Crayfish ecosystem engineering effects on riverbed disturbance and topography are mediated by size and behavior

Lindsey K. Albertson[1,2,3] and Melinda D. Daniels[2,4]

[1]Department of Ecology, 310 Lewis Hall, Montana State University, Bozeman, Montana 59717 USA
[2]Stroud Water Research Center, 970 Spencer Road, Avondale, Pennsylvania 19311 USA

Abstract: Animals that burrow, forage, or produce physical structures can have substantial impacts on transport processes related to erosion. However, the influence of behavior and body size on regulating the magnitude of engineering effects by animals is not well understood. For example, crayfish are common and abundant freshwater organisms that disturb sediments in ways that influence gravel transport, fine sediment suspension, and bank stability. Animals such as crayfish also display complex territorial and aggressive behaviors, often related to body size, which might influence their ability to influence sediment transport dynamics. We conducted an experiment with spiny-cheek crayfish (*Faxonius limosus*) to investigate the influence of behavior and body size on substrate disturbance. The experiment included 4 enclosure (0.31-m long × 0.21-m wide × 0.17-m deep) treatments that differed in the body size of individual crayfish and the amount of biomass: 1) 2 small young-of-the-year (YOY) crayfish of 15-mm carapace length (CL) (abbreviated SS), 2) 2 larger, 1+ y-old crayfish of 25-mm CL (abbreviated LL), 3) 1 crayfish of 15- and one crayfish of 25-mm CL (abbreviated SL), and 4) a control with no crayfish. We monitored construction of pits within the gravel bed and the proportion of streambed over which crayfish exhumed subsurface gravels. We also used videography to quantify aggressive encounters between crayfish individuals. We found that body size strongly influenced the amount and type of disturbance, with large crayfish creating a significantly greater number of pit structures than small crayfish. Additionally, surface gravels were moved over 11.4, 9.3, 1.3, and 0.003% of the bed surface area in LL, SL, SS, and control treatments, respectively. On average, 77% of interactions between crayfish individuals were aggressive regardless of size, which may explain why the amount of change in bed topography in the LL treatments did not always exceed that in the SL treatments. Successfully incorporating animal behavior into sediment transport models may require consideration of both behavior and body size.
Key Words: ecogeomorphology, biophysical interactions, bioturbation, sediment transport, territoriality

Transport of sediment is one of the fundamental disturbance processes that can regulate benthic community composition and productivity in freshwater ecosystems (Resh et al. 1988, Lake 2000). In recent years, a growing body of research has investigated how animals and plants can influence sediment transport dynamics. This research has emphasized how biological forces can affect the timing and magnitude of sediment movement (Viles et al. 2008, Jones 2012, Statzner 2012) and has resulted in the development of integrative disciplines, such as ecogeomorphology (Viles 1988, Jones et al. 1994, Allen et al. 2014).

Despite significant advances in ecogeomorphological research, there is still limited understanding of the ecological factors that influence when and where ecosystem engineers (those species capable of influencing ecosystem physical structures and function) are important (Jones et al. 1994). For example, population density, organism body size, and behavior are all expected to regulate the ability of animals

to engineer their environment (Moore 2006), and recent evidence suggests that organism density and individual biomass are positively correlated with the magnitude of engineering effects (Albertson and Allen 2015). The role of behavior and interactions between individuals is less well understood but has the potential to regulate physical engineering impacts through biotic interactions (Wright and Jones 2006, Gribben et al. 2009, Sanders et al. 2014).

Crayfish are a diverse, abundant, and globally distributed group of omnivorous invertebrates that inhabit lentic and lotic ecosystems (Momot et al. 1978, Taylor et al. 1996) and that can act as ecosystem engineers. Crayfish can alter several features of the benthic habitat, including gravel erosion and fine sediment suspension (Statzner et al. 2003, Creed and Reed 2004, Harvey et al. 2014). They can also alter riverbed microtopography by creating pit and mound structures within the substrate and reduce bank stabilization through burrowing activities (Guan 1994, Barbaresi et al. 2004, Johnson et al. 2010). These activities can alter various biotic features of freshwater habitats as well, including macroinvertebrate and fish community composition and density (Bobeldyk and Lamberti 2010), processes of detrital breakdown (Schofield et al. 2001, Bobeldyk and Lamberti 2008, 2010), and standing stock of macrophytes (Roth et al. 2007). As such, crayfish can represent a potentially important biological force that can influence ecosystem function.

Crayfish are territorial and display complex inter- and intraspecific aggressive behaviors. Behavior between individuals of the same species is sex and size dependent (Bruski and Dunham 1987, Bergman and Moore 2003), and dominance hierarchies, typically established by fighting behaviors, can influence access to food resources and space (Herberholz et al. 2007, Chibucos et al. 2015). Links between behavior and engineering capability are still rare, but some evidence suggests that at relatively high density crayfish fighting behaviors may result in a reduced impact on transport processes and riverbed topography (Statzner et al. 2003). Additionally, evidence suggests that conspecific interactions between crayfish individuals can occur frequently, but further work is needed to understand if these behaviors might alter propensity to influence geomorphic processes (Rice et al. 2012).

To explore how body size and aggressive behaviors influenced the magnitude at which crayfish engineer riverbed sediments, we used a laboratory mesocosm experiment to manipulate the presence or absence of crayfish that varied in body size. We documented aggressive interactions between crayfish individuals, changes to the gravel bed through the development of pit and mound topography, and tracked the movement of 2 size classes of gravels. We predicted that larger crayfish would have a stronger engineering effect than smaller crayfish but that aggressive interactions between large crayfish would diminish their engineering effects compared with treatments containing both small and large crayfish. Our findings provide insight into the mechanisms related to body size, age, and behaviors that might regulate the magnitude of animal ecosystem engineering in streams.

METHODS
Study site and organism

This experiment was conducted in the stream house at the Stroud Water Research Center (SWRC) in Avondale, Pennsylvania (PA), USA between 10 and 27 October, 2014. The experimental units were 8 replicate recirculating flumes that were each individually fed with stream water from neighboring White Clay Creek. Each flume had a gravel bed composed of surface gravels with a median diameter of 16 to 22 mm and subsurface gravels with a median diameter of 5.6 to 8 mm. Subsurface gravels were colored pink to distinguish surface from subsurface layers. Gravels were water worked for 24 h before crayfish were added to the flumes to encourage settling of hand-placed gravels into a stable arrangement.

We studied *Faxonius limosus* [Rafinesque, 1817], a native crayfish in North America with abundant populations in the mid-Atlantic region of the USA (Crandall and De Grave 2017). Commonly called the spiny-cheek crayfish, *F. limosus* is found in a wide range of habitat types from rivers with moderate current to ponds. It typically inhabits cobble and gravel substrate but can be found under muddy, undercut banks or vegetation (Swecker et al. 2010, Nuttall 2013). *Faxonius limosus* omnivorously feeds on invertebrates, detritus, and plant material. This species has been introduced to Europe, where it reaches extremely high population densities with substantial and often negative impacts on native crayfish species, spread of disease, fish biodiversity, and foodweb dynamics (Hobbs 1948, Holdich and Black 2007, Lodge et al. 2000). At our study site, crayfish were collected by hand from White Clay Creek and housed individually in aquaria for 24 h before the start of the experiment. Crayfish were categorized as either small YOY (born summer 2014 and approximately 5 mo old) with 15-mm CL or large (born summer 2013 or earlier and at least 1.5 y old) with 25-mm CL. Although size structure descriptions of *F. limosus* populations in PA are unavailable to our knowledge, evidence from nearby populations in New England suggests that individuals with a CL of ~15 mm are likely in age class 0 and CL of ~25 mm are likely in age class 1 (Smith 1981). For another group in the same crayfish family, the *Cambarus acuminatus* complex, in Valley Creek near our study site, 2 distinct size classes of 9 to 18 and 23 to 38 mm CL are common in the fall when our study took place (Lieb et al. 2008). We did not sex individuals in our experiment, but male and female Cambaridae in Valley Creek appear to show no significant differences in body size in the fall (Lieb et al. 2008). To further describe differences in the body size-class categories we used in the experiment, we sacrificed 2 representative individuals from each size class to measure claw length

and dry mass by drying at 60°C until moisture was removed. We found that large crayfish bodies were 7× more massive and claws were 2× longer than small crayfish. The small crayfish category contained individuals weighing approximately 0.18 ± 0.03 g with claw lengths of 7.35 ± 0.15 mm, and the large crayfish category contained individuals weighing approximately 1.20 ± 0.10 g with claw lengths of 12.20 ± 0.40 mm.

Experimental design

The experiment was run as a complete block design with 4 crayfish treatments: control with no crayfish, 2 small crayfish (SS), 1 small and 1 large crayfish (SL), and 2 large crayfish (LL). Two replicates of each treatment were run per each of 4 blocks for a total of 8 replicates per crayfish treatment. Each block lasted 48 h. During the 48-h period, crayfish were placed into porous mesh (100-mm^2 openings) cages that were 0.31-m long × 0.21-m wide × 0.17-m deep. The cages contained gravel of median surface grain size 16 to 22 mm and median subsurface grain size 5.6 to 8 mm in an arrangement identical to the surrounding riverbed. The mesh cage was necessary to contain the crayfish within the flumes and minimize escape from the experimental units, and the mesh structure had minimal influence on current velocity (outside cage: 0.0432 ± 0.0036 m/s, inside cage: 0.0428 ± 0.0038 m/s). Crayfish density equaled $30/m^2$, which is at the high end of the range of densities for *Faxonius* spp. measured in natural freshwater habitats and used in previous laboratory studies (Momot et al. 1978, Hill and Lodge 1999, Haertel-Borer et al. 2005). Following the completion of block 1, crayfish were housed in individual aquaria for 24 h, assigned a new partner to ensure novel interactions among individuals, and then reintroduced to the flumes for block 2. New individuals collected by hand from White Clay Creek were used for block 3, after which they were housed in individual aquaria for 24 h, assigned a new partner, and then reintroduced to the flumes for block 4. Macroinvertebrates were screened from the water pump supply, and additional food was not provided during the experiment, although it is possible that some aquatic insects were introduced to the flumes through the water source coming from White Clay Creek. One large crayfish escaped the SL treatment cage during the 2nd evening of block 1 but the response variables we measured for that replicate were within 1 standard deviation (±SD) of the mean for that treatment. We, thus, included that replicate in further data analyses. There was no crayfish mortality in the cages during the experiment.

Measuring changes to gravel morphology

Changes to the gravel bed were quantified after a 48-h exposure to crayfish activity. To document changes to surface bed topography, an important variable that can regulate roughness, near-bed velocity, and bedload transport (Church 2006), we counted pit structures per unit area of the bed, and used a ruler and level to measure the depth of each pit depression (the level was held flush with the surrounding bed surface). We defined pits as visually obvious topographic alterations of the gravel-bed surface made by crayfish resulting in a decrease in bed elevation at the pit and subsequent increase in bed elevation in an immediately neighboring mound (Johnson et al. 2010, Rice et al. 2012). Twenty gravels in size class 16 to 22 mm and 20 gravels in size class 5.6 to 8 mm (intermediate orthogonal *b*-axis) were marked at the bed surface with white paint at the start of each block. We tracked movement of these marked gravels by counting any gravel that was flipped, turned, or transported within the mesh enclosure. We counted the number of marked gravels that moved within each grain size class and recorded the longest orthogonal axis (*a*-axis) of each gravel particle to the nearest 10th of a mm with ImageJ (Rasband 1997) to calculate the proportion and average size of gravels that had been moved. ImageJ was also used to quantify the area of the bed that contained visible, exposed subsurface colored gravels upon completion of each block. Exposure of subsurface gravel represents potential for wholesale grain-size changes, an increase in the fine fraction of the grain-size distribution at the bed surface, and movement of material, such as fine particulate organic matter or biofilm from the hyporheic subsurface zone to the surface where it could interact with channel water or benthic organisms. Upon completion of data collection, sediments were removed from the cages, regraded smooth by hand, allowed to be water worked for 24 h, and the next block was started.

Measuring interactions between crayfish

A GoPro™ video camera (Hero 3+ Silver; GoPro, Los Angeles, California) was mounted above each cage that contained crayfish to document interactions between crayfish individuals. Although the mesh mesocosms confined the crayfish to a restricted space and reduced the distance over which competitively inferior individuals might be able to retreat, research suggests that agonistic interactions in the laboratory are representative of and overlap well with field observations (Bergman and Moore 2003). Videos were initiated immediately after crayfish were introduced to each flume and continued for 3 h during the first evening of each block. Videos were used to enumerate the number of times individuals contacted each other. Contacts were categorized as aggressive if 1 or both individuals either displayed their claws or moved away.

Data analyses

We used 2-way analysis of variance (ANOVA) with treatment and block as fixed effects to assess if the number of pit structures, gravel size moved, or proportion of riverbed with subsurface gravels exposed differed across crayfish treatments. If no evidence of a block effect was detected (using $\alpha \leq 0.05$), we selected the most parsimonious model

by removing the nonsignificant effect and followed with a 1-way ANOVA with a fixed treatment effect. No block effects were significant, and all treatments were significant, so we compared all pairwise differences in each response variable across crayfish treatments with Tukey's Honestly Significant Difference (HSD) post-hoc tests. We conducted similar analyses on behavioral responses. Prior to any ANOVA analyses, all response variable data distributions were tested for normality using Shapiro–Wilk tests and appropriately transformed if the assumptions of normality were not met ($\sqrt{x}$-transformation for counts and arcsine transformation for proportions). Data in our figures display untransformed data. All analyses were conducted in R (Version 3.1.0; R project for statistical computing, Vienna, Austria; R Development Core Team 2008).

RESULTS

Crayfish significantly influenced bed topography compared with controls (Fig. 1). No evidence for a block effect was detected for any of the analyses (all $p > 0.05$). On average, 2 large crayfish (LL) dug the deepest pits (mean = 3.4 cm), whereas the small and large crayfish (SL) pits averaged 3.1 cm, and the 2 small crayfish (SS) pits were 2.3-cm deep on average ($p < 0.001$). A significantly greater number

Figure 2. The average size (length of orthogonal a-axis) of gravels moved was 14.2 ± 0.3, 13.8 ± 1.0, and 11.3 ± 1.2 mm for LL, SL, and SS treatments, respectively. Values are means (±1 SE) for $n = 8$. Treatments with different lowercase letters are significantly different from one another based on post-hoc comparisons.

of pit depressions were found in the gravel bed after 48 h in treatments with crayfish compared with controls (Fig. 1; all $p < 0.001$). However, no difference existed in pit density between SL and LL treatments ($p = 0.878$).

Some of the marked gravels in the control treatments moved, which likely occurred as flow was introduced to the flumes following experimental set up and the grains were water worked. The size of gravel moved in the control enclosures was, however, significantly smaller than the size of gravels moved in any treatments with crayfish present (all $p < 0.001$). Between crayfish treatments, however, there were no differences in the average size of gravels moved (all $p > 0.8$), suggesting that both large and small crayfish were capable of moving similarly sized gravels in this experiment (Fig. 2). However, larger crayfish may ultimately be capable of moving larger gravels if presented with them, because we also found that the single largest marked gravel that was moved in SS, SL, and LL treatments was 22.8, 25.5, and 29.3 mm, respectively.

The proportion of marked 5.6- to 8-mm gravels that moved (Fig. 3A) was higher in the SL ($p = 0.001$) and LL ($p < 0.001$) treatments than the controls, but no differences were detected between the SS treatment and control ($p = 0.980$). Within crayfish treatments, a higher proportion of 5.6- to 8-mm gravels moved in both the SL ($p = 0.003$) and LL ($p < 0.001$) treatments than the SS treatment, but no differences existed between the SL and LL treatments ($p = 0.168$). The proportion of marked 16- to 22-mm gravels that were moved (Fig. 3B) was higher in the LL treatment than the control ($p = 0.044$) but was not different between
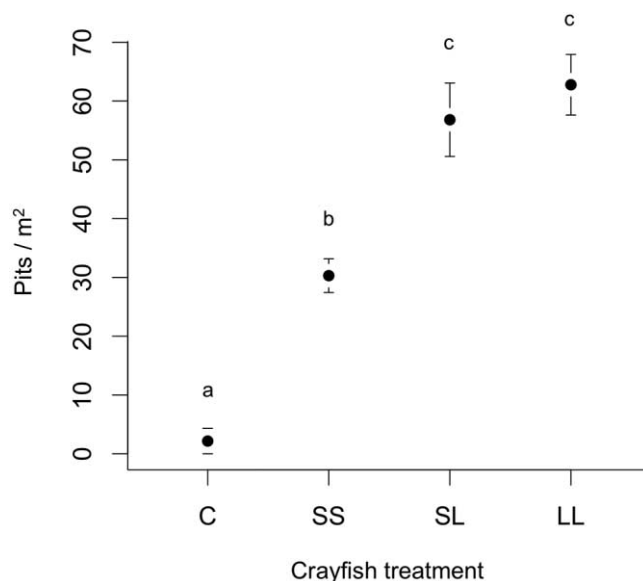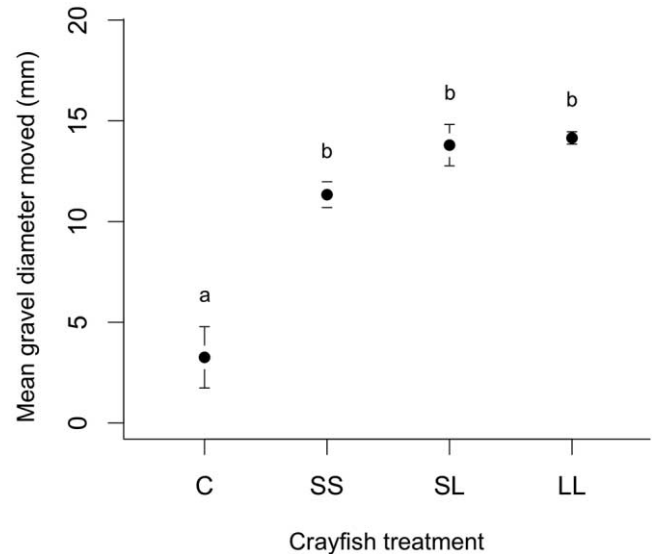

Figure 1. Changes in riverbed morphology caused by crayfish activity. Crayfish treatments were 2 large individuals (LL), 1 small and 1 large individual (SL), 2 small individuals (SS), or a control (C) with no crayfish present. Enclosures with large crayfish present (either SL or LL treatments) had a significantly greater number of pit and mound structures than those with only small crayfish (SS) or controls with no crayfish, but there was no difference between the SL and LL treatments. Values are means (±1 SE) for $n = 8$. Treatments with different lowercase letters are significantly different from one another based on post-hoc comparisons.
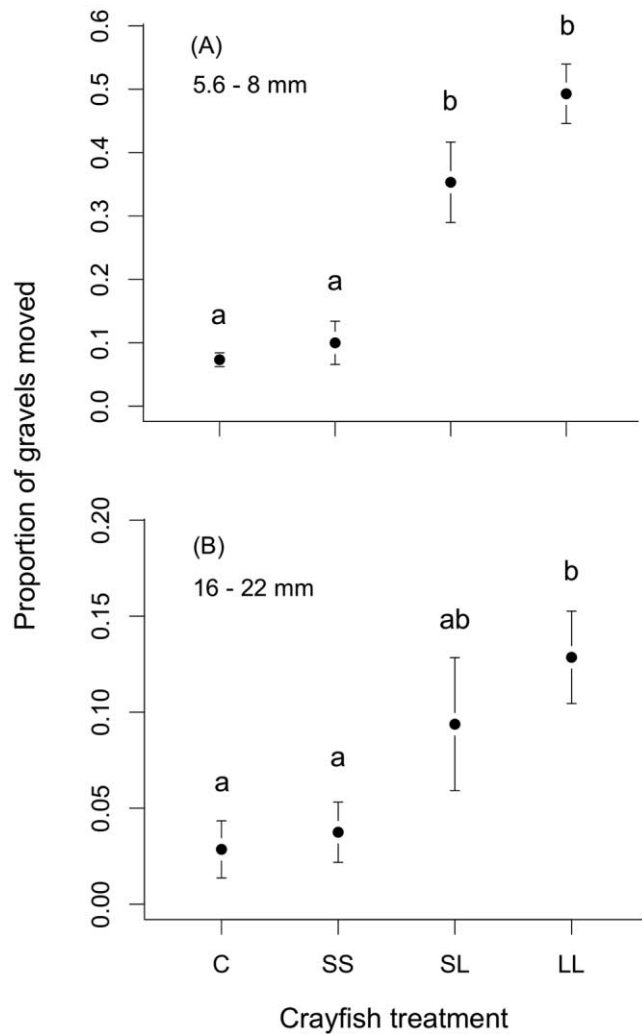
Figure 3. Crayfish activity at the riverbed surface. Crayfish moved marked gravels that were categorized by size as either 5.6- to 8-mm diameter (A) or 16- to 20-mm diameter (B). Values are means (±1 SE) for $n = 8$. Treatments with different lowercase letters are significantly different from one another based on post-hoc comparisons.

the control and SS treatment ($p = 0.994$) or control and SL ($p = 0.254$) treatment. Within crayfish treatments, a marginally higher proportion of 16- to 22-mm gravels moved in the LL treatment than the SS treatment ($p = 0.063$), but no difference was observed between the SS and SL treatments ($p = 0.346$) or between the SL and LL treatments ($p = 0.751$).

Crayfish of all body sizes were capable of moving grains of similar size, but there were significant differences among treatments in the proportion of bed gravels that moved and the amount of exposed subsurface gravels (Fig. 4). The proportion of subsurface material exposed was higher in SL ($p = 0.026$) and LL ($p = 0.006$) treatments than controls but was not different between the SS treatment and the control ($p = 0.990$). Within crayfish treatments, there was more material

exposed in SL ($p = 0.043$) and LL ($p = 0.010$) treatments than in the SS treatment, but no differences were detected between the SL and LL treatments ($p = 0.892$). Crayfish in the LL and SL treatments exposed, on average, 11.4 and 9.3% of the bed, respectively, and as much as 27.4% was recorded for 1 LL replicate.

Crayfish in all cages contacted and interacted with each other repeatedly when they were introduced to the streams (Fig. 5). As predicted, a significantly greater number of contacts occurred between 2 large individuals (LL) than either a small and large individual (SL) ($p = 0.009$) or 2 small individuals (SS) (Fig. 5A, $p < 0.001$). Contacts/h in the LL treatments occurred 2× as often as in the SL treatments ($p = 0.009$) and 3× more often than in the SS treatments (Fig. 5B, $p < 0.001$). The small individuals contacted each other the least, averaging only 3 contacts/h. Compared with the contacts in the SS treatments, contacts in the SL ($p = 0.013$) and LL treatments ($p < 0.001$) were significantly more aggressive (Fig. 5C), but no difference in the proportion of aggressive contacts were detected between the SL and LL treatments ($p = 0.145$). Interactions between large individuals were aggressive ~90% of the time, between small and large individuals ~80% of the time, and between 2 small individuals ~60% of the time. When averaged across all treatments, interactions between individuals were aggressive 77% of the time.
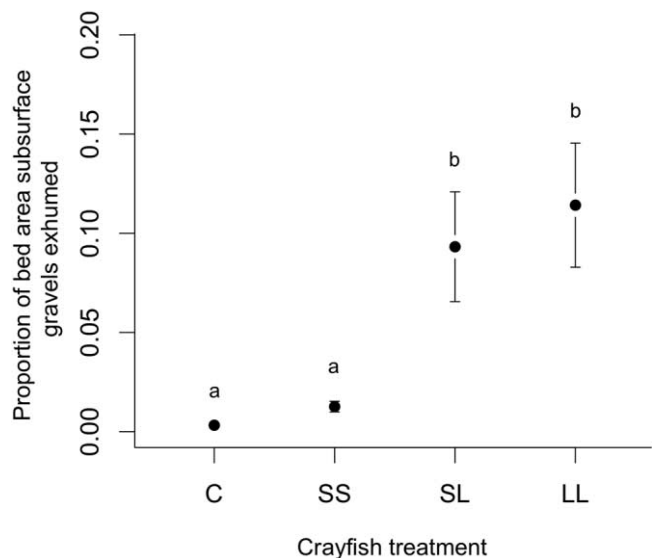

Figure 4. The proportion of the bed surface area over which surface gravels were moved and subsurface gravels were exhumed by crayfish. Exposure of subsurface material was higher, on average, in LL and SL crayfish treatments compared with controls, but exposed subsurface material was no different in enclosures with 2 small crayfish (SS) than in controls. Values are means (±1 SE) for $n = 8$. Treatments with different lowercase letters are significantly different from one another based on post-hoc comparisons.
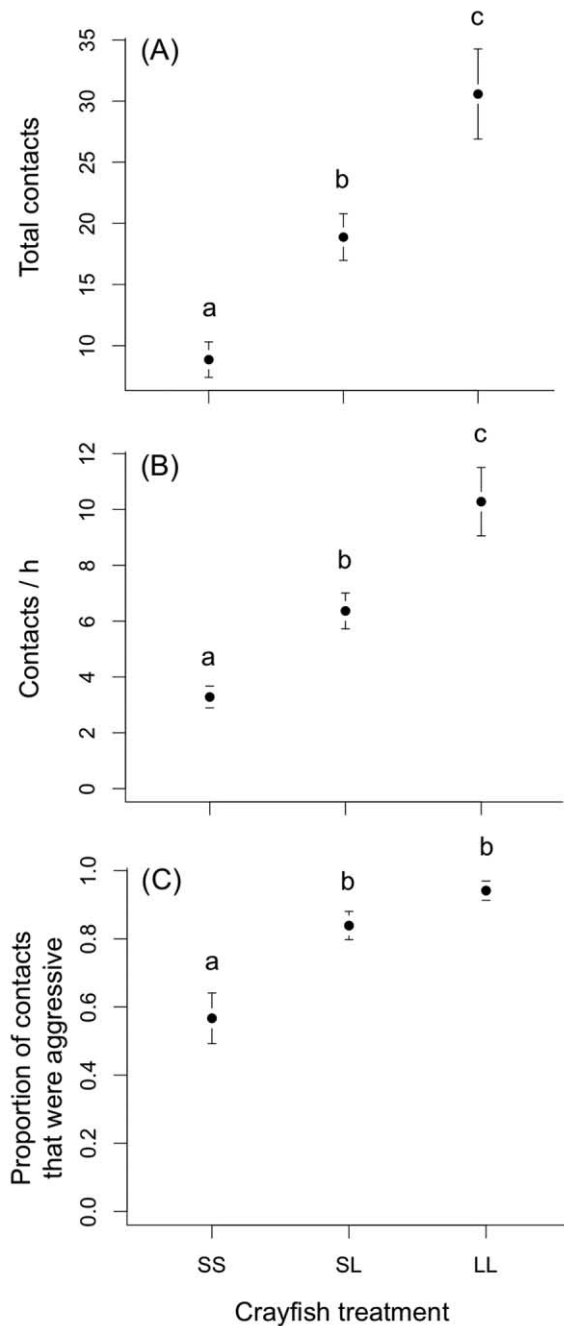
Figure 5. Interactions between crayfish individuals in the experiment. Total number of contacts (A) and contacts per h (B) during the first evening the crayfish were present in the enclosures was highest for treatments with large crayfish present (SL, LL). Large crayfish were almost always aggressive in their interactions (C), but small crayfish also displayed territorial and aggressive behavior during the majority of their interactions. Values are means (±1 SE) for $n = 8$. Treatments with different lowercase letters are significantly different based on post-hoc comparisons.

DISCUSSION

We demonstrated that *Faxonius limosus*, a common crayfish in the northeast USA, can alter surface and subsurface gravel arrangement and bed topography. Bioturbation by crayfish has been recognized for decades, but only a few studies have quantified how effectively crayfish engineer riverbed topography, loosen the surface gravel matrix, and sort grain layers by digging and exposing subsurface material (Johnson et al. 2010). Our study provides further insight into crayfish-induced gravel movement by assessing how agonistic behaviors and conspecific territoriality between individuals influenced gravel movement. We found support for our hypothesis that behavioral interactions might reduce crayfish-induced gravel movements. These findings contradict some previous work showing that limited shelter space leading to increased interactions between crayfish does not reduce crayfish engineering activity (Statzner and Peltret 2006). However, they are consistent with other observations that showed 2 similarly sized crayfish spent only slightly more time digging than a single crayfish, perhaps because they spent more time interacting, and thus, resulting in little additional effect on bed topography or grain entrainment rates than 1 crayfish (Rice et al. 2012). Given these conflicting findings, future work is needed to untangle just how important behaviors are in regulating biotic engineering activity.

We also found support for our hypothesis that body size might regulate how actively crayfish engineer gravel substrate. Given that the large crayfish almost universally altered the gravel bed more than small crayfish in our experiment, and because crayfish often reach a larger body size than the 'large' individuals used in this study (Holdich and Black 2007, Loughman 2010), our results may represent a conservative estimate of the effects of crayfish size on riverbed gravel movement. However, the relative importance of larger body or claw sizes compared with a parallel increase in behavioral interactions that might arise from larger, more aggressive individuals is unknown. Limitations deriving from the small spatial and temporal scale of our flume study require that these biological effects be measured under field conditions to best evaluate their prevalence and their relative importance compared with other forces affecting sediments in natural streams. Compared to physical forces associated with high flows, for example, the effects of crayfish on gravel movement may be minimal or restricted to certain locations or times of year (Harvey et al. 2014). In addition, other biological forces associated with, for example, biofilm or vegetative root structures may have a larger magnitude or even opposing (stabilizing) effects on gravel movements (Albertson and Allen 2015).

As predicted, small YOY crayfish showed only a minor effect on movement of gravels. This finding is consistent with recent evidence indicating that individual mass can regulate engineering effect sizes, with larger individuals typically having a stronger influence on transport processes (Albertson and Allen 2015). We found that both small and

large crayfish were capable of moving grains of similar size, and our results are similar to previous findings that crayfish can move gravels up to 38 mm in size (Johnson et al. 2010). However, the proportion of the subsurface layer visible at the end of 48 h was not different between enclosures with 2 small crayfish and controls with no crayfish. These results suggest that small crayfish are capable of moving grains of the same size as large crayfish, but their activity is less than that of large crayfish. In Valley Creek near our study site, cambarid crayfish assemblages were dominated (>80%) by juveniles in spring and fall, suggesting that seasonal differences in the presence of small crayfish may influence population-level effects on sediment engineering. In addition, some evidence suggests that smaller individuals may move to shallow, lateral areas to avoid fish predation (Englund and Krupa 2000), but similarly sized crayfish have also been found to occupy both riffles and pools without showing a location preference (Lieb et al. 2008). Future work might address how variation in location of occupation influences crayfish body size and, thus, the magnitude of effects on grain arrangement and bed topography. The mechanisms controlling body-size related effects on substrate alterations remain to be fully tested, but we hypothesize that they could be related to energetic and metabolic constraints as small crayfish become tired during digging activities or to the size of pore spaces available relative to body size that allows YOY crayfish to hide in existing pores without needing to alter the gravel arrangement.

Small YOY crayfish are relatively more abundant than larger crayfish in natural streams (Lieb et al. 2008), but juvenile crayfish populations typically make up only 21 to 65% of the biomass of adult crayfish (Haertel-Borer et al. 2005), and the importance of this difference is understudied. We detected minimal difference between the SL and LL treatments across all response variables, despite the difference in total biomass in the two treatments owing to the presence of the 2nd large individual in the LL treatment. These findings suggest that 25-mm CL crayfish at a density of 15 and 30/m^2 in the SL and LL treatments, respectively, are capable of moving similar amounts of gravel. Crayfish modification of gravel beds could be occurring regularly in natural streams, because these crayfish densities are representative (but high) of those found in natural streams (Hill and Lodge 1999, Kuhlmann 2016). However, the restriction of individuals in our study to small mesocosm cages may have influenced either the duration or intensity of both sediment-modifying behaviors and aggressive interactions among individuals. Our study did not address trade-offs between population and life-history attributes, such as density, body mass, sex, and sexual maturity in regulating the effects crayfish can have on the gravel matrix. These are potentially important factors that remain to be investigated in natural streams where crayfish can disperse to, and select from, a wider range of habitats.

A growing body of research illustrates how species traits can influence the effects ecosystem engineers have on physical transport processes (Statzner and Sagnes 2008, Albertson et al. 2014). Our study begins to identify how the intra- and interspecific behavioral interactions that occur among crayfish of varying size might shape their ability to affect sediment dynamics. Ecosystem engineers are predicted to influence multiple trophic levels, but effects within trophic levels are rarely studied (Sanders et al. 2014, van der Zee et al. 2016). Additionally, interactions between multiple species of engineers that live in the same community are well-recognized in marine systems (Angelini et al. 2011), but the spatial and temporal scales over which these interactions influence freshwater ecosystems is unknown. Crayfish are pervasive invaders across the globe (Lodge et al. 2012), so they may be ideal study organisms with which to investigate the importance of interspecific competition, coexisting ecosystem engineers, and trait variation on animal alteration of physical transport processes. Across the northeast USA, invasive rusty crayfish are displacing native crayfish species such as *F. limosus* (Lieb et al. 2008, Kuhlmann and Hazelton 2007). Species interactions and species-specific differences in engineering activity during and after invasion are relatively unknown but could be substantial given larger body sizes and higher densities often are documented for invasive rusty crayfish compared with natives (Hill and Lodge 1999, Wilson et al. 2004). Incorporating behavior related to competition and predation into ecosystem engineering frameworks is an important next step for better understanding biotic controls on erosion regimes (Gribben et al. 2009).

Sediment dynamics regulate fundamentally important processes in streams, including nutrient cycling, carbon storage, and habitat availability to benthic organisms (Allan 1995). If crayfish are altering grain-size distributions and the gravel matrix in natural streams, this activity may affect bedload flux, critical shear stress, and fine sediment retention (Church 2006). However, it is important to note that our study was conducted in laboratory flumes and, as such, may not represent the complexity of real streams. The range of grain sizes and heterogeneity of pore spaces that might provide refuge for larger crayfish was limited in our experiment. Crayfish were not allowed use of cobble refugia where they often shelter. Previous studies suggest that crayfish bioturbation is greater when refugia are not present (Statzner et al. 2000), implying the rates of gravel movement that we observed may be higher than observed in streams with refugia present. Conducting experiments in a field setting is an important next step for understanding the role of crayfish behavior in altering sediment dynamics.

Crayfish are one of the most widespread groups of aquatic macroinvertebrates. They are also prolific invaders in freshwater ecosystems (Savini et al. 2010), causing striking changes to native crayfish diversity, macrophyte cover, and benthic communities (Lodge et al. 2000, Wilson et al.

2004, Twardochleb et al. 2013). Understanding the impact of crayfish on ecosystem functions, including sediment transport dynamics, is becoming increasingly important as we seek to better understand the role of animals in structuring physical habitats in freshwater ecosystems.

LITERATURE CITED

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.

Albertson, L. K., L. S. Sklar, P. Pontau, M. Dow, and B. J. 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.

Allan, J. D. 1995. Stream ecology: structure and function of running waters. Springer, New York.

Allen, D. C., B. J. Cardinale, and T. Wynn-Thompson. 2014. Toward a better integration of ecological principles into interdisciplinary ecogeoscience research. BioScience 64:444–454.

Angelini, C., A. H. Altieri, B. R. Silliman, and M. D. Bertness. 2011. Interactions among foundation species and their consequences for community organization, biodiversity, and conservation. BioScience 61:782–789.

Barbaresi, S., E. Tricarico, and F. Gherardi. 2004. Factors inducing the intense burrowing activity of the red-swamp crayfish, *Procambarus clarkii*, an invasive species. Naturwissenschaften 91:342–345.

Bergman, D. A., and P. A. Moore. 2003. Field observations of intraspecific agonistic behavior of two crayfish species, *Orconectes rusticus* and *Orconectes virilis*, in different habitats. Biological Bulletin 205:26–35.

Bobeldyk, A. M., and G. A. Lamberti. 2008. A decade after invasion: evaluating the continuing effects of rusty crayfish on a Michigan River. Journal of Great Lakes Research 34:265–275.

Bobeldyk, A. M., and G. A. Lamberti. 2010. Stream food web responses to a large omnivorous invader, *Orconectes rusticus* (Decapoda, Cambaridae). Crustaceana 83:641–657.

Bruski, C. A., and D. W. Dunham. 1987. The importance of vision in agonistic communication of the crayfish *Orconectes rusticus*. I: An analysis of bout dynamics. Behaviour 103:83–107.

Chibucos, K., S. J. Wofford, and P. A. Moore. 2015. Hierarchical decision-making: resource distribution exhibits stronger effect on crayfish dominance relationships and shelter occupation than prior social experience and resource ownership. Behaviour 152:1063–1082.

Church, M. 2006. Bed material transport and the morphology of alluvial river channels. Annual Review of Earth and Planetary Sciences 34:325–354.

Crandall, K. A., and S. De Grave. 2017. An updated classification of the freshwater crayfishes (Decapoda: Astacidea) of the world, with a complete species list. Journal of Crustacean Biology 37:615–653.

Creed, R. P., and J. M. Reed. 2004. Ecosystem engineering by crayfish in a headwater stream community. Journal of the North American Benthological Society 23:224–236.

Englund, G., and J. J. Krupa. 2000. Habitat use by crayfish in stream pools: influence of predators, depth and body size. Freshwater Biology 43:75–83.

Gribben, P. E., J. E. Byers, M. Clements, L. A. McKenzie, P. D. Steinberg, and J. T. Wright. 2009. Behavioural interactions between ecosystem engineers control community species richness. Ecology Letters 12:1127–1136.

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

Haertel-Borer, S. S., D. Zak, R. Eckmann, U. Baade, and F. Hölker. 2005. Population density of the crayfish, *Orconectes limosus*, in relation to fish and macroinvertebrate densities in a small mesotrophic lake – implications for the lake's food web. International Review of Hydrobiology 90:523–533.

Harvey, G. L., A. J. Henshaw, T. P. Moorhouse, N. J. Clifford, H. Holah, J. Grey, and D. W. Macdonald. 2014. Invasive crayfish as drivers of fine sediment dynamics in rivers: field and laboratory evidence. Earth Surface Processes and Landforms 39: 259–271.

Herberholz, J., C. McCurdy, and D. H. Edwards. 2007. Direct benefits of social dominance in juvenile crayfish. Biological Bulletin 213:21–27.

Hill, A. M., and D. M. Lodge. 1999. Replacement of resident crayfishes by an exotic crayfish: the roles of competition and predation. Ecological Applications 9:678–690.

Hobbs, H. H., Jr. 1948. On the crayfishes of the limosus section of the genus *Orconectes* (Decapoda, Astacidae). Journal of the Washington Academy of Sciences 38:14–21.

Holdich, D., and J. Black. 2007. The spiny-cheek crayfish, *Orconectes limosus* (Rafinesque, 1817) [Crustacea: Decapoda: Cambaridae], digs into the UK. Aquatic Invasions 2:1–16.

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.

Jones, C. G. 2012. Ecosystem engineers and geomorphological signatures in landscapes. Geomorphology 157:75–87.

Jones, C. G., J. H. Lawton, and M. Shachak. 1994. Organisms as ecosystem engineers. Ecosystem Management 69:130–147.

Kuhlmann, M. L. 2016. Invasion-related change in crayfish density affects a stream macroinvertebrate community. Northeastern Naturalist 23:434–453.

Kuhlmann, M. L., and P. D. Hazelton. 2007. Invasion of the upper Susquehanna River watershed by rusty crayfish (*Orconectes rusticus*). Northeastern Naturalist 14:507–518.

Lake, P. S. 2000. Disturbance, patchiness, and diversity in streams. Journal of the North American Benthological Society 19:573–592.

Lieb, D. A., R. F. Carline, J. L. Rosenberger, and V. M. Mengel. 2008. The discovery and ecology of a member of the *Cambarus acuminatus* complex (Decapoda: Cambaridae) in Valley Creek, Southeastern Pennsylvania. Journal of Crustacean Biology 28: 439–450.

Lodge, D. M., C. A. Taylor, D. M. Holdich, and J. Skurdal. 2000. Nonindigenous crayfishes threaten North American freshwater biodiversity: lessons from Europe. Fisheries 25(8):7–20.

Lodge, D. M., A. Deines, F. Gherardi, D. C. J. Yeo, T. Arcella, A. K. Baldridge, M. A. Barnes, W. L. Chadderton, J. L. Feder, C. A. Gantz, G. W. Howard, C. L. Jerde, B. W. Peters, J. A. Peters, L. W. Sargent, C. R. Turner, M. E. Wittmann, and Y. Zeng. 2012. Global introductions of crayfishes: evaluating the impact of species invasions on ecosystem services. Annual Review of Ecology, Evolution, and Systematics 43:449–472.

Loughman, Z. J. 2010. Crayfishes of western Maryland: conservation and natural history. Southeastern Naturalist 9:33–62.

Momot, W. T., H. Gowing, and P. D. Jones. 1978. The dynamics of crayfish and their role in ecosystems. American Midland Naturalist 99:10–35.

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

Nuttall, T. R. 2013. Key to PA crayfishes. Lock Haven University, Lock Haven, Pennsylvania. (Available from: http://community .lhup.edu/tnuttall/crayfish%20key%20-%20couplet%201.htm)

R Development Core Team. 2008. R: a language and environment for statistical computing. Foundation for Statistical Computing, Vienna, Austria. (Available from: http://www.r-project.org/)

Rasband, W. S. 1997. ImageJ. US National Institutes of Health, Bethesda, Maryland.

Resh, V. H., A. V. Brown, A. P. Covich, M. E. Gurtz, H. W. Li, G. W. Minshall, S. R. Reice, A. L. Sheldon, J. B. Wallace, and R. C. Wissmar. 1988. The role of disturbance in stream ecology. Journal of the North American Benthological Society 7:433–455.

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. Biron, and A. G. Roy (editors). Gravel-bed rivers: processes, tools, environments. John Wiley and Sons, Chichester, UK.

Roth, B. M., J. C. Tetzlaff, M. L. Alexander, and J. F. Kitchell. 2007. Reciprocal relationships between exotic rusty crayfish, macrophytes, and *Lepomis* species in northern Wisconsin Lakes. Ecosystems 10:75–86.

Sanders, D., C. G. Jones, E. Thébault, T. J. Bouman, T. van der Heide, J. van Belzen, and S. Barot. 2014. Integrating ecosystem engineering and food webs. Oikos 123:513–524.

Savini, D., A. Occhipinti-Ambrogi, A. Marchini, E. Tricarico, F. Gherardi, S. Olenin, and S. Gollasch. 2010. The top 27 animal alien species introduced into Europe for aquaculture and related activities. Journal of Applied Ichthyology 26:1–7.

Schofield, K. A., C. M. Pringle, J. L. Meyer, and A. B. Sutherland. 2001. The importance of crayfish in the breakdown of rhododendron leaf litter. Freshwater Biology 46:1191–1204.

Smith, D. G. 1981. Life history parameters of the crayfish *Orconectes limosus* (Raf.) in southern New England. Ohio Journal of Science 81:169–172.

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

Statzner, B., E. Fièvet, J.-Y. Champagne, R. Morel, and E. Herouin. 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., and O. Peltret. 2006. Assessing potential abiotic and biotic complications of crayfish-induced gravel transport in experimental streams. Geomorphology 74:245–256.

Statzner, B., O. Peltret, and S. Tomanova. 2003. Crayfish as geomorphic agents and ecosystem engineers: effect of a biomass gradient on baseflow and flood-induced transport of gravel and sand in experimental streams. Freshwater Biology 48:147–163.

Statzner, B., and P. Sagnes. 2008. Crayfish and fish as bioturbators of streambed sediments: assessing joint effects of species with different mechanistic abilities. Geomorphology 93:267–287.

Swecker, C. D., T. D. Jones, J. V. Kilian, and L. F. Roberson. 2010. Key to the crayfish of Maryland. Maryland Department of Natural Resources, Annapolis, Maryland. (Available from: http://dnr .maryland.gov/streams/Documents/KeytotheCrayfishesofMD_8 _18_10.pdf)

Taylor, C. A., M. L. Warren Jr., J. F. Fitzpatrick Jr., H. H. Hobbs III, R. F. Jezerinac, W. L. Pflieger, and H. W. Robison. 1996. Conservation status of crayfishes of the United States and Canada. Fisheries 21:25–38.

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.

van der Zee, E. M., C. Angelini, L. L. Govers, M. J. Christianen, A. H. Altieri, K. J. van der Reijden, B. R. Silliman, J. van de Koppel, M. van der Geest, J. A. van Gils, H. W. van der Veer, T. Piersma, P. C. de Ruiter, H. Olff, and T. van der Heide. 2016. How habitat-modifying organisms structure the food web of two coastal ecosystems. Proceedings of the Royal Society of London Series B: Biological Sciences 283:20152326.

Viles, H. A. 1988. Biogeomorphology. Blackwell, Oxford, UK.

Viles, H. A., L. A. Naylor, N. E. A. Carter, and D. Chaput. 2008. Biogeomorphological disturbance regimes: progress in linking ecological and geormorphological systems. Earth Surface Processes and Landforms 33:1419–1435.

Wilson, K. A., J. J. Magnuson, D. M. Lodge, A. M. Hill, T. K. Kratz, W. L. Perry, and T. V. Willis. 2004. A long-term rusty crayfish (*Orconectes rusticus*) invasion: dispersal patterns and community change in a north temperate lake. Canadian Journal of Fisheries and Aquatic Sciences 61:2255–2266.

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.