esa ECOSPHERE

Predator, prey, and substrate interactions: the role of faunal activity and substrate characteristics

K. L. Mathers,[1],† S. P. Rice,[2] and P. J. Wood[2]

[1]*Eawag, Swiss Federal Institute of Aquatic Science and Technology, Department of Surface Waters Research and Management, 6047 Kastanienbaum, Switzerland*
[2]*Geography and Environment, Centre for Hydrological and Ecosystem Science, Loughborough University, Loughborough, Leicestershire LE11 3TU UK*

Citation: Mathers, K. L., S. P. Rice, and P. J. Wood. 2019. Predator, prey, and substrate interactions: the role of faunal activity and substrate characteristics. Ecosphere 10(1):e02545. 10.1002/ecs2.2545

Abstract. Many taxa possess a range of strategies to reduce the risk of predation, including actively seeking suitable refuge habitats; however, the global spread of invasive species may disrupt these behavioral responses. In lotic ecosystems, interstitial spaces in the substrate are important refugia for small organisms. Some predators are ecosystem engineers that exhibit zoogeomorphic agency—the ability to modify the geomorphology of their environment. It is therefore possible that direct ecological effects of predators on prey may be realized through modifications to the prey's habitat, including the availability of refugia, by predators that are zoogeomorphic agents or via external stressors such as fine sediment loading. This study examined three research questions in a mesocosm study across a gradient of sediment-stress treatments: (1) What affects do predators (*Pacifastacus leniusculus*, invasive crayfish) and prey (*Gammarus pulex*, amphipods) have on the ingress of fine sediment into gravel substrates and therefore on available interstitial refugia? (2) Do prey taxa seek refuge from (invasive) predators in the form of vertical movement into subsurface sediments? and (3) How does fine sediment ingress influence predator–prey interactions and prey survival through predator avoidance behavior. Here, we provide direct evidence demonstrating that fine sediment ingress into gravel river beds can be facilitated by zoogeomorphic activity with *P. leniusculus* increasing the infiltration of fine sand particles (but not coarse sand) during foraging activities. Predator–prey interactions were found to be a primary factor mediating zoogeomorphic activity, with the isolation of crayfish from prey (*G. pulex*) leading to increased fine sand ingress. When present with signal crayfish, *G. pulex* displayed vertical avoidance behavior, entering subsurface substrates to evade predation by *P. leniusculus*. Coarse sand treatments resulted in higher predation rates of *G. pulex*, most likely due to clogging of interstitial pore spaces between gravels limiting the effectiveness of the prey's vertical avoidance behavior strategy. A new conceptual model that captures the interactions between predator, prey, zoogeomorphic processes and habitat availability is presented. This model highlights how predator–prey interactions can be strongly mediated by dynamic bi-directional interactions between organisms and the physical environment they inhabit as ecological and geomorphological processes are intrinsically linked.

Key words: amphipods; crayfish; ecosystem engineering; fine sediment; hyporheic zone; ingress; invasive species; lotic invertebrates; predator avoidance behavior; refuge; sediment transport; zoogeomorphology.

Received 2 November 2018; accepted 12 November 2018. Corresponding Editor: Debra P. C. Peters.

† **E-mail:** kate.mathers@eawag.ch

INTRODUCTION

Predation and the associated behavior of both predator and prey are important drivers of evolutionary change (Vermeij 1982), with predator–prey interactions receiving considerable research attention (e.g., Heck and Crowder 1991, Chivers and Smith 1998, Schmitz et al.

2017). Many species display a repertoire of strategies and defense mechanisms to reduce the risks associated with predation that reflect adaptations developed over millennia (Strauss et al. 2006, Belgrad and Griffen 2016, Alberti et al. 2017). For instance, prey may respond to the presence of a predator by reducing activity levels and by increasing or timing their use of safe microhabitats to reduce the risk of predation (Lima and Dill 1990, Sih and McCarthy 2002). However, the rapid spread of non-native species across the globe (Early et al. 2016) may disrupt the behavioral response of indigenous native taxa. The overall effect of non-native predators may therefore be enhanced if they possess predation strategies that prey do not recognize or are ill-equipped to counter (Sol and Maspons 2016, Segev et al. 2017). Understanding the behavioral adaptions that taxa employ to successfully evade and survive predation pressures by native and non-native taxa is therefore important in the context of managing contemporary ecosystems.

Crayfish (order Decapoda) are one of the most widely translocated groups of aquatic organisms (Kouba et al. 2014). Where crayfish invade they typically reduce biodiversity and biomass of the wider faunal community (Twardochleb et al. 2013, Mathers et al. 2016). The most widely recorded taxa affected by invasive crayfish colonization are Mollusca, with reductions in species richness, abundances, and biomass (e.g., Dorn 2013, Ruokonen et al. 2014). Despite a large number of studies centered on crayfish–prey interactions (Crowl and Covich 1990, Alexander and Covich 1991), studies examining the behavioral response of ubiquitous prey taxa within crayfish invaded ecosystems are limited (but see Haddaway et al. 2014). In response to predation by non-native crayfish, several natural avoidance strategies have been observed in macroinvertebrate species, including rapid locomotion, increased voluntary drift, and vertical migration into the subsurface sediments (Alexander and Covich 1991, Nyström 1999, Haddaway et al. 2014). However, utilization of subsurface sediments as a refuge is dependent on the availability of open, interstitial pore spaces.

River bed gravels typically form a structural framework within which finer sand (<2.0 mm) and silt (<0.063 mm) particles are stored (Church et al. 1987). The amount of available pore space depends on (1) the grain size distribution of the framework gravels and their packing density (Frostick et al. 1984, Cui and Parker 1998), and (2) the amount and size of fine sediment delivered to and stored within the framework. The relative size of the framework and fine sediment is a key control on bed porosity because it directly affects the propensity of fine sediment to infiltrate into or block (clog) gravel interstices (Frings et al. 2008, Wooster et al. 2008). If interstitial space is sufficient, particles infiltrate and infill from the base of the substrate in a process called unimpeded static percolation (Lunt and Bridge 2007). In contrast, where interstitial spaces are small, large sand grains may block pore throats, impeding the infiltration of fine sediments in a process known as bridging (Gibson et al. 2009*a*). The availability of interstitial refugia for prey species (e.g., freshwater amphipods) in riverine systems is therefore linked to the bed sedimentology and the fine sediment regime (Gayraud and Philippe 2003, Jones et al. 2012).

Anthropogenic modifications have altered the quantity and composition of fine sediment delivered to rivers globally (Walling and Collins 2016), with sediment yields of many rivers currently exceeding background levels (Owens et al. 2005, Collins and Zhang 2016). Consequent filling (or colmation) of interstitial spaces within the river bed can lead to the disconnection of river bed (benthic) and subsurface (hyporheic) habitats (Descloux et al. 2013, Mathers et al. 2014). Where this occurs, taxa that possess predator avoidance adaptations that rely on vertical movement into the river bed may be subject to reduced refuge availability and therefore enhanced predation pressure.

However, the classic view of fine sediment dynamics at the water–substrate interface has been conceived entirely around geophysical principles in which bed shear and fluid turbulence drive entrainment, transport, and deposition of fine sediment (Beschta and Jackson 1979, Diplas and Parker 1992, Kuhnle et al. 2016). There is a growing body of literature demonstrating that animals including fish and macroinvertebrates can also alter the accumulation and distribution of fine sediment (Statzner et al. 1996, Zanetell and Peckarsky 1996, Nogaro et al. 2006, Pledger et al. 2017) via the expenditure of biotic energy

(Rice et al. 2016). For example, macroinvertebrate prey may winnow fine sediment from interstitial spaces and thereby maintain and/or re-establish vertical connectivity and migration pathways within the river bed (Visoni and Moulton 2003, Mermillod-Blondin et al. 2004, Mermillod-Blondin and Rosenberg 2006, Nogaro et al. 2006, Stumpp and Hose 2017). This is an example of fluvial zoogeomorphology (Butler 1995) the process through which animals alter the geomorphology and sedimentology of their environment (Rice et al. 2012, Statzner 2012, Albertson and Allen 2015, Vu and Pennings 2017). Crayfish are widely recognized zoogeomorphic agents that manipulate coarse sediments and bedload flux (Johnson et al. 2011), recruit fine sediment to rivers via their burrowing activities (Faller et al. 2016, Rice et al. 2016), entrain detritus into the flow when foraging and fighting (Usio and Townsend 2004, Harvey et al. 2011), and increase the suspended sediment load in rivers (Rice et al. 2014, 2016). It is therefore likely that crayfish may also have a direct influence on the infiltration of sediment into subsurface habitats, a process which has yet to be tested for any biota.

This research therefore sought to examine the engineering of a shared physical environment by a predator and its prey, and the effect of their geomorphological work on predator–prey interactions. These interactions are situated within a broader framework in which ecosystems are subject to multiple external stressors (Sih et al. 2004, Strayer 2010, Jackson et al. 2016) that may drive and/or mediate the interactions between predator, prey, and the physical environment, in this case biological invasions and increased fine sediment loading. Predator–prey interactions are a recurrent theme in ecology, but the typical assumption (conceptualized in Fig. 1A) is that the physical environment is a fixed template in which predation occurs. The growing recognition that organisms can engineer their environments (Jones et al. 1997, Moore 2006, Wright and Jones 2006), in this case via zoogeomorphological processes (Rice et al. 2012, Statzner 2012), means that both predator and prey may modify their shared habitats (Fig. 1B).

In this study, we examine the effect that predators (invasive crayfish) and prey (freshwater amphipods) have on the ingress of contrasting surface fine sediment treatments into experimental substrates and how changes in the physical environment influence predator–prey interactions. Amphipods are diverse and keystone organisms in marine and freshwater systems with over 2000 freshwater species recorded to date (Väinölä et al. 2008). *Gammarus pulex* (L.) (Amphipoda: Crustacea) is the most widely distributed and abundant amphipod species in the UK (Gledhill et al. 1993), often dominating macroinvertebrate communities by biomass and abundance (MacNeil et al. 1997). *G. pulex* are a highly mobile taxon, capable of burrowing into fine sediment to find trophic resources and habitat (Vadher et al.

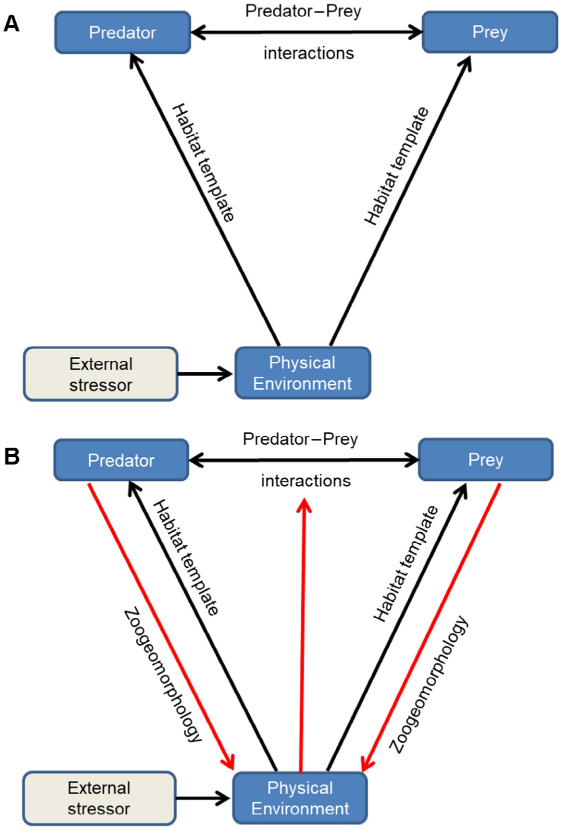

Fig. 1. Conceptual framework of the interactions between predator–prey relations, the physical environment, and the addition of an external stressor. Panel (A) represents the traditional view of predator–prey interactions; panel (B) characterizes the additional processes and interactions between biotic and abiotic factors which take place in the natural environment. Red arrows represent the additional mediating factors considered in this study for the first time.

2015) and are therefore an ideal model prey organism. The North American signal crayfish (*Pacifastacus leniusculus*; Dana) is one of the most prevalent non-native decapod species globally (Kouba et al. 2015), including in UK freshwaters (Holdich et al. 2014), and was therefore chosen as the model predator organism.

We address the following research questions: (1) Does the presence of *G. pulex* and *P. leniusculus* (alone and in combination) modify fine sediment infiltration rates? (2) Does *G. pulex* display predator avoidance behavior in the presence of *P. leniusculus* in the form of vertical movement into subsurface sediments? (3) Does elevated sediment ingress into subsurface habitats result in reduced survivorship of *G. pulex* due to predation? Each of these questions were examined across a gradient of infiltration scenarios, as defined by sediment loading and grain size, thereby providing different environmental conditions in which to examine the interaction of predator–prey relationships and zoogeomorphic activity. Fine sand treatments were used to assess the role of pore infilling and therefore reduction in refuge volume, while coarse sand allowed the assessment of surface-pore bridging and therefore a reduction in refuge access. Differentiation between these processes is ecologically important as pore space may still be available but inaccessible should coarse sand bridge pathways, prohibiting the transfer of resources and organisms below the level of clog development. In contrast, a reduction in pore volume renders the interstitial space unusable regardless of the grain size present (Mathers et al. 2019).

MATERIALS AND METHODS

Experimental setup

Experiments were undertaken in three identical sediment columns (following Mathers et al. 2014) comprising two interlocking substrate sections representing surface (benthic) and subsurface (hyporheic) substrates (Fig. 2). Each section was 32 cm in diameter and contained a 50 mm thickness of coarse fluvial sediment (gravel particles 20–64 mm in diameter). This size distribution is consistent with natural coarse river framework gravels and included particles that *Pacifastacus leniusculus* are known to displace (up to 38 mm in diameter; Johnson et al. 2010). The two sections were stacked vertically to provide a total substrate depth of 100 mm. Six mm holes (at a density of 0.06 cm^{-1}) allowed water, fine sediment and *Gammarus pulex* to move between the sections. The bottom section (50–100 mm) was perforated with smaller holes (2 mm diameter at a density of 0.09 cm^{-1}) to prevent emigration of *G. pulex* and limit fine sediment loss from the base of the column, while also permitting vertical hydrological exchange. In addition, 0.25-mm netting was secured around the base of the column and a 5-mm rubber seal created around the base of the top section. The column was covered to prevent movement of crayfish out of the column. Experiments were conducted under natural ambient light conditions as *G. pulex* are phototactic and display negative migration behavior in response to light (movement away from the light source; MacNeil et al. 1999) and *P. leniusculus* activity is strongly diurnal with most activity occurring at night (Guan and Wiles 1998, Nyström 2005).

Downwelling flow conditions were employed during all experiments. Previous experiments using the mesocosm facility have documented the affinity of *G. pulex* for surface substrates under downwelling hydrological exchange (Mathers et al. 2014). Application of downwelling flow conditions therefore provided a baseline distribution of *G. pulex* for this set of experiments and facilitated the detection of avoidance behavior as increased occupancy of subsurface substrates. The sediment columns were placed inside separate cylindrical water containers (97 × 57 cm, volume = 210 L). External pumps delivered flowing water to the columns which passed through the column under gravity. A sprinkler rosette was attached to the end of the pump outlet to disperse water (2.7–2.8 L/min). Preliminary observations indicated that this flow of water was sufficient to maintain low interstitial flow through the sediments but was not great enough to initiate sediment transport. Consequently, any vertical movement of fine sediment during the experimental period was primarily a function of gravity or the direct activity of *G. pulex* and/or *P. leniusculus*.

The experimental containers were aerated throughout the experiments using an aquarium pump and temperature was held constant (15 ± 0.4°C) via an external water cooler (Aqua Medic, Titan 150, Bissendorf, Germany). The

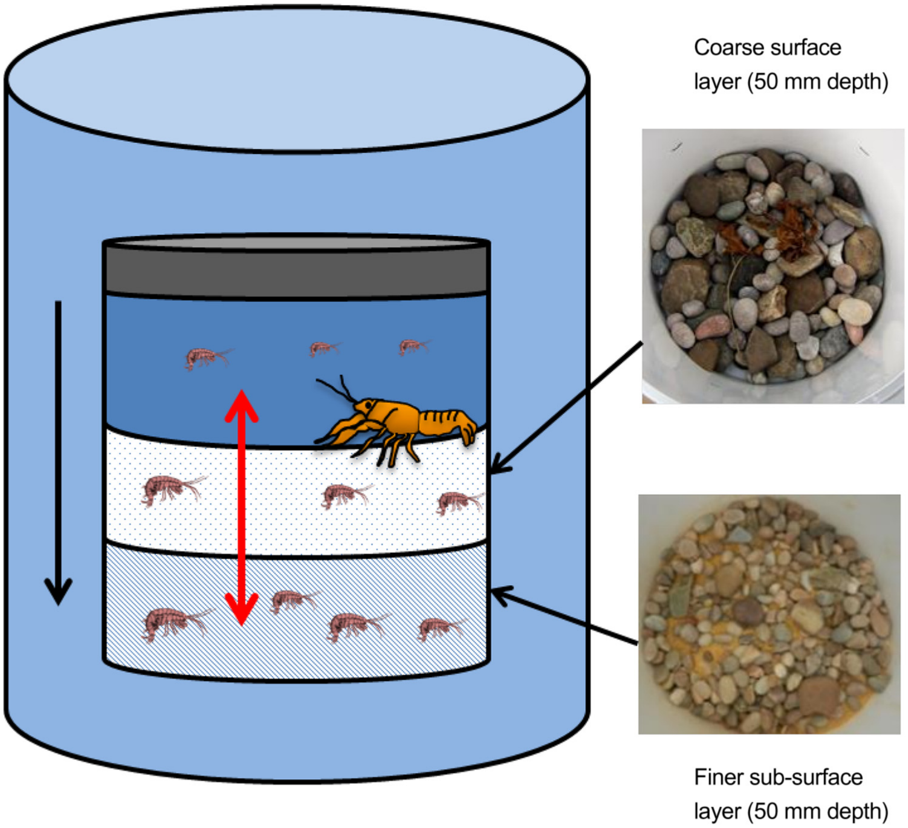

Fig. 2. Conceptual diagram of the experimental setup consisting of a coarse surface layer and finer subsurface layer. The red arrow represents the migration pathways available to *Gammarus pulex*, and the black arrow represents the flow of downwelling water and direction of sediment transport. Photographs illustrate the grain size matrix prior to sediment addition.

temperature selected for the experiments corresponds with peaks in crayfish activity under field conditions in the summer months within the UK (Bubb et al. 2004, Johnson et al. 2014) and is comparable to that employed during other laboratory studies (Basil and Sandeman 2000). Experiments were undertaken during late spring and summer (May–July) to coincide with the main period of crayfish activity in the Northern Hemisphere.

The fine sediments used in the experiment consisted of two prewashed fluvial size fractions: fine sand (0.125 µm–1 mm) and coarse sand (1–4 mm). Finer fractions (<0.125 µm) were removed by wet sieving to ensure that turbidity did not vary between experimental trials. Prior to each experimental run, fine sediment was applied evenly to the surface of wet gravel in the top section of the column using a 1 or 4 mm sieve, respectively. Preliminary tests indicated that the application of 5 kg/m^2 filled all interstices (100% of pore framework volume) under the fine sediment treatment and covered the surface of all gravel particles. In addition to this heavy sediment loading, a moderate sediment loading of 3 kg/m^2 was used. The two size fractions were chosen to include grains with a low propensity to clog interstitial spaces (0.125 µm–1 mm) and grains with a high propensity to bridge between framework clasts and thus limit further infiltration (1–4 mm). Appropriate grain sizes were determined using calculations based on studies by Gibson et al. (2009*b*) and Frings et al. (2008), who provide ratios to discriminate between pore filling loads and bed structure (framework) clasts. For each experimental trial, a mixture of both fine sand fractions (equivalent to

2 kg/m^2 of each size fraction) was mixed thoroughly with the gravel matrix and placed in the bottom section. This poorly sorted grain size mixture acted as sediment trap but did not reduce interstitial space sufficiently to preclude *G. pulex* from migrating into the subsurface layer.

Five sediment treatments were examined: (1) an open gravel framework without application of fine sediment; (2) 3 kg/m^2 fine sand sedimentation in the surface section; (3) 5 kg/m^2 fine sand sedimentation in the surface section; (4) 3 kg/m^2 coarse sand sedimentation in the surface section and; (5) 5 kg/m^2 coarse sand sedimentation in the surface section. These treatments represented a gradient of fine sediment loading (Appendix S1). Each treatment was undertaken for four different scenarios: (1) no organisms present; (2) 75 *G. pulex*; (3) one *P. leniusculus;* and (4) one *P. leniusculus* and 75 *G. pulex*. The sediment treatments (n = 5) and organism presence/absence (n = 4) were combined in a full factorial design giving 20 treatment combinations. Each combination was replicated five times to give a total of 100 experimental runs. Treatments were randomly allocated to an experimental trial.

Animals used in experiments

All crayfish were collected from a local stream (Wood Brook, Loughborough, UK; 52°75′69″ N., −1°22′74″ W.) using baited traps and immediately transported to the laboratory. To limit variability that might be associated with differing size and age, only medium-sized individuals with a carapace length of 40 ± 5 mm were selected. Selected individuals did not display any obvious injury (such as damaged carapace or loss of chelae, legs, or antennae), or regenerating chelae which might have affected their foraging behavior (Basil and Sandeman 2000, Koch et al. 2006). The sex was recorded, although males and females have been documented as exhibiting no significant differences in behavior (Guan 1994), so this influence was not considered in experiments. Only intermolt individuals were used in the experiments (Kuhlmann et al. 2008) because activity and feeding behavior is known to be modified during ecdysis (molting; Reynolds 2002).

Each crayfish was housed individually between experiments and lettuce was provided ad libitum and supplemented with crayfish pellets (Tetra: TetraCrusa Menu) every other day when not involved in experiments. Preliminary tests indicated that when *P. leniusculus* were not fed in the days prior to experiments, insufficient numbers of *G. pulex* survived the experimental trials to enable analysis. All *G. pulex* specimens were collected from a local stream (Burleigh Brook, Loughborough, UK; 52°76′09″ N., −1°24′58″ W) where they occurred at high abundances (>100 individuals per m^2) using a standard pond net (mesh size, 1 mm) prior to each experimental trial. Individuals used in the experiments consisted of mixed size classes; 1–10 mm length.

Experimental procedure

For experiments in which no organisms were present (control application experiments), sediment was applied to the surface of the top section and left for 24 h. Experiments with *P. leniusculus* present were initiated in the same manner but with the addition of one crayfish on the surface section immediately after the application of the sediment treatment. For experimental trials which included only *G. pulex*, seventy-five individuals were released onto the top section of the columns and left for 24 h to redistribute themselves. Preliminary experiments indicated that this was a sufficient number for appropriate survival rates at the termination of the experiments to enable the detection of an avoidance behavior if present. In experimental trials where *P. leniusculus* and *G. pulex* were present at the same time, all *G. pulex* individuals were placed in the experimental facility and left to acclimatize for an hour prior to the addition of crayfish. A single pre-conditioned (soaked in water) horse chestnut (*Aesculus hippocastanum*) leaf was placed in both sections of the sediment columns as a food source for the *G. pulex* to reduce intraspecific predation (Dick 1995). A slice of carrot (~10 g) and crayfish pellets were provided as alternative food sources for *P. leniusculus* (following Bubb et al. 2002, Kuhlmann et al. 2008), to avoid excessive predation due to the absence of an alternate sedentary food source (Dorn 2013, Ruokonen et al. 2014). Shelter, in the form of an open-ended cylinder (110 × 100 mm), was provided for the crayfish in order to reduce pit digging behavior triggered by the absence of refuge (Johnson et al. 2010). This allowed the direct effect that foraging activities had on the ingress of fine sediment to be identified. New *G. pulex* specimens were used for each experimental trial. One crayfish was used per experimental trial, and each individual was used once for each treatment.

At the end of each experimental run (24 h), *G. pulex* individuals were collected and counted from each of the two substrate sections by washing the contents of each section through 4-mm sieves. All fine sediment was removed from the column and subsequently oven dried at 60°C until a constant weight was recorded to determine mass per section. For the subsurface section, the mass of fine sediment initially placed in the section was subtracted from the total fine sediment mass to calculate the fraction which had infiltrated down into the subsurface. These masses were converted to infiltration rates ($\text{kg}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$) as a measure of the amount of sediment mobilized.

Statistical analysis

Differences in infiltration rates between organism combinations for each sediment treatment were examined via a linear model using the function lm in the stats package in R version 3.12 (R Development Core Team 2013). Differences between all experimental treatments were tested using a Tukey post-hoc test via the glht function in the multcomp package (Hothorn et al. 2012).

Differences in the abundance of *G. pulex* in the subsurface as a function of sediment treatment, *P. leniusculus* presence, and the interaction of the two factors were examined via a linear model and tested using a Tukey post-hoc test. To assess differences in the vertical distribution of *G. pulex* (associated with avoidance behavior) within each sediment treatment and each organism combination (*P. leniusculus* presence or absence), a linear mixed effects model was employed with treatment specified as a fixed factor and substrate section nested within the experimental replicate (column) as a random factor (reflecting the fact that sections within individual columns were not independent). Post-hoc tests were conducted using a Tukey post-hoc test to determine the effect of the different sediment loadings on *G. pulex* movement patterns with and without *P. leniusculus*. Survivorship of *G. pulex* (number of individuals retrieved at the termination of the experimental trial) in the presence and absence of *P. leniusculus* and as a function of the sediment treatment was examined within a general linear model using the glm function in the stats package. A Poisson error distribution and log link structure were fitted to account for non-normal residuals.

RESULTS

Sediment infiltration rates

3 kg/m^2 fine sand sedimentation.—Infiltration rates of fine sand into the subsurface layer were greatest in experiments with *P. leniusculus* present (mean 1.93 kg/m^2 ± SEM 0.10, 63.3% of the sediment initially applied on the surface of the upper layer). These rates were significantly greater ($P = 0.026$ Tukey) than under control conditions with no organisms present (1.61 kg/m^2 ± SEM 0.06, 53.6%; Fig. 3A).

5 kg/m^2 fine sand sedimentation.—Fine sand sedimentation experiments with *P. leniusculus* present had the greatest infiltration rates (mean 3.06 kg/m^2 ± SEM 0.37, 61% of initial sediment, Fig. 3B); however, none of the pairwise comparisons were statistically different (Table 1).

3 kg/m^2 coarse sand sedimentation.—No significant differences between infiltration rates with or without organisms were determined (Table 2). All organism treatments displayed similar low sediment infiltration rates with surface clogging being evident (range 0.095–0.111 kg/m^2, 3.1–3.7% of initial sediment application Fig. 3C).

5 kg/m^2 coarse sand sedimentation.—Infiltration of sand into the subsurface was greatest when both *P. leniusculus* and *G. pulex* were present, and the rate was statistically greater than for control conditions ($P < 0.001$ Tukey), *G. pulex* ($P < 0.001$ Tukey), and for an individual crayfish ($P = 0.009$ Tukey; Table 1). However, infiltration rates for all organism treatments were low when compared to fine sand treatments (range 0.082–0.286 kg/m^2, representing only 1.6–5.7% of the initial sediment application; Fig. 3D).

Vertical migration of G. pulex *in response to* P. leniusculus *presence and fine sediment treatment*

The distribution of *G. pulex* between layers was dependent on the presence of *P. leniusculus* ($P < 0.001$) and fine sediment treatment

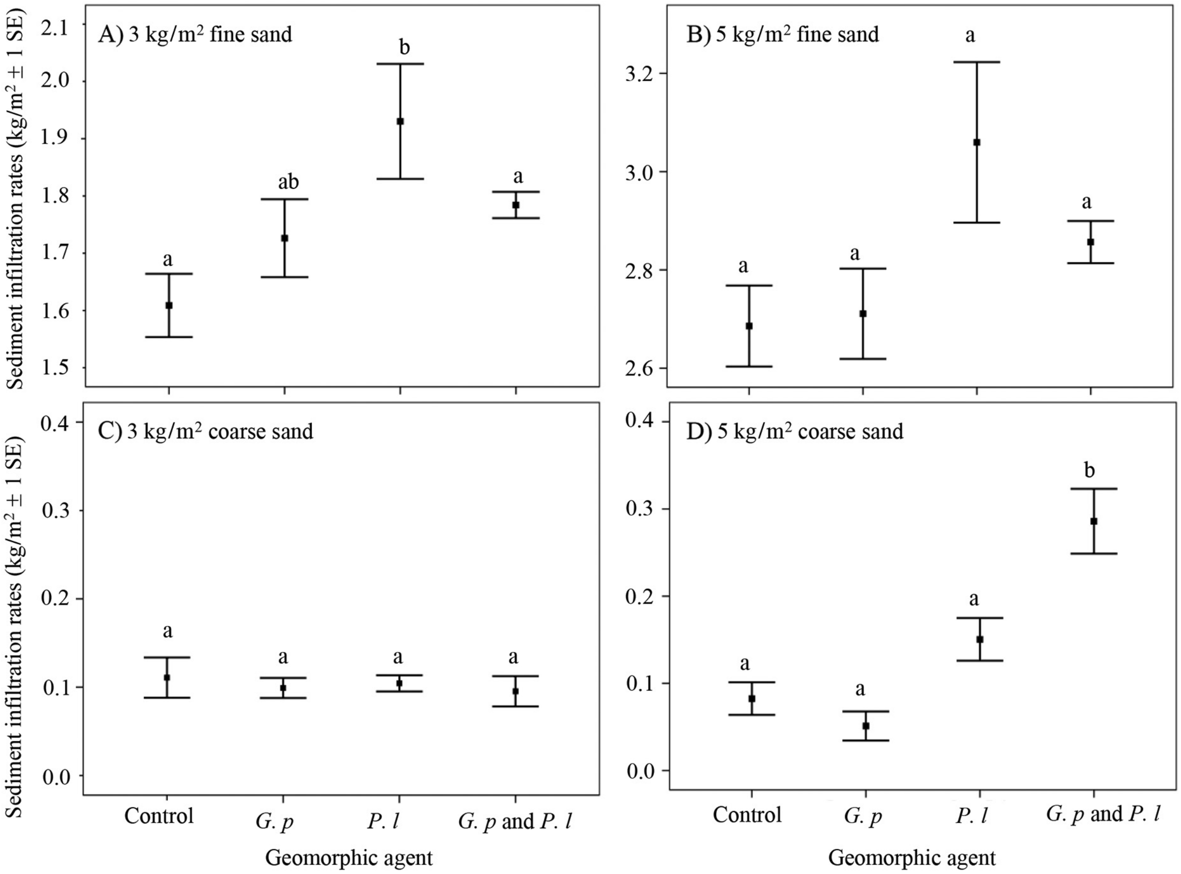

Fig. 3. Mean infiltration rates (kg·m^{-2}·day^{-1} ± 1 SE) for each biotic treatment: (A) 3 kg/m^2 fine sedimentation; (B) 5 kg/m^2 fine sedimentation; (C) 3 kg/m^2 coarse sedimentation; and (D) 5 kg/m^2 coarse sedimentation. Treatments where infiltration rates were not significantly different are denoted with the same letter (Tukey post-hoc test $P < 0.05$). Note the order of magnitude reduction in vertical (infiltration rate) scale between fine (upper row) and coarse (lower row) sediment treatments.

($P < 0.001$) but did not vary as a function of the interaction of these factors ($P = 0.247$; Table 2; LMM).

*Clean gravel.—*In the absence of *P. leniusculus*, the majority of *G. pulex* remained in the surface layer, but in the presence of *P. leniusculus, G. pulex* were more equally distributed between the surface and subsurface layers (Fig. 4). Statistical differences were apparent in the number of *G. pulex* recorded in the surface or subsurface layers for treatments when *P. leniusculus* were absent with a greater number of *G. pulex* recorded in the surface layer ($t_{1,8} = -6.770$, $P = <0.001$; Table 3). The presence of *P. leniusculus* resulted in no differences between the layers.

*3 kg/m^2 fine sand sedimentation.—*The presence of *P. leniusculus* resulted in a greater number of *G. pulex* migrating into the subsurface (Fig. 4). In the absence of *P. leniusculus*, 25% of individuals were located in the subsurface layer at the end of the experiment, but when crayfish were present, this proportion increased significantly to 50%. During experiments without *P. leniusculus*, there were significant differences in the vertical distribution of *G. pulex* ($t_{1,8} = -6.856$, $P = <0.001$), but no differences were evident when *P. leniusculus* were present ($P > 0.05$; Table 3).

*5 kg/m^2 fine sand sedimentation.—*There were no significant differences in surface and subsurface abundances of *G. pulex* when crayfish were present ($P > 0.05$), but when *P. leniusculus* were

Table 1. Tukey post-hoc comparisons of sediment infiltration rates over the 24-h experimental period for each sediment treatment.

Organism by sediment treatment	*Gammarus pulex*	*Pacifastacus leniusculus*	*G. pulex* and *P. leniusculus*
3 kg/m^2 fine sedimentation			
Control	0.609	**0.026**	0.343
G. pulex		0.172	0.926
P. leniusculus			0.497
5 kg/m^2 fine sedimentation			
Control	0.998	0.098	0.673
G. pulex		0.110	0.774
P. leniusculus			0.546
3 kg/m^2 coarse sedimentation			
Control	0.955	0.992	0.902
G. pulex		0.996	0.998
P. leniusculus			0.978
5 kg/m^2 coarse sedimentation			
Control	0.821	0.275	**<0.001**
G. pulex		0.062	**<0.001**
P. leniusculus			**0.009**

Notes: P values are presented for pairwise comparisons between organisms. Significant ($P < 0.05$) results appear in boldface.

Table 2. Univariate linear model (LM) analysis for the abundance of *Gammarus pulex* within the subsurface associated with the presence of *Pacifastacus leniusculus*, sediment treatments ($n = 5$), and the interaction between these factors.

Factor	df	F	P
P. leniusculus presence	1, 40	22.14	<0.001
Sediment treatment	4, 40	13.42	<0.001
Sediment treatment × *P. leniusculus* presence	4, 40	1.42	0.247

absent the surface layer contained a greater number of individuals ($t_{1,8} = -5.815$, $P = <0.001$; Table 3; Fig. 4).

3 kg/m² coarse sand sedimentation.—Unlike the control and fine sand treatments, when coarse sand was applied the majority of amphipods remained in the surface layer whether or not *P. leniusculus* was present (Fig. 4). The number of *G. pulex* in surface and subsurface layers was significantly different in experiments with ($t_{1,8} = -11.109$, $P = 0.010$) and without *P. leniusculus* ($t_{1,8} = 4.197$, $P = <0.001$; Table 3).

5 kg/m² coarse sand sedimentation.—The greater loading of coarse sand was associated with the highest counts of *G. pulex* in the surface layer irrespective of *P. leniusculus* presence (Fig. 4; Table 3). The surface layer contained significantly greater numbers of *G. pulex* than the subsurface layer with ($t_{1,8} = -4.587$, $P = <0.001$) and without crayfish ($t_{1,8} = -4.587$, $P = <0.001$; Table 3).

Between sediment treatment comparisons.—Overall, there were significant differences in the number of *G. pulex* in subsurface substrates when comparisons between sediment treatments, with or without *P. leniusculus* (Table 4), were considered. In the absence of *P. leniusculus*, only the addition of the greatest loading of coarse sand (5 kg/m^2) resulted in significant differences in the distribution of *G. pulex* compared to 3 kg/m^2 fine sand ($P = 0.022$) and 5 kg/m^2 fine sand ($P = 0.005$; Table 4). In contrast, in the presence of *P. leniusculus*, the addition of 3 and 5 kg/m^2 coarse sand treatments resulted in reduced numbers of *G. pulex* in the subsurface layer compared to clean gravel ($P = 0.030$ and $P < 0.001$, respectively), 3 kg/m^2 fine sand ($P = 0.006$ and $P < 0.001$, respectively), and 5 kg/m^2 fine sand (both instances $P = <0.001$; Table 4).

Survivorship to crayfish presence as a function of sediment load

Survivorship rates of *G. pulex* averaged 80% for all experiments but were highly variable as a function of crayfish presence/absence (Fig. 5). Experiments conducted in the absence of *P. leniusculus* had a mean survivorship of

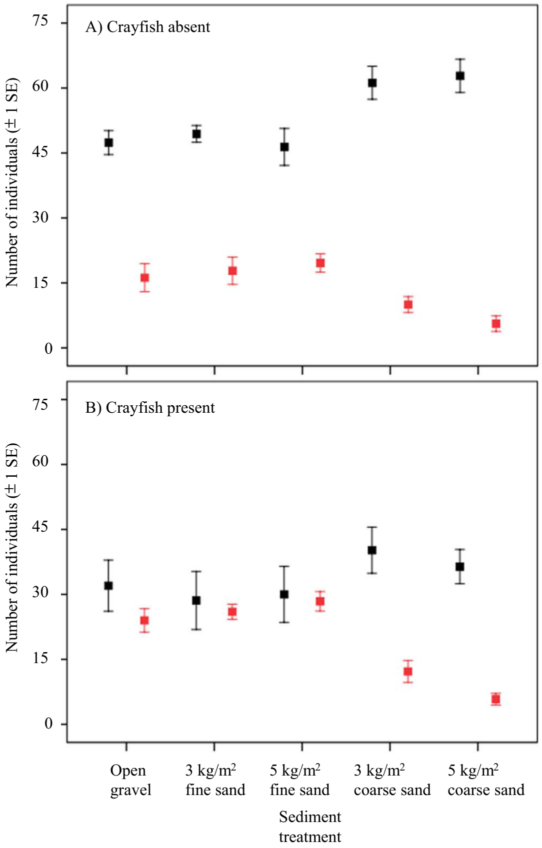

Fig. 4. Mean number of *Gammarus pulex* (± 1 SE) recorded at the end of the 24-h experiment within surface (black) and subsurface (red) substrates for each sediment treatment in: (A) the absence and (B) presence of *Pacifastacus leniusculus*. For post-hoc tests see Tables 3 and 4.

89% ± SEM 1.59 (range = 80–100%) compared to 70% ± SEM 3.52 when crayfish were present (range = 45–100%). The survivorship of *G. pulex* was dependent on the sediment treatment ($P < 0.001$) and the interaction of sediment treatment and *P. leniusculus* presence ($P = 0.003$; Table 5; LMM). Pairwise comparisons across all treatment combinations indicated that the addition of 5 kg/m^2 of coarse sediment in the presence of crayfish resulted in significantly lower survivorship (mean 56.27% ± SEM 5.04) of individuals compared to all substrate conditions when *P. leniusculus* were absent (all $P \leq 0.001$; Table 6; Fig. 5). The addition of 3 kg/m^2 of coarse sand and 3 kg/m^2 fine sand in the presence of *P. leniusculus* resulted in significantly lower survivorship than both coarse sand treatments in the absence of crayfish (all $P < 0.05$; Table 6, Fig. 5).

Table 3. Tukey post-hoc comparisons for the abundance of *Gammarus pulex* between the surface and subsurface sections.

Sediment treatment	*t*	*P*
Crayfish absent		
Open framework	−6.770	**<0.001**
3 kg/m^2 fine	−6.856	**<0.001**
5 kg/m^2 fine	−5.815	**<0.001**
3 kg/m^2 coarse	−11.109	**<0.001**
5 kg/m^2 coarse	−12.411	**<0.001**
Crayfish present		
Open framework	−1.199	0.972
3 kg/m^2 fine	−0.390	1.000
5 kg/m^2 fine	−0.240	1.000
3 kg/m^2 coarse	−4.197	**<0.001**
5 kg/m^2 coarse	−4.587	**<0.001**

Notes: *P* values are presented for pairwise comparisons in the presence/absence of *Pacifastacus leniusculus* for each sediment treatment. Significant ($P < 0.05$) results appear in boldface.

Discussion

This research sought to examine the behavioral strategies prey may use to evade predation, the engineering of a shared physical environment by a predator and its prey, and the impact that modifications to the prey's habitat as a result of biotic engineering and anthropogenic sediment loading may have for predator–prey interactions. In this study, freshwater amphipods utilized vertical avoidance behavior by actively moving into subsurface substrates to evade crayfish predation. However, the deposition of coarse fine sand clogged the surface layers of the substrate and reduced the effectiveness of this behavioral strategy resulting in increased predation (Fig. 6). When considering the zoogeomorphic potential of taxa, crayfish influenced fine sand ingress but predator–prey interactions themselves were found to be a primary mediating factor, with the availability of prey resources controlling the foraging activity of crayfish and subsequently their direct effect on the sedimentology of the physical environment (Fig. 6). The extent of this effect was, however, dependent on differences in the amount and grain size of the sediment loads applied. In

Table 4. Tukey post-hoc comparisons of *Gammarus pulex* abundance in the subsurface layer. *P* values are presented for pairwise comparisons between sediment treatment.

Sediment treatment	3 kg/m^2 fine	5 kg/m^2 fine	3 kg/m^2 coarse	5 kg/m^2 coarse
Pacifastacus leniusculus absent				
Open framework	1.000	0.989	0.069	0.073
3 kg/m^2 fine		1	0.380	**0.022**
5 kg/m^2 fine			0.140	**0.005**
3 kg/m^2 coarse				0.942
P. leniusculus present				
Open framework	1.000	0.942	**0.030**	**<0.001**
3 kg/m^2 fine		1.000	**0.006**	**<0.001**
5 kg/m^2 fine			**<0.001**	**<0.001**
3 kg/m^2 coarse				0.651

Note: Significant ($P < 0.05$) results appear in boldface.

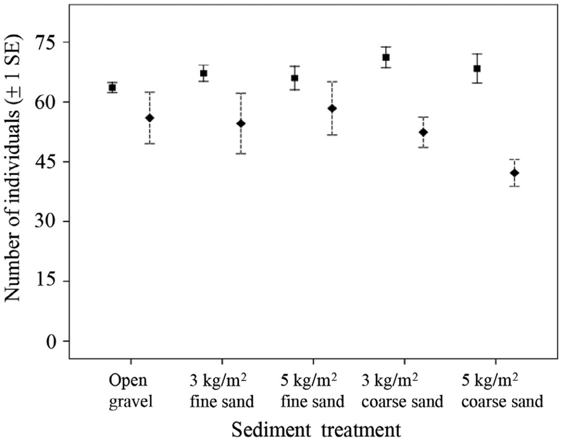

Fig. 5. Survivorship of *Gammarus pulex* ($n = 75$) at the end of the 24-h experiment in the absence (solid squares) and presence (dashed rhombus) of *Pacifastacus leniusculus*.

Table 5. Univariate linear model (general linear model) analysis for the survivorship of *Gammarus pulex* associated with the presence of *Pacifastacus leniusculus*, sediment treatments ($n = 5$), and the interaction between these factors.

Factor	df	*z*	*P*
P. leniusculus	1, 40	−0.190	0.850
Sediment treatment	4, 40	2.449	**<0.001**
Sediment treatment × *P. leniusculus*	4, 40	−2.949	**0.003**

Note: Significant ($P < 0.05$) results appear in boldface.

the current experiments, large pore spaces prevented crayfish-initiated infiltration of sand from reducing refuge habitat availability to the point that prey capture was more likely than for clean gravels. However, within a mixed, poorly sorted framework it is likely that crayfish-augmented infiltration may have the potential to reduce interstitial refuge availability and as a result prey avoidance behavior (Fig. 6). These ideas are captured in Fig. 6, which develops predator–prey–environment interactions (Fig. 1) into a more complex model in which the fuller sets of interactions are recognized (Fig. 6). This conceptual model emphasizes that predator–prey interactions should not be studied in isolation from the physical environment, and that the role of zoogeomorphic activity should be considered in the context of resource availability and other biotic drivers. The results also highlight the tantalizing prospect that predators may increase foraging success by inadvertently engineering changes in the environment (crayfish may increase fine sediment infiltration sufficiently to reduce available pore space), which requires further investigation in future studies. Each of the research questions we sought to address will be considered in the following sections where we examine the complex and three-way relationship between predator–prey and the physical environment and the critical role that external factors may play.

Impact of organisms on fine sediment infiltration rates and the role of predator–prey relationships

Many studies have examined the ingress of fine sands into gravel beds (e.g., Beschta and Jackson 1979, Frostick et al. 1984, Wooster et al. 2008, Franssen et al. 2014), but to date none have

Table 6. Tukey pairwise post-hoc comparisons of *Gammarus pulex* survivorship at the end of the 24-h experiment in the absence and presence of *Pacifastacus leniusculus*.

	P. leniusculus absent					*P. leniusculus present*			
	Fine		Coarse			Fine		Coarse	
Substrate	3 kg/m^2	5 kg/m^2	3 kg/m^2	5 kg/m^2	Control	3 kg/m^2	5 kg/m^2	3 kg/m^2	5 kg/m^2
P. leniusculus absent									
Control	1.000	1.000	0.906	0.996	0.870	0.702	0.989	0.373	**<0.001**
3 kg/m^2 fine		1.000	1.000	1.000	0.418	0.241	0.763	0.075	**<0.001**
5 kg/m^2 fine			0.993	1.000	0.582	0.376	0.883	0.140	**<0.001**
3 kg/m^2 coarse				1.000	0.080	**0.032**	0.262	**0.007**	**<0.001**
5 kg/m^2 coarse					0.277	0.144	0.610	**0.039**	**<0.001**
P. leniusculus present									
Control						1.000	1.000	0.999	0.060
3 kg/m^2 fine							1.000	1.000	0.132
5 kg/m^2 fine								0.959	**0.012**
3 kg/m^2 coarse									0.361

Note: Significant ($P < 0.05$) results appear in boldface.

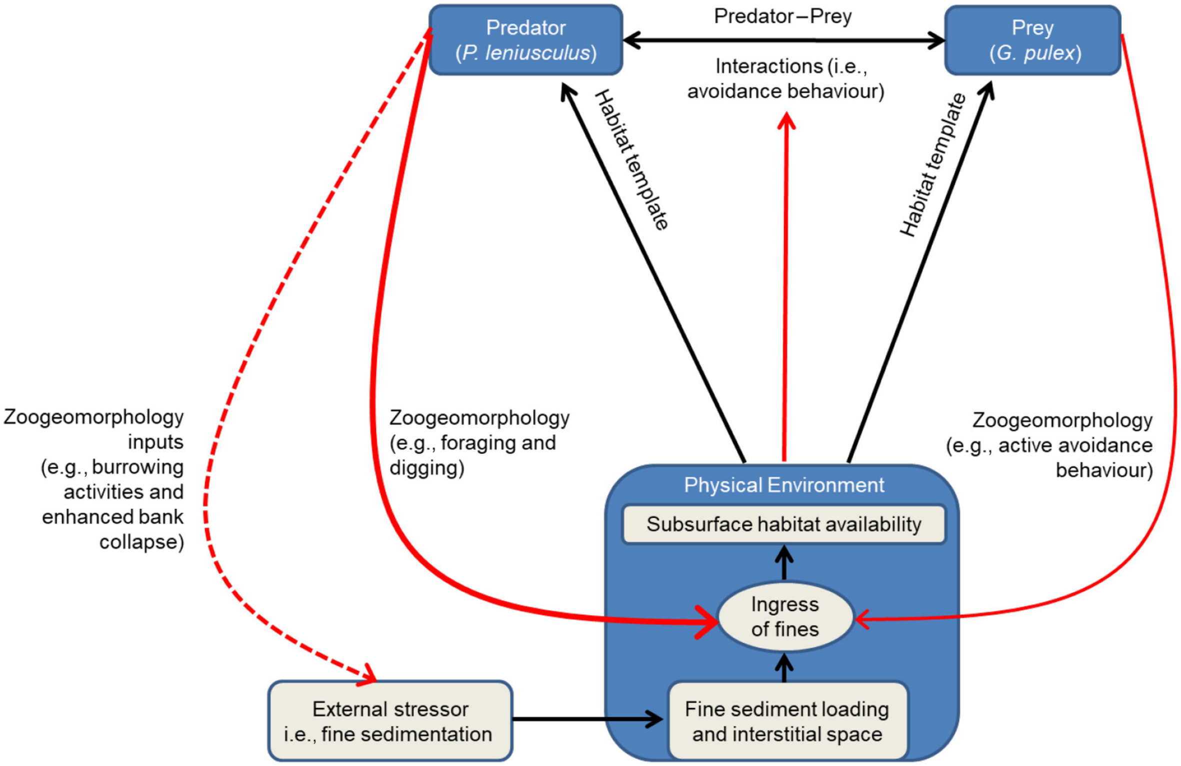

Fig. 6. Conceptualization of the work conducted in this study examining the interactions between predator–prey relations, the physical environment, and the addition of an external stressor building on the traditional concepts presented in Fig. 1. Specific examples in relation to fine sediment dynamics, *Pacifastacus leniusculus* and *Gammarus pulex,* are provided. Dashed arrows indicate processes which require further investigation to fully understand the implications for predator–prey–environment dynamics.

examined how this process is affected by the zoogeomorphic activity of a single organism or the interaction(s) among multiple organisms. This study provides direct evidence that the presence of *P. leniusculus* alone and of *G. pulex* and *P. leniusculus* together can increase infiltration rates depending on the characteristics of the sediment involved. For fine sand treatments (grain size 0.125 μm–1 mm), the greatest geomorphic effect was associated with crayfish foraging and resulted in ~10% increase in fine sediment infiltration into the bed compared to control conditions (no organisms present) or when 75 *G. pulex* were present. The significant effect of a single crayfish suggests that under field conditions, and where interstitial spaces in the subsurface exist, sediment infiltration may occur at greater rates if crayfish densities are high. Given that *P. leniusculus* can reach densities up to 15 m^{-2} (Guan and Wiles 1996), the presence of this organism may significantly modify fine sediment movements between river bed surface and subsurface layers. No significant difference in infiltration rates was detected for *G. pulex* when in isolation, most likely associated with their relatively small body size (Moore 2006).

When both predator and prey were present (*P. leniusculus* and 75 *G. pulex*), sediment infiltration rates were on average 5% higher than control conditions or when only 75 *G. pulex* were present. It is likely that infiltration rates were reduced during these experiments because of direct prey–predator interactions that affected the zoogeomorphic behavior of prey and predator. First, for experiments without crayfish, the majority of *G. pulex* were in the surface layer and therefore had a greater opportunity to cause ingress of fine sediment over the course of the experiment. In contrast, in the presence of *P. leniusculus*, on average 25% more *G. pulex* migrated into subsurface habitats, and consequently, the sum influence on ingress was reduced. Second, in experiments where *P. leniusculus* were the only organism present, a large proportion of energy was expended in foraging for food. In a number of experiments, *P. leniusculus* exhibited bulldozing behavior by piling and moving the substrate (Helms and Creed 2005, Johnson et al. 2010). This foraging behavior and the disturbance of surface sediments significantly affected the vertical movement of fine-grained sediments into the bed. The addition of prey (*G. pulex*) resulted in a reduction in foraging activity due to the greater availability and number of encounters with food resources. It is assumed that during the experiments foraging activity would gradually decline over the 24-h period as prey were consumed (Haddaway et al. 2014) and time between foraging activity would have increased. The overall effect was a reduction in bed disturbance caused by foraging, and therefore, a reduction in fine sediment ingress compared with that when *P. leniusculus* were alone. Prey availability may therefore be a key driver of zoogeomorphic activity. Reductions in prey availability may increase foraging behavior and inter-species competition (especially for *P. leniusculus* which exhibits a high degree of intraspecific aggression; Pintor et al. 2008); this in turn may enhance fine sediment mobilization (suspension and ingress). These results support findings of other studies on predaceous stoneflies, which surmise that prey scarcity increases predator movement and thus the stability of fine sediments (Statzner et al. 1996, Zanetell and Peckarsky 1996).

In contrast to fine sand deposition, the greater propensity of coarse sand to form a bridge between clasts and thus prevent further infiltration meant that biota had little effect on overall infiltration rates. Under 3 kg/m^2 loadings, no significant differences in infiltration rates were recorded for any of the organism combinations, with only 3–4% (0.1 kg/m^2) of the initial sediment application infiltrating into the subsurface. Application of 5 kg/m^2 coarse sand resulted in limited differences in infiltration rates when animals were present, and although significant, the total mass of sediment was low compared to fine sand treatments (mean 0.14 kg/m^2 ingress). For coarse sand sediment treatments, *P. leniusculus* generated significantly greater infiltration rates (an extra 0.1 g/m^2 on average) compared to control or 75 *G. pulex* treatments. However, in contrast to fine sand applications, the combination of both *G. pulex* and *P. leniusculus* resulted in the greatest infiltration rates. With clogging of the surface layers of the substrate by coarse sands (Mathers et al. 2019), *G. pulex* were unable to migrate into the subsurface, and therefore, around 95% of individuals remained in the surface layer. This had a significant effect on infiltration rates in the coarse sediment experiment but at an order of magnitude lower than for the fine sand treatments.

Predator avoidance and the interaction with the physical environment

The application of fine sediment (grain size 0.125 μm–1 mm) under both loadings (3 and 5 kg/m^2) resulted in high infiltration rates under control conditions (gravity and downwelling flow) and all organism combinations. However, vertical connectivity was maintained due to the large interstitial spaces between gravel particles relative to the sand grain size (Xu et al. 2012, Mathers et al. 2014). As a result, around 50% of *G. pulex* were able to migrate vertically into the subsurface when predatory crayfish were present. In the equivalent treatments without the predator, the majority of prey remained in the surface layer, probably reflecting the rheophilic preferences of *G. pulex* (Gledhill et al. 1993). The results therefore indicate that the presence of the crayfish predator significantly modified the vertical distribution of *G. pulex* and provides evidence of predator avoidance behavior.

In contrast, the addition of coarse sand sediments (1–4 mm) resulted in bridging of interstitial spaces within the surface layer of the substrates and clogging that disconnected the surface and subsurface layers regardless of zoogeomorphic activity. Infiltration rates were significantly lower for coarse sand than for fine sand treatments, with the majority of sand particles being retained in the surface layer for both organism combinations. As a result, no significant difference in the vertical distribution of *G. pulex* (with or without *P. leniusculus*) was observed. The formation of surface-layer clogs probably restricted the ability of *G. pulex* to migrate into subsurface sediments (sensu Mathers et al. 2019) and influenced predator–prey relationships, in this instance through survivorship of *G. pulex* (Figs. 1B, 6). In experiments where *G. pulex* could easily migrate, survivorship averaged 77% (± SEM 4.5) with no significant differences evident for any of the fine sand sediment or control treatments. The addition of coarser sand clogged the substrate interstices and prevented vertical avoidance behavior resulting in lower survivorship rates. 3 kg/m^2 coarse sand resulted in moderately lower survivorship (70% ± SEM 5.1) and 5 kg/m^2 reduced *G. pulex* survival to 56% (± SEM 4.5); a reduction of 28% compared to the control treatment (open gravel framework).

Despite *P. leniusculus* being a significant zoogeomorphic agent within fine sand treatments, in this set of experiments only the coarse sand treatment affected the vertical avoidance behavior and subsequent predation rates. This result is predominately a function of the open gravel framework used in the experiments (Xu et al. 2012) and we therefore hypothesize that under natural conditions, where poorly sorted mixed gravel frameworks exist, ingress of sand augmented by *P. leniusculus* may influence pore space sufficiently to affect avoidance behavior in many instances. If this is the case, *P. leniusculus* may inadvertently improve their predatory success by increasing fine sediment content within the river bed, an example of extended phenotype engineering, whereby the organism creates structures or effects that directly influence their fitness and survival (Jones et al. 1994, Wright and Jones 2006). This hypothesis requires further detailed investigation to fully understand the feedbacks between predator–prey and the physical environment (sensu Fig. 6).

Mediation of predator–prey interaction by sediment characteristics

This research illustrates how the structure of the physical environment potentially influences predator–prey interactions (Figs. 1B, 6). In each experiment, the nature of the physical environment was a key control on these interactions and feedback, with different outcomes dependant on the amount and grain size of the fine sediment applied. The deposition of coarser sand grains has the potential to reduce the effectiveness of a prey's avoidance behavior and render them susceptible to enhanced predation. This suggests that in nature, spatial and temporal variations in fine sediment dynamics will partly regulate these interactions and further field experimentation is required to test this more rigorously. Sediment dynamics in rivers vary as a function of the abiotic hydro-geomorphological regime, but anthropogenic activities (agriculture, urbanization, forestry, construction, mining) increase sediment loading (Owens et al. 2005) and, in the UK, sediment recruitment to rivers may be further increased in the presence of *P. leniusculus* through burrowing activities (Faller et al. 2016, Rice et al. 2016). It is therefore possible that anthropogenic sedimentation has facilitated the success of invasive *P. leniusculus* by reducing the availability of hyporheic refugia for prey species.

CONCLUSIONS

The results of this study demonstrate that fine sediment ingress into gravel river beds can be caused by expenditure of biological energy under certain environmental conditions; that prey utilize avoidance strategies to evade predation; that predator–prey interactions themselves mediate the zoogeomorphic effectiveness of an organism and that these interactions and feedbacks are dependent on the environmental context. We present a new conceptual model that captures the interactions between predator, prey, zoogeomorphic processes, and habitat availability (Fig. 6) highlighting that interactions between ecosystem processes may be strongly mediated by dynamic bi-directional interactions between organisms and the physical environment they inhabit. Ecological (predation, avoidance) and geomorphological processes (sediment infiltration) are intrinsically linked and should not be studied in isolation.

ACKNOWLEDGMENTS

KLM acknowledges the support of a Glendonbrook doctoral studentship and co-funding from the Environment Agency to undertake this study. Thanks go to Stuart Ashby and Richard Harland for providing technical and laboratory support and to Nigel Wilby and Nicholas Clifford for useful discussions pertaining to the study outcomes. The comments of two anonymous reviewers have significantly improved the clarity of this study.

LITERATURE CITED

Alberti, M., J. Marzluff, and V. M. Hunt. 2017. Urban driven phenotypic changes: empirical observations and theoretical implications for eco-evolutionary feedback. Philosophical Transactions of the Royal Society B 372:20160029.

Albertson, L. K., and D. C. Allen. 2015. Meta-analysis: abundance, behavior, and hydraulic energy shape biotic effects on sediment transport in streams. Ecology 96:1329–1339.

Alexander, J. E., and A. P. Covich. 1991. Predation risk and avoidance behaviour in two freshwater snails. Biological Bulletin 180:387–393.

Basil, J., and D. Sandeman. 2000. Crayfish (*Cherax destructor*) use tactile cues to detect and learn topographical changes in their environment. Ethology 106:247–259.

Belgrad, B. A., and B. D. Griffen. 2016. Predator–prey interactions mediated by prey personality and predator hunting mode. Proceedings of the Royal Society B 283:20160408.

Beschta, R. L., and W. L. Jackson. 1979. The intrusion of fine sediments into a stable gravel bed. Journal of the Fisheries Board of Canada 36:204–210.

Bubb, D. H., M. C. Lucas, T. J. Thom, and P. Rycroft. 2002. The potential use of PIT telemetry for identifying and tracking crayfish in their natural environment. Hydrobiologia 483:225–230.

Bubb, D. H., T. J. Thom, and M. C. Lucas. 2004. Movement and dispersal of the invasive signal crayfish *Pacifastacus leniusculus* in upland rivers. Freshwater Biology 49:357–368.

Butler, D. R. 1995. Zoogeomorphology: animals as geomorphic agents. Cambridge University Press, Cambridge, UK.

Chivers, D. P., and R. J. F. Smith. 1998. Chemical alarm signalling in aquatic predator-prey systems: a review and prospectus. Ecoscience 5:338–352.

Church, M. A., D. G. McLean, and J. F. Wolcott. 1987. River bed gravels: sampling and analysis. Pages 43–88 *in* C. R. Thorne, J. C. Bathurst, and R. D. Hey, editors. Sediment transport in gravel-bed rivers. John Wiley & Sons, New York, New York USA.

Collins, A. L., and Y. Zhang. 2016. Exceedance of modern 'background' fine-grained sediment delivery to rivers due to current agricultural land use and uptake of water pollution mitigation options across England and Wales. Environmental Science and Policy 61:61–73.

Crowl, T. A., and A. P. Covich. 1990. Predator-induced life-history shifts in a freshwater snail. Science 247:949–951.

Cui, Y., and G. Parker. 1998. The arrested gravel front: stable gravel-sand transitions in rivers, part 2: General numerical solution. Journal of Hydraulic Research 36:159–182.

Descloux, S., T. Datry, and P. Marmonier. 2013. Benthic and hyporheic invertebrate assemblages along a gradient of increasing streambed colmation by fine sediment. Aquatic Sciences 75:493–507.

Dick, J. T. 1995. The cannibalistic behaviour of two *Gammarus* species (Crustacea: Amphipoda). Journal of Zoology 236:697–706.

Diplas, P., and G. Parker. 1992. Deposition and removal of fines in gravel-bed streams. Pages 313–329 *in* P. Billi, R. D. Hey, C. R. Thorne, and P. Tacconi, editors. Dynamics of gravel-bed rivers. Wiley, Chichester, UK.

Dorn, N. J. 2013. Consumptive effects of crayfish limit snail populations. Freshwater Science 32:1298–1308.

Early, R., et al. 2016. Global threats from invasive alien species in the twenty-first century and national response capacities. Nature Communications 7: Article 12485.

Faller, M., G. Harvey, A. J. Henshaw, W. Bertoldi, M. C. Bruno, and J. England. 2016. River bank burrowing by invasive crayfish: spatial distribution, biophysical controls and biogeomorphic significance. Science of the Total Environment 569:1190–1200.

Franssen, J., M. Lapointe, and P. Magnan. 2014. Geomorphic controls on fine sediment reinfiltration into salmonid spawning gravels and the implications for spawning habitat rehabilitation. Geomorphology 211:11–21.

Frings, R. M., M. G. Kleinhans, and S. Vollmer. 2008. Discriminating between pore-filling load and bed-structure load: a new porosity-based method, exemplified for the river Rhine. Sedimentology 55:1571–1593.

Frostick, L., P. M. Lucas, and I. Reid. 1984. The infiltration of fine matrices into coarse-grained alluvial sediments and its implications for stratigraphical interpretation. Journal of the Geological Society 141:955–965.

Gayraud, S., and M. Philippe. 2003. Influence of bed sediment features on the interstitial habitat available for macroinvertebrates in 15 French streams. International Review of Hydrobiology 88:77–93.

Gibson, S., D. Abraham, R. Heath, and D. Schoellhamer. 2009*a*. Vertical gradational variability of fines deposited in a gravel framework. Sedimentology 56:661–676.

Gibson, S., D. Abraham, R. Heath, and D. Schoellhamer. 2009*b*. Bridging process threshold for sediment infiltrating into a coarse substrate. Journal of Geotechnical and Geoenvironmental Engineering 136:402–406.

Gledhill, T., D. W. Sutcliffe, and W. D. Williams. 1993. British Freshwater Crustacea Malacostraca: A Key with Ecological Notes. Freshwater Biological Association Publication No. 52.

Guan, R.-Z. 1994. Burrowing behaviour of signal crayfish, *Pacifastacus leniusculus* (Dana), in the River Great Ouse, England. Freshwater Forum 4:155–168.

Guan, R.-Z., and P. R. Wiles. 1996. Growth, density and biomass of crayfish, *Pacifastacus leniusculus*, in a British lowland river. Aquatic Living Resources 9:265–272.

Guan, R.-Z., and P. R. Wiles. 1998. Feeding ecology of the signal crayfish *Pacifastacus leniusculus* in a British lowland river. Aquaculture 169:177–193.

Haddaway, N. R., D. Vielle, R. J. G. Mortimer, M. Christmas, and A. M. Dunn. 2014. Aquatic macroinvertebrate responses to native and non-native predators. Knowledge and Management of Aquatic Ecosystems 415. https://doi.org/10.1051/kmae/2014036

Harvey, G., T. P. Moorhouse, N. J. Clifford, A. Henshaw, M. F. Johnson, D. W. MacDonald, I. Reid, and S. P. Rice. 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.

Heck, Jr. K., and L. B. Crowder. 1991. Habitat structure and predator–prey interactions in vegetated aquatic systems. Pages 281–299 *in* S. S. Bell, E. D. McCoy, and H. R. Mushinsky, editors. Habitat structure. Springer, Dordrecht, The Netherlands.

Helms, B. S., and R. P. Creed. 2005. The effects of 2 coexisting crayfish on an Appalachian river community. Journal of the North American Benthological Society 24:113–122.

Holdich, D. M., J. James, C. Jackson, and S. Peay. 2014. The North American signal crayfish, with particular reference to its success as an invasive species in Great Britain. Ethology Ecology and Evolution 26:232–262.

Hothorn, T., F. Bretz, P. Westfall, and R. M. Heiberger. 2012. Multcomp: simultaneous inference for general linear hypotheses. http://CRAN. R-project. org/package=multcomp, R package version.

Jackson, M. C., C. J. Loewen, R. D. Vinebrooke, and C. T. Chimimba. 2016. Net effects of multiple stressors in freshwater ecosystems: a meta-analysis. Global Change Biology 22:180–189.

Johnson, M. F., S. P. Rice, and I. Reid. 2010. Topographic disturbance of subaqueous gravel substrates by signal crayfish (*Pacifastacus leniusculus*). Geomorphology 123:269–278.

Johnson, M. F., S. P. Rice, and I. Reid. 2011. Increase in coarse sediment transport associated with disturbance of gravel river beds by signal crayfish (*Pacifastacus leniusculus*). Earth Surface Processes and Landforms 36:1680–1692.

Johnson, M. F., S. P. Rice, and I. Reid. 2014. The activity of signal crayfish (*Pacifastacus leniusculus*) in relation to thermal and hydraulic dynamics of an alluvial stream, UK. Hydrobiologia 724:41–54.

Jones, C. G., J. H. Lawton, and M. Shachak. 1994. Organisms as ecosystem engineers. Oikos 69:373–386.

Jones, C. G., J. H. Lawton, and M. Shachak. 1997. Positive and negative effects of organisms as physical ecosystem engineers. Ecology 78:1946–1957.

Jones, J. I., J. F. Murphy, A. L. Collins, D. A. Sear, P. S. Naden, and P. D. Armitage. 2012. The impact of fine sediment on Macroinvertebrates. River Research and Applications 28:1055–1071.

Koch, L. M., B. W. Patullo, and D. L. Macmillan. 2006. Exploring with damaged antennae: do crayfish compensate for injuries. Journal of Experimental Biology 209:3226–3233.

Kouba, A., M. Buřič, and A. Petrusek. 2015. Crayfish species in Europe. Pages 79–164 *in* P. Kozák, Z. Ďuriš, A. Petrusek, M. Buřič, A. Horká Kouba, E. Kozubikova-Balcarová, and T. Policar, editors. Crayfish biology and culture. University of South Bohemia, Zátiŝi, Czech Republic.

Kouba, A., A. Petrusek, and P. Kozák. 2014. Continental-wide distribution of crayfish species in Europe: update and maps. Knowledge and Management of Aquatic 413. https://doi.org/10.1051/kmae/2014007

Kuhlmann, M. L., S. M. Badylak, and E. L. Carvin. 2008. Testing the differential predation hypothesis for the invasion of rusty crayfish in a stream community: laboratory and field experiments. Freshwater Biology 53:113–128.

Kuhnle, R. A., D. G. Wren, and E. J. Langendoen. 2016. Erosion of sand from a gravel bed. Journal of Hydraulic Engineering 142:04015052.

Lima, S. L., and L. M. Dill. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. Canadian Journal of Zoology 68:619–640.

Lunt, I. A., and J. S. Bridge. 2007. Formation and preservation of open-framework gravel strata in unidirectional flows. Sedimentology 54:71–87.

MacNeil, C., J. T. Dick, and R. W. Elwood. 1997. The trophic ecology of freshwater *Gammarus* spp. (Crustacea: Amphipoda): problems and perspectives concerning the functional feeding group concept. Biological Reviews 72:349–364.

MacNeil, C., J. T. Dick, and R. W. Elwood. 1999. The dynamics of predation on *Gammarus* spp.] (Crustacea: Amphipoda). Biological Reviews 74:375–395.

Mathers, K. L., R. P. Chadd, M. J. Dunbar, C. A. Extence, J. Reeds, S. P. Rice, and P. J. Wood. 2016. The long-term effects of invasive signal crayfish (*Pacifastacus leniusculus*) on instream macroinvertebrate communities. Science of the Total Environment 556:207–218.

Mathers, K. L., M. J. Hill, C. D. Wood, and P. J. Wood. 2019. The role of fine sediment characteristics and body size on the vertical movement of a freshwater amphipod. Freshwater Biology 64:152–163.

Mathers, K. L., J. Millett, A. L. Robertson, R. Stubbington, and P. J. Wood. 2014. Faunal response to benthic and hyporheic sedimentation varies with direction of vertical hydrological exchange. Freshwater Biology 59:2278–2289.

Mermillod-Blondin, F., J.-P. Gaudet, M. Gérino, G. Desrosiers, J. Jose, and M. Creuzé des Châtelliers. 2004. Relative influence on bioturbation and predation on organic matter processing in river sediments: a microcosm experiment. Freshwater Biology 49:895–912.

Mermillod-Blondin, F., and R. Rosenberg. 2006. Ecosystem engineering: the impact of bioturbation on biogeochemical processes in marine and freshwater benthic habitats. Aquatic Science 68:434–442.

Moore, J. W.. 2006. Animal ecosystem engineers in streams. BioScience 56:237–246.

Nogaro, G., F. Mermillod-Blondin, F. François-Carcaillet, J.-P. Gaudet, M. Lafont, and J. Gibert. 2006. Invertebrate bioturbation can reduce the clogging of sediment: an experimental study using infiltration sediment columns. Freshwater Biology 51:1458–1473.

Nyström, P. 1999. Ecological impact of introduced and native crayfish on freshwater communities. Pages 63–85 *in* F. Gheradi and D. M Holdich, editors. Crayfish in Europe as alien species. AA Balkema, Rotterdam, The Netherlands.

Nyström, P. 2005. Non-lethal predator effects on the performance of a native and an exotic crayfish species. Freshwater Biology 50:1938–1949.

Owens, P. N., et al. 2005. Fine-grained sediment in river systems: environmental significance and management issues. River Research and Applications 21:693–717.

Pintor, L. M., A. Sih, and M. L. Bauer. 2008. Differences in aggression, activity and boldness between native and introduced populations of an invasive crayfish. Oikos 117:1629–1636.

Pledger, A. G., S. P. Rice, and J. Millett. 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.

R Development Core Team. 2013. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Reynolds, J. D. 2002. Growth and reproduction. Pages 152–191 *in* D. M. Holdich, editor. Biology of freshwater crayfish. Blackwell Science, Oxford, UK.

Rice, S. P., M. F. Johnson, C. Extence, J. Reeds, and H. Longstaff. 2014. Diel patterns of suspended sediment flux and the zoogeomorphic agency of invasive crayfish. Cuadernos de Investigación Geográfic 40:7–27.

Rice, S. P., M. F. Johnson, K. Mathers, J. Reeds, and C. Extence. 2016. The importance of biotic entrainment for base flow fluvial sediment transport. Journal of Geophysical Research: Earth Surface 121:890–906.

Rice, S. P., M. F. Johnson, and I. Reid. 2012. Animals and the geomorphology of gravel-bed rivers. Pages 225–241 *in* M. Church, P. M. Biron, and A. G. Roy, editors. Gravel-bed rivers: Processes, tools, environments. John Wiley & Sons, Chichester, UK.

Ruokonen, T. J., J. Karjalainnen, and H. Hamalainen. 2014. Effects of an invasive crayfish on the littoral macroinvertebrates of large boreal lakes are habitat specific. Freshwater Biology 59:12–25.

Schmitz, O. J., J. R. Miller, A. M. Trainor, and B. Abrahms. 2017. Toward a community ecology of landscapes: predicting multiple predator-prey interactions across geographic space. Ecology 98:2281–2292.

Segev, O., R. Verster, and C. Weldon. 2017. Testing the link between perceived and actual risk of predation: mosquito oviposition site selection and egg predation by native and introduced fish. Journal of Applied Ecology 54:854–861.

Sih, A., A. M. Bell, and J. L. Kerby. 2004. Two stressors are far deadlier than one. Trends in Ecology and Evolution 19:274–276.

Sih, A., and T. M. McCarthy. 2002. Prey responses to pulses of risk and safety: testing the risk allocation hypothesis. Animal Behaviour 63:437–443.

Sol, D., and J. Maspons. 2016. Life history, behaviour and invasion success. Pages 63–81 *in* J. S. Weis and D. Sol, editors. Biological invasions and animal behaviour. Cambridge University Press, Cambridge, UK.

Statzner, B. 2012. Geomorphological implications of engineering bed sediments by lotic animals. Geomorphology 157–158:49–65.

Statzner, B., U. Fuchs, and L. W. G. Higler. 1996. Sand erosion by mobile predaceous stream insects: implications for ecology and hydrology. Water Resources Research 32:2279–2287.

Strauss, S. Y., J. A. Lau, and S. P. Carroll. 2006. Evolutionary responses of natives to introduced species: What do introductions tell us about natural communities? Ecology Letters 9:357–374.

Strayer, D. L. 2010. Alien species in fresh waters: ecological effects, interactions with other stressors, and prospects for the future. Freshwater Biology 55:152–174.

Stumpp, C., and G. C. Hose. 2017. Groundwater amphipods alter aquifer sediment structure. Hydrological Processes 31:3452–3454.

Twardochleb, L. A., J. D. Olden, and E. R. Larson. 2013. A global meta-analysis of the ecological impacts of nonnative crayfish. Freshwater Science 32:1367–1382.

Usio, N., and C. R. Townsend. 2004. Roles of crayfish: consequences of predation and bioturbation for stream invertebrates. Ecology 85:807–822.

Vadher, A. N., R. Stubbington, and P. J. Wood. 2015. Fine sediment reduces vertical migrations of *Gammarus pulex* (Crustacea: Amphipoda) in response to surface water loss. Hydrobiologia 753:61–71.

Väinölä, R., J. D. S. Witt, M. Grabowski, J. J. Bradbury, K. Jazdzewski, and B. Sket. 2008. Global diversity of amphipods (Amphipoda; Crustacea) in freshwater. Hydrobiologia 595:241–255.

Vermeij, G. J. 1982. Phenotypic evolution in a poorly dispersing snail after arrival of a predator. Nature 299:349–350.

Visoni, S. B. C., and T. P. Moulton. 2003. Effects of shrimp on periphyton and sediments in Atlantic forest streams: an exclusion experiment. Acta Limnologica Brasil 15:19–26.

Vu, H. D., and S. C. Pennings. 2017. Ecosystem engineers drive creek formation in salt marshes. Ecology 98:162–174.

Walling, D. E., and A. L. Collins. 2016. Fine sediment transport and management. Pages 37–60 *in* D. J. Gilvear, M. T. Greenwood, M. C. Thoms, and P. J. Wood, editors. River science: Research and management for the 21st century. John Wiley & Sons, Chichester, UK.

Wooster, J. K., S. R. Dusterhoff, Y. Cui, L. S. Sklar, W. E. Dietrich, and M. Malko. 2008. Sediment supply and relative size distribution effects on fine sediment infiltration into immobile gravels. Water Resource Research 44:18.

Wright, J. P., and C. G. Jones. 2006. The concept of organisms as ecosystem engineers ten years on: progress, limitations, and challenges. BioScience 56:203–209.

Xu, M., Z. Wang, B. Pan, and N. Zhou. 2012. Distribution and species composition of macroinvertebrates in the hyporheic zone of bed sediment. International Journal of Sediment Research 27: 129–140.

Zanetell, B. A., and B. Peckarsky. 1996. Stoneflies as ecological engineers – hungry predators reduce fine sediments in stream beds. Freshwater Biology 36:569–577.

Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.2545/full