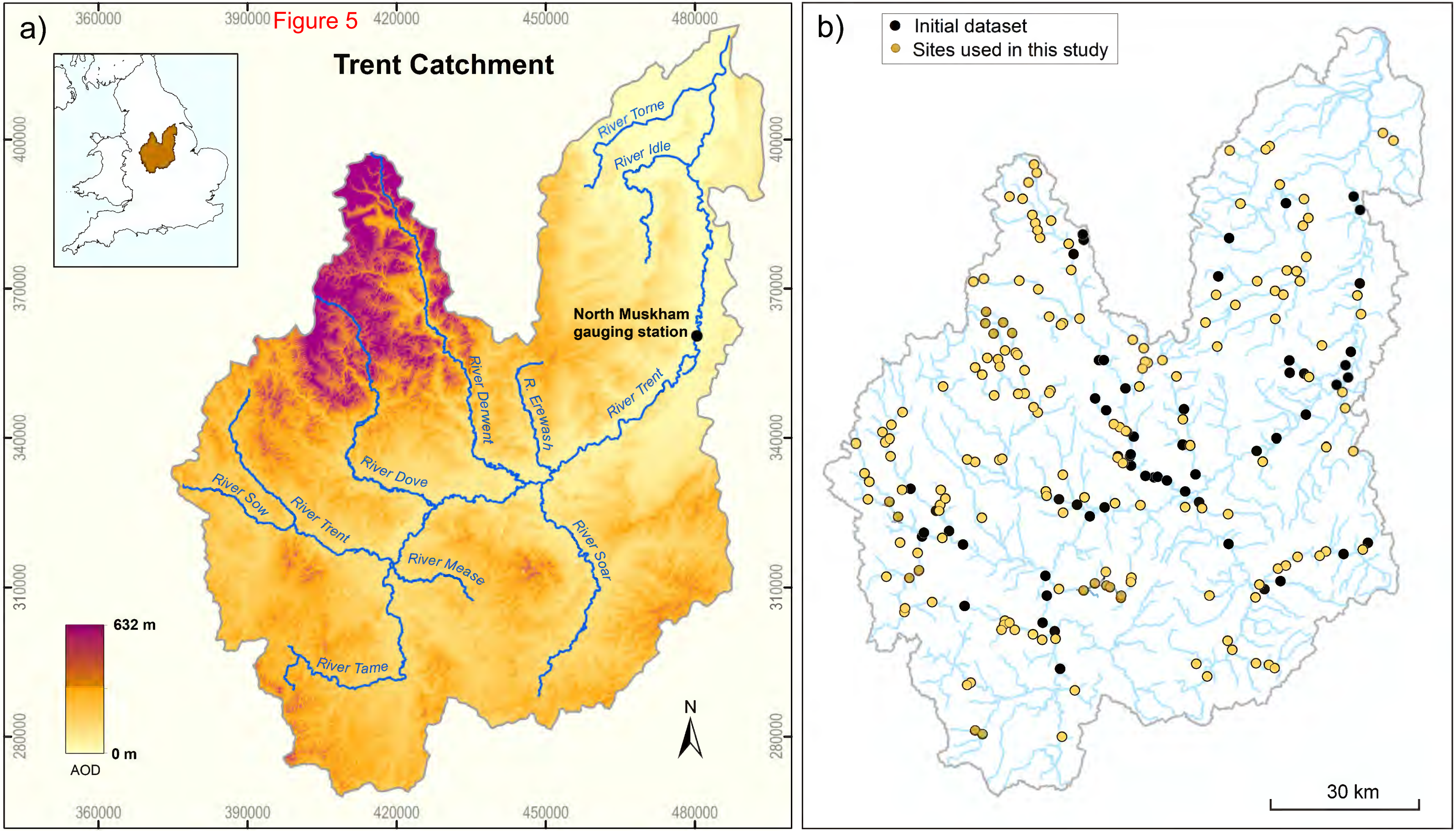

Environmental factors
Flow
Bed material
Temperature
Air pressure
Predator factors
Feeding behaviour
Body size
Abundance
Species interactions
Shoaling
Prey factors
Density
Nutritional value
FORAGING
Bed particle disturbance and displacement
Grain - size sorting
Bed particle structure and fabric
Microtopographic roughness
Critical entrainment stress
Bed shear stress
Bed material transport

Figure 5



Created using ESRI ArcMap 10.5 and OS Terrain 50, OS Open Rivers products © Crown copyright and database rights 2018. Ordnance Survey (Digimap Licence). British National Grid.

Figure 6

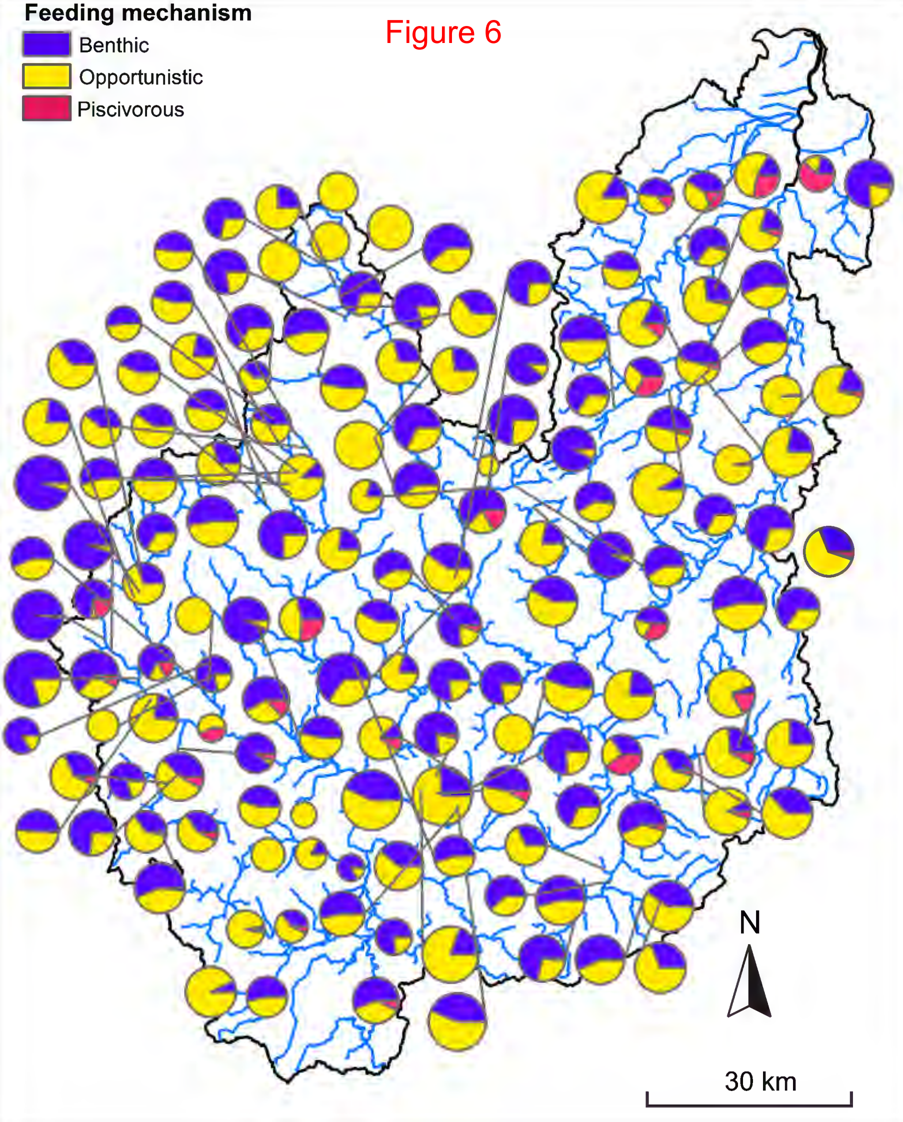

Feeding mechanism
🟦 Benthic
🟨 Opportunistic
🟥 Piscivorous
N
30 km

Figure 7

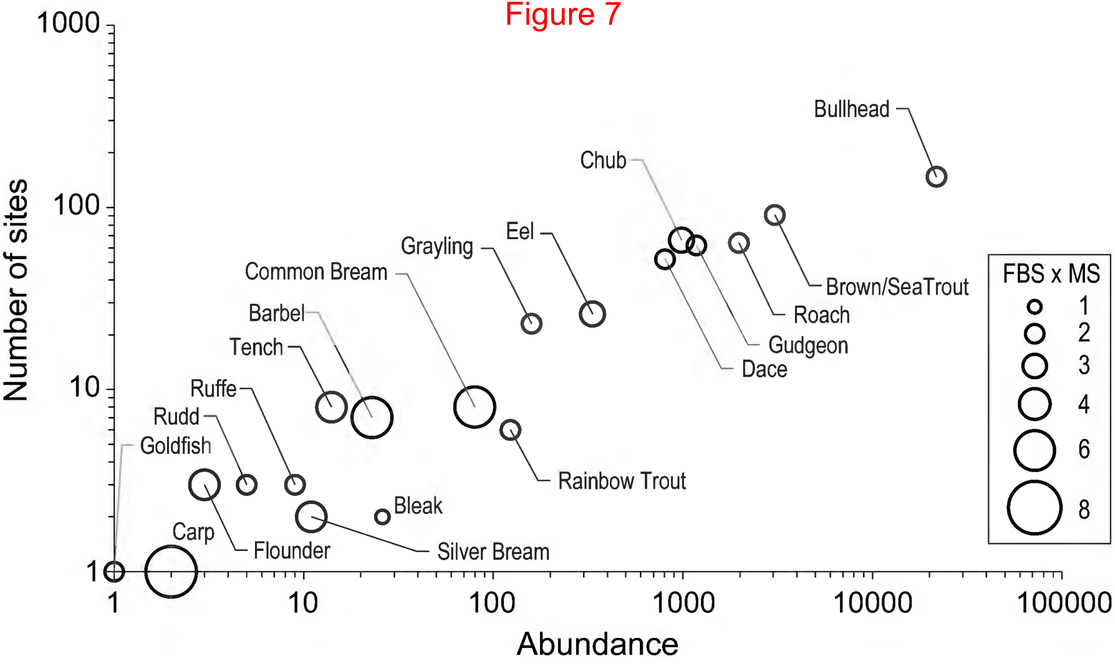
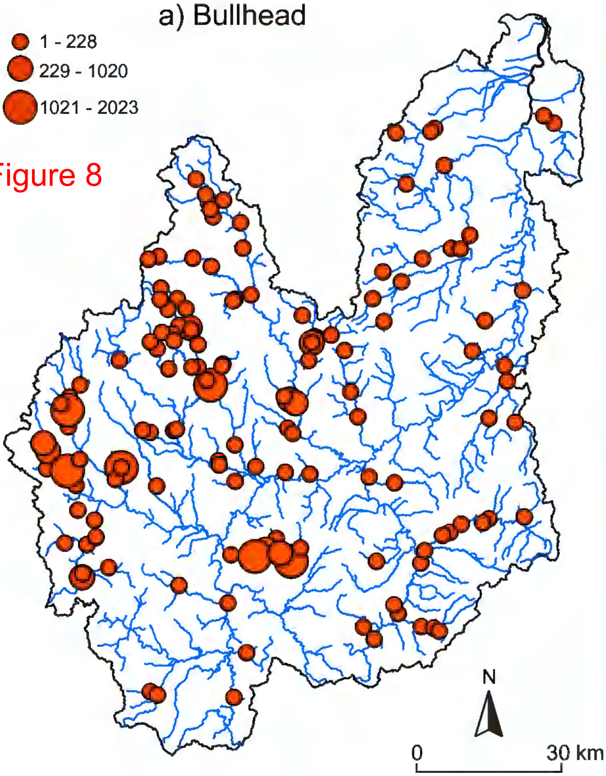
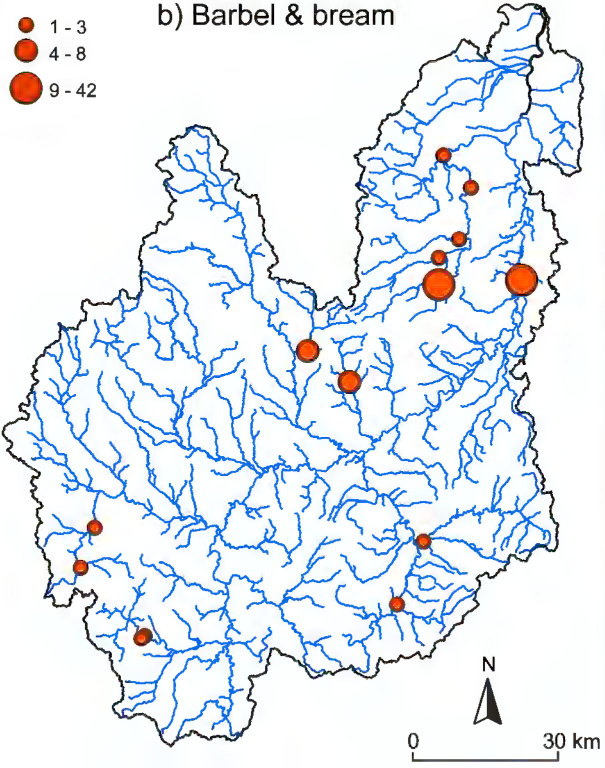

1000
100
10
1
Number of sites
1
10
100
1000
10000
100000
Abundance
Bullhead
Chub
Eel
Grayling
Common Bream
Barbel
Tench
Ruffe
Rudd
Goldfish
Carp
Flounder
Bleak
Silver Bream
Rainbow Trout
Brown/SeaTrout
Roach
Gudgeon
Dace
FBS x MS
1
2
3
4
6
8

Figure 8



a) Bullhead



b) Barbel & bream

Figure 9

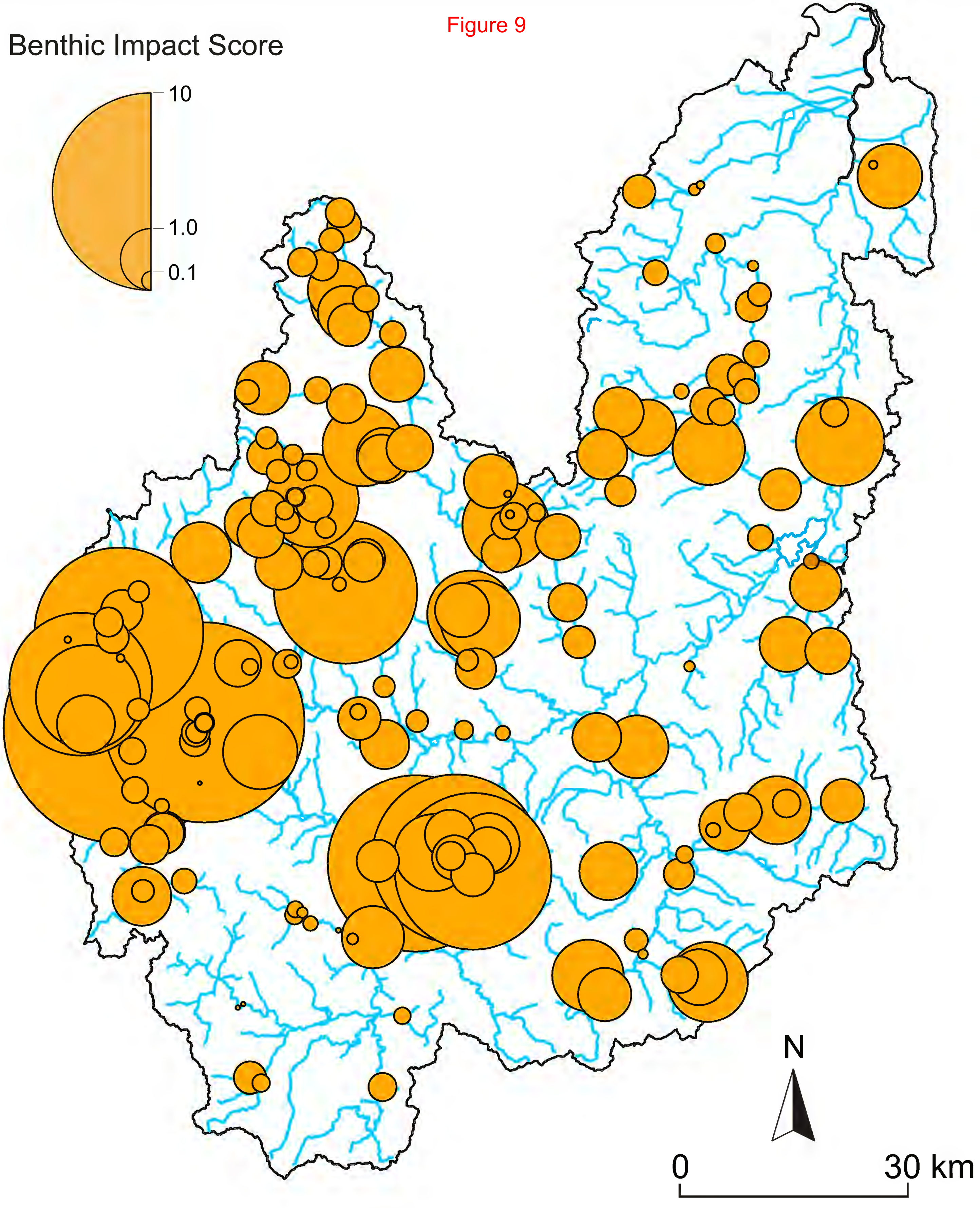
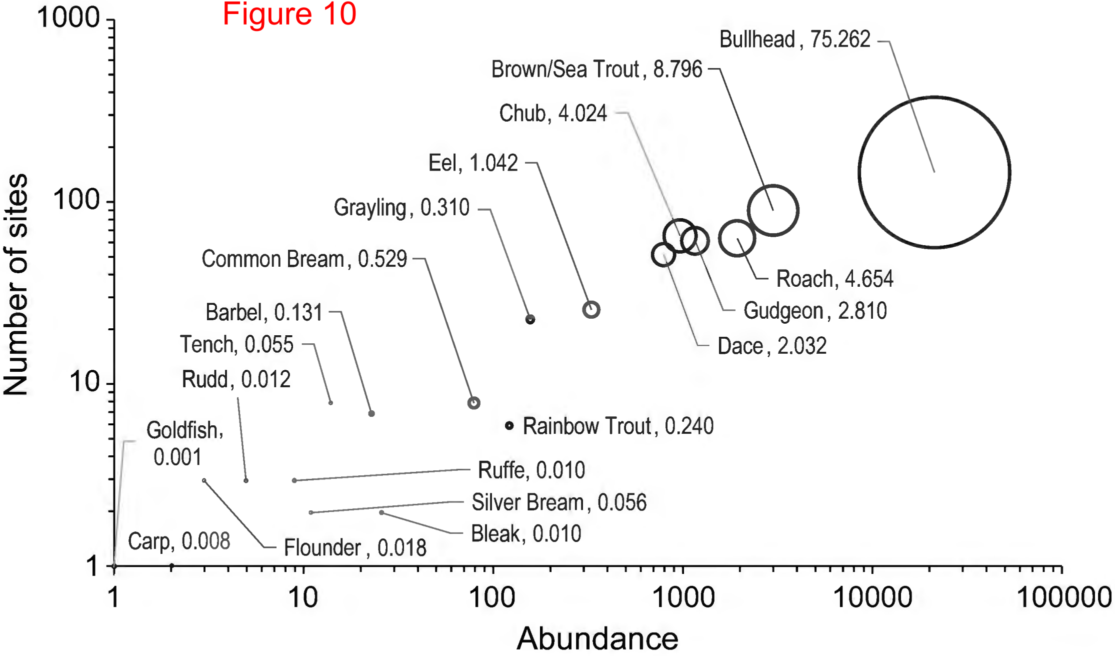


Figure 10


1000
100
10
1
Number of sites
1
10
100
1000
10000
100000
Abundance
Bullhead , 75.262
Brown/Sea Trout , 8.796
Chub, 4.024
Eel, 1.042
Grayling , 0.310
Common Bream , 0.529
Barbel, 0.131
Tench, 0.055
Rudd, 0.012
Goldfish,
0.001
Carp, 0.008
Flounder , 0.018
Roach, 4.654
Gudgeon , 2.810
Dace , 2.032
Rainbow Trout , 0.240
Ruffe, 0.010
Silver Bream , 0.056
Bleak, 0.010