Effects of invasive crayfish on fine sediment accumulation, gravel movement, and macroinvertebrate communities

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

[1]Stroud Water Research Center, 970 Spencer Road, Avondale, Pennsylvania 19311 USA

Abstract: Crayfish are one of the most prolific freshwater invaders, yet the role of crayfish as ecosystem engineers that structure benthic substrates in their nonnative habitat is rarely studied. We used an in situ experimental manipulation to document changes in sediment dynamics and macroinvertebrate density and richness caused by the presence or absence of invasive rusty crayfish (*Orconectes rusticus*). Rusty crayfish reduced fine-sediment accumulation and increased pit and mound structures in the river bed by moving gravels at the bed surface. We predicted that this omnivorous species would directly reduce macroinvertebrate density and richness, but we found that macroinvertebrate density was higher in treatments with rusty crayfish present and that macroinvertebrate richness did not differ between treatments with and without crayfish. Our findings suggest that rusty crayfish, which are spreading throughout the northeast USA, are probably important engineers of physical habitat structure in stream ecosystems. Rusty crayfish may also have unexpected, facilitative consequences for other benthic species by reducing fine-sediment accumulation in streams that are sediment impaired. Our study illustrates that biological forces can influence benthic gravel-size distributions and topography and suggests that crayfish may be important drivers of substrate-sorting dynamics and disturbance regimes, with consequences for community structure in streams where they are invasive.
Key words: ecosystem engineering, biophysical interactions, exotic, streams, sediment transport

Invasive species pose one of the world's most pressing environmental problems (Vitousek et al. 1997, Jenkins 2003). Invasions are occurring across a variety of habitats, but freshwater systems are particularly sensitive to invasion by nonnative species compared with their terrestrial counterparts (Ricciardi and Rasmussen 1999). For example, in freshwater ecosystems, invaders such as carp (Cyprinidae; Koehn 2004, Gozlan et al. 2010) and Zebra Mussels (*Dreissena polymorpha*; MacIsaac 1996) have dramatically influenced native species diversity, productivity, and ecosystem function (Strayer 2010). A significant amount of funding is allocated toward invasive control and reintroduction of natives because of substantial changes to natural habitats and the loss of ecosystem function attributed to invasive species in many instances (Bernhardt et al. 2005, Pimentel et al. 2005). However, the effects of invasive species on the structure of ecosystems in the growing number of urbanized and impaired streams are not well studied and may differ from effects in pristine systems (Ricciardi 2001, Smucker and Detenbeck 2014).

Many invaders are ecosystem engineers (Crooks 2002), which are organisms that affect abiotic features of ecosystems, including physical habitat characteristics and biogeochemical cycles (Jones et al. 1994, Jones 2012). In streams, animals can substantially alter habitat structure, sediment transport, and nutrient cycling (Moore 2006, Albertson and Allen 2015). Aquatic animals ranging from nutria to fishes to macroinvertebrates move gravels, alter riverbank formation, and make changes to bed topography. For example, fish can create divots as they build nests for egg protection, and insects can agitate fine sediments as they search for food (Zanetell and Peckarsky 1996, Moore et al. 2004). Biota can regulate substrate dynamics, including grain-size distributions, sediment erosion during floods, and fine-sediment suspension levels (Montgomery et al. 1996, Albertson et al. 2014, Harvey et al. 2014).

Crayfish are one of the most prolific groups of invaders across the globe (Lodge et al. 2000, 2012, Savini et al. 2010, Twardochleb et al. 2013). Invasive crayfish pose a particu-

larly significant threat to freshwater ecosystems because crayfish are ecosystem engineers of both aquatic community structure and physical habitat. Current evidence for the effects of crayfish on benthic communities suggests a significant reduction in macroinvertebrate, fish, and macrophyte density, shifts in macroinvertebrate and fish community composition, and an increase in the breakdown of detritus (Momot et al. 1978, Wilson et al. 2004, Bobeldyk and Lamberti 2008, 2010). Crayfish are bioturbators that also can engineer physical habitat by disrupting benthic sediments as they forage or build shelters (Parkyn et al. 1997, Statzner et al. 2003, Creed and Reed 2004). Disturbance by crayfish can loosen riverbed gravels, which subsequently increases sediment erosion during floods (Statzner et al. 2003, Statzner and Peltret 2006). The bioturbating activities of some crayfish species can be extensive and cause complete riverbank collapse (Guan 1994, Barbaresi et al. 2004), and the role of crayfish as agents of disturbance may have important consequences for biodiversity and benthic community recovery following high-flow events (Resh et al. 1988, Lake 2000). Crayfish also can alter fine-sediment dynamics (Harvey et al. 2014), which may influence feedbacks between sediment suspension, turbidity, and biofilm communities (Wood 1997, Lawler et al. 2006) and regulate suitable habitat for fish egg development (Suttle et al. 2004). In invasions of Europe by *Pacifastacus leniusculus* and *Procambarus clarkii*, crayfish altered aquatic communities and substantially affected gravel-bed morphology, erosion, and fine-sediment suspension (Barbaresi et al. 2004, Johnson et al. 2011, Harvey et al. 2014).

The rusty crayfish (*Orconectes rusticus*) is native to the Ohio River basin and has become invasive in the northeastern USA. Spread of the invasive rusty crayfish has been identified as a threat for >4 decades (Lodge et al. 2000, Wilson et al. 2004) and has significantly reduced native crayfish diversity (Taylor et al. 1996). *Orconectes rusticus* moved into southern Pennsylvania (PA), the location of our research, in the 1960s–1970s (Kuhlmann and Hazelton 2007, Lieb et al. 2011). It can outcompete native crayfish species, reduce macroinvertebrates and detritus (Lodge et al. 1986, Olden et al. 2006), cause shifts in fish populations (Roth and Kitchell 2005), and reduce standing stock of macrophytes (Roth et al. 2007).

Several studies now illustrate the strong physical-engineering role of invasive crayfishes, but despite its rapid spread, few investigators have explored the role of invasive *O. rusticus* in structuring benthic substrate dynamics. We conducted a field experiment to investigate the influence of rusty crayfish on benthic substrates and macroinvertebrate communities. We used an in situ manipulation of the presence or absence of *O. rusticus* to address the following questions: 1) Does *O. rusticus* change riverbed topography, sediment sorting, and fine-sediment accumulation? 2) How does *O. rusticus* influence macroinvertebrate communities? Our study provides some of the first evi-

dence of the physical effects of *O. rusticus* invasions on gravel disturbance and consequences for benthic communities and ecosystem processes.

METHODS
Study site

We conducted our study in Valley Creek (lat 40°04′N, long 75°27′W), situated in Valley Forge National Historic Park, King of Prussia, PA, from 24 October to 14 November 2014. Valley Creek is an urbanized, perennial 3rd-order tributary of the Schuylkill River. In autumn, it is ~10 m wide and 0.24 m deep. In the heavily populated Schuylkill River basin, 77% of streams are in fair or poor condition, and forest buffer zones have been reduced along many waterways (Jackson 2009). Valley Creek is classified as an impaired stream (VFNHP and PFBCCP 2004, Jackson 2009). Excessive sedimentation, excessive stormwater, polychlorinated biphenyl (PCB) contamination, and channel instability have been identified as primary drivers of impairment. The hydrologic regime is flashy. Base flows range from 0.28 m^3/s in autumn to 1.70 m^3/s in spring, interspersed with frequent flood events. Discharge averaged 0.57 m^3/s during the study period, and 2 moderate flow events peaked at 1.12 m^3/s on 1 November and 0.85 m^3/s on 6 November (US Geological Survey gage 01473169; Fig. 1). Rusty crayfish were first documented in Valley Creek in 2008 (http://www.nps.gov/kids/features /2014/crayfishCorps.cfm#). The National Park Service manages rusty crayfish populations in Valley Creek primarily by using an intensive, volunteer-based removal effort called the Crayfish Corps.
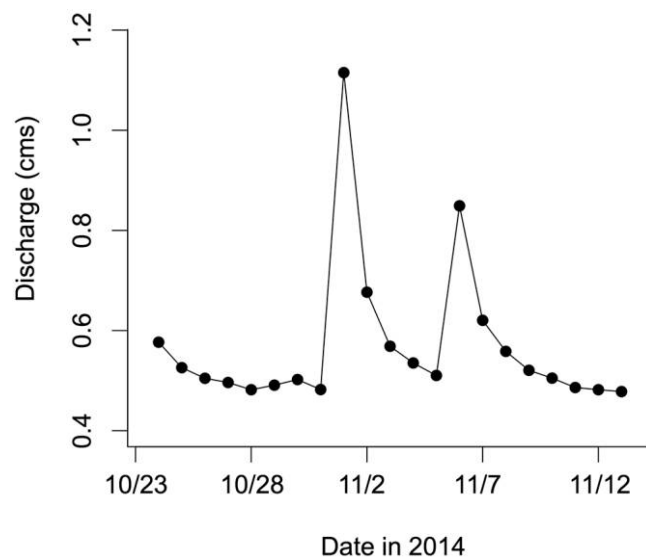

Figure 1. Discharge in Valley Creek during the study period. Over the course of the experiment, discharge averaged 0.57 m^3/s (cms). Closed circles indicate mean discharge per day.

Experimental design

The experiment contained 2 treatments: crayfish present or absent (control). We ran the experiment as a complete block design in which 4 replicates of each treatment were run in 2 consecutive temporal blocks for a total of $n = 8$ for each treatment. We placed 2 wire-mesh (100-mm^2 opening) enclosures (0.41 m long × 0.31 m wide × 0.41 m high) within 0.5 m of each other at the downstream end of each of 4 riffles (= replicates). We selected cage locations that were similar in physical condition; velocity averaged 0.3 m/s. We secured cages to rebar and made them flush with the surrounding substrate. Cages were oriented so that width was perpendicular and length parallel to the direction of flow. Leaves and other small debris accumulated on the front of each cage, but we allowed the debris to remain for the duration of each temporal block. We filled cages with gravel mined from the river bed nearby. At the start of each block, we scrubbed gravel clean and passed it through sieves to create 2 heterogeneous gravel mixtures of grain diameters between 5.6 and 11 mm or 22 and 31 mm. We carefully placed a layer of subsurface gravel (5.6–11 mm) in the bottom of each enclosure, graded it smooth by hand, and then covered it by a layer of surface gravel (22–31 mm) to represent an armored surface layer typical of gravel-bedded rivers (Dietrich et al. 1989).

The crayfish-present treatment contained 3 crayfish that were selected to be similar in size (25-mm carapace length). Crayfish density within the mesh enclosure was 24/m^2, which is on the high end but in the range of densities reported for this species (Momot et al. 1978, Hill and Lodge 1999). The control treatment was identical but contained no crayfish. Each block ran for 2 wk, after which we fully disturbed and cleaned sediments to remove any macroinvertebrates. After the 1st block, we resieved and graded the sediments smooth to reset for the 2nd block. All crayfish survived for the duration of the experiment.

Measurement of the abiotic response

We took photographs of each replicate crayfish cage with a GoPro Hero 3+ Silver (GoPro, Riverside, California) at the start and end of each block to estimate changes in the gravel-bed matrix. We analyzed photos in the laboratory with ImageJ (Rasband 1997) to calculate the proportion of the total surface area of the bottom of each cage where surface gravels had been moved to expose subsurface material or the bottom of the cage. To estimate fine-sediment accumulation in the benthos, we measured total suspended solids (TSS) in a subset of enclosures ($n = 3$ control cages and $n = 4$ crayfish cages) during block 2. At the end of block 2, we enclosed each cage with a modified Hess sampler (0.6 m × 0.4 m × 0.5 m), vigorously disturbed all gravels by hand, and collected a 1-L water sample. For the purposes of this experiment, measures of agitated TSS served as a proxy for benthic sediment accumulation. We processed water sam-

ples in the laboratory by filtering a known volume of well-mixed sample through a 0.45-μm mixed cellulose ester membrane, drying the sample at 60°C for 24 h, and weighing the sample to estimate g/L.

Measurement of the biotic response

At the end of each 2-wk block, we used the same Hess sampler to isolate each cage and sample macroinvertebrates (Hauer and Lamberti 2007). We dislodged macroinvertebrates from surface gravels by hand and swept them into a mesh (500-μm) drift net secured to a solid frame. This sampling technique ensured that any collected invertebrates were from the enclosure. To compare macroinvertebrate communities and abundances in the experiment to ambient conditions in Valley Creek, we used Surber samplers on 30 October 2015 to collect macroinvertebrates in $n = 2$ riffles at the study site. Because of permitting restrictions, we kept all macroinvertebrates alive during all macroinvertebrate sampling efforts and enumerated them on site. We identified insects >500 μm to family to estimate taxon richness (count of all families/sample) and density (number of individuals/m^2; Merritt et al. 2008) and returned macroinvertebrates to the stream.

Data analyses

We compared TSS levels across crayfish and control treatments with a mixed model in which TSS was a function of the fixed effect of crayfish treatment and the random effect of riffle location. We compared changes in bed topography across crayfish treatments by means of linear mixed effects models in which density of pit structures or proportion of river bed with subsurface exposed was a function of the fixed effect of crayfish treatment and random effects of replicate nested within block and of riffle location. We compared macroinvertebrate density and diversity by means of mixed models in which density or richness was a function of the fixed effect of crayfish treatment and the random effect of replicate nested within block and of riffle location. Shannon–Wiener diversity index (H) was calculated as:

$$H = -\Sigma P_i \ln P_i, \qquad \text{(Eq. 1)}$$

where P_i is the number of the ith species divided by the total number of individuals counted. In studies conducted in the field, high variation among sampling replicates is often expected. Thus, we accepted $p \leq 0.1$ as a marginally significant effect. All analyses were conducted using R (version 3.1.0; R Project for Statistical Computing, Vienna, Austria).

RESULTS

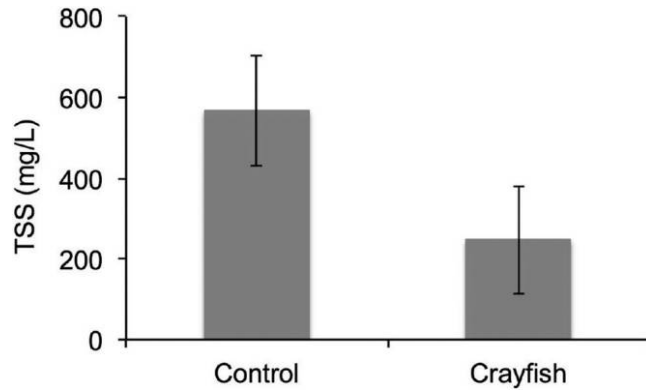TSS levels were consistently lower in sediment patches with crayfish present than in controls, suggesting that cray-

Figure 2. Mean (±1 SE) total suspended solids (TSS) from enclosures with and without crayfish at the end of the second 2-wk temporal block. $n = 3$ control cages (no crayfish) and $n = 4$ crayfish cages.

fish activity increased suspension and reduced settling of fine sediments ($t = -2.7$, $p = 0.1$; Fig. 2). Comparison of photographs of control and crayfish cages before and after each 2-wk block showed substantial amounts of fine-sediment material covering the benthos in control cages without crayfish (Fig. 3A–D). We found evidence of gravel movement in the control treatments resulting from small changes in base flow during the sampling period, but after 2 wk the number of pit and depression structures was significantly higher in treatments with crayfish present than in controls ($t = 8.5$, $p < 0.001$; Fig. 4A). Crayfish activity also exposed a significantly greater amount of subsurface material composed of the smaller grain-size class than was exposed in control treatments ($t = 5.0$, $p < 0.001$; Fig. 4B).

Crayfish activity significantly affected macroinvertebrate communities, but not in the direction predicted. Macroinvertebrate density was significantly higher in crayfish treatments than in controls ($t = 2.4$, $p = 0.04$; Fig. 5A). Species richness did not differ between treatments ($t = 1.0$, $p = 0.35$; Fig. 5B). Hydropsychid caddisfly larvae (Hydropsychidae) and amphipods (Gammaridae) were the most common macroinvertebrates sampled across all treatments, and the Shannon–Wiener diversity index was similar between the crayfish and control treatments ($H = 1.57$ and 1.59, respectively). Macroinvertebrate density was lower in the experimental enclosures (crayfish present and absent)
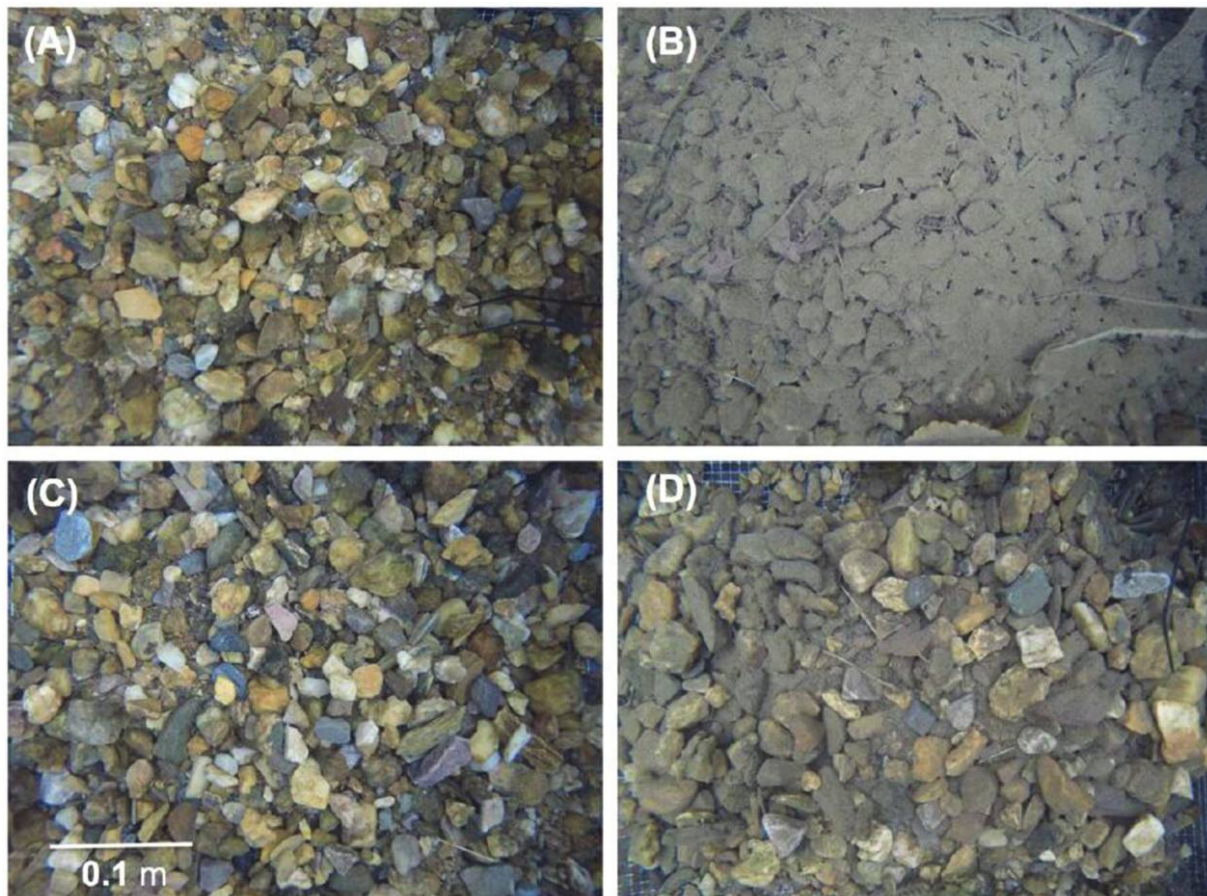

Figure 3. A control enclosure at the start (A) and end (B) of a 2-wk experiment, and a crayfish cage at the start (C) and end (D) of a 2-wk experiment.
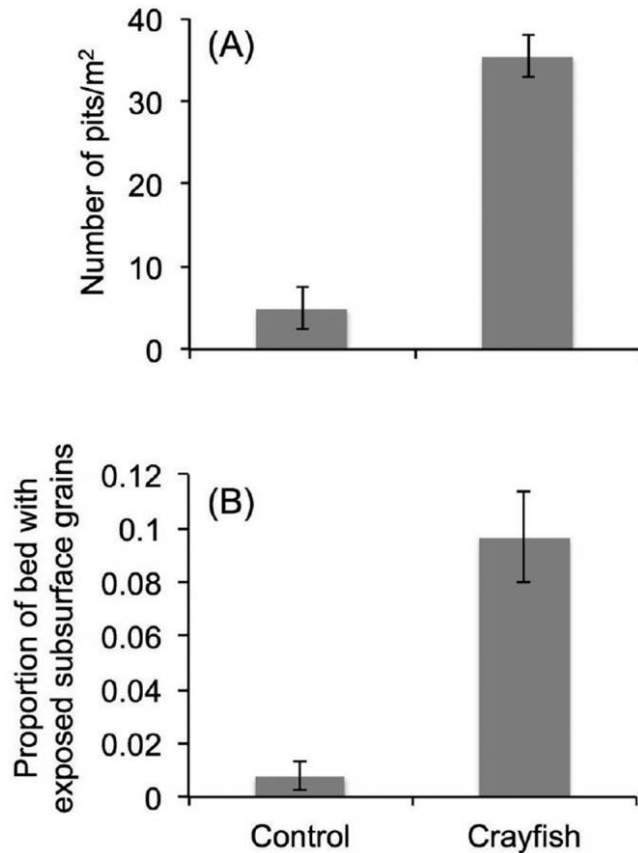
Figure 4. A.—Mean (±1 SE) density of pit structures in the gravel bed in treatments with and without crayfish present. B.—Mean (±1 SE) proportion of bed with exposed subsurface grains. $n = 8$.

than the ambient macroinvertebrate density in Valley Creek (Table 1).

DISCUSSION

We have shown that the rusty crayfish, an invasive species spreading throughout the northeastern USA, can influence substrate dynamics, with potential cascading effects for aquatic communities. Our results illustrate that rusty crayfish activity can suspend benthic sediments, reduce fine-sediment accumulation, and increase pit and mound morphology within the river bed. Our results further reveal an increase in macroinvertebrate abundance in the presence of rusty crayfish. These findings emphasize the need to understand better the invasion ecology of crayfish because their engineering effects on the physical habitat of streams may be more widespread than previously documented.

In support of findings for other crayfish species, we found a substantial change in sediment dynamics when rusty crayfish were present. *Orconectes rusticus* altered bed topography similarly to other species for which de-

tailed measurements of physical substrate dynamics have been monitored. Crayfish are often associated with gravel and cobble substrate that provides shelter and refuge from predators, and crayfish disturb both fine sediments and gravels (Kershner and Lodge 1995, Statzner et al. 2003, Johnson et al. 2011, Harvey et al. 2014, Magoulick 2014). Changes to grain sorting and movement initiated by crayfish activity have important implications for erosion regimes. Gravel arrangement can influence grain protrusion and friction angles that control when grains move downstream (Buffington and Montgomery 1999). Grain orientation can regulate critical shear stress and initial movement during floods (Carling et al. 1992). In addition, changes in grain-size distributions associated with the movement of finer, subsurface gravels toward the surface are likely to increase bed-material movement during high flows (Church 2006). Selective removal of fine silt from the gravel matrix can produce infilling of downstream pool volume (Lisle and Hilton 1999), and alteration of the fine component of a gravel matrix also can influence gravel movement (Curran and Wilcock 2005). Although a growing number of studies illustrate the effects of crayfish on substrate-sorting dynamics, many of these studies, including ours, have been conducted in laboratory flumes or in small spatial patches that lack the complexity and heterogeneity of natural streams. For example, our enclosures did not con-
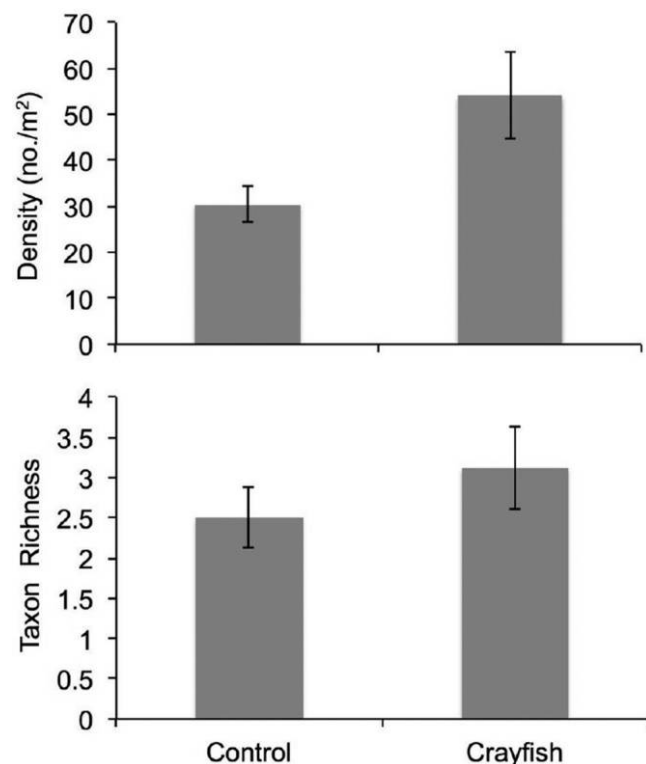

Figure 5. Mean (±1 SE) macroinvertebrate density (A) and taxon richness (B) in crayfish and control treatments. $n = 8$.

Table 1. Macroinvertebrate density in Valley Creek and experimental enclosures. Density in Valley Creek was estimated on 30 October 2015 during the first 2-wk experimental block for $n = 2$ riffles. Density in the experimental treatments was estimated across 4 replicates and 2 temporal blocks for $n = 8$. Values for total macroinvertebrate density are mean ±1 SE.

| | | Experiment | |
| | Valley Creek (no./m^2) | Crayfish enclosure (no./m^2) | Control enclosure (no./m^2) |
Taxon and total			
Baetidae	11	3	3
Chironomidae	11	5	4
Dugesiidae	6	6	2
Gammaridae	150	16	7
Hydrachnidiae	6	0	1
Hydropsychidae	278	22	13
Rhyacophilidae	0	1	1
Simulidae	0	1	0
Tubificidae	6	1	0
Total	462 ± 161	54 ± 9	31 ± 4

tain larger gravels that provide shelter space for the crayfish, a factor that could be considered in future studies because shelter may alter crayfish engineering effects and change behavioral interactions between individual crayfish (Statzner and Peltret 2006). As such, our findings are limited but suggest the need for additional research linking invasion ecology and geomorphology at larger field scales (Reinhardt et al. 2010).

We found that macroinvertebrates were more abundant in treatments with rusty crayfish present than in controls. A large portion of crayfish diets consists of detritus and plant material, but many investigators have shown that crayfish directly reduce the abundance of their macroinvertebrate prey across a variety of habitat types, including lakes and streams, and across a variety of substrates, including rocks and leaves (Momot et al. 1978, Bobeldyk and Lamberti 2010, Twardochleb et al. 2013). However, some evidence suggests that crayfish control of macroinvertebrates is taxon specific. For example, Lodge et al. (1994) found that in sandy-bottomed lakes, *O. rusticus* reduced snail macroinvertebrate abundance by 99% but had minimal influence on other macroinvertebrate taxa. We hypothesize that effects of rusty crayfish on gravel movement and the removal of fine sediments is context dependent and particular to food availability, substrate size, and substrate heterogeneity. In our experiment, the indirect, facilitative effect of removing fine sediment may have improved habitat for macroinvertebrates that are sensitive to sediment accumulation (Richards and Bacon 1994, Wood 1997). Overall macroinvertebrate colonization

in the experiment was lower in both experimental treatments than natural, ambient macroinvertebrate densities in Valley Creek, suggesting that colonization of the enclosures may have been limited, potentially because of the short time scale of our study. Nevertheless, colonization was higher in treatments with rusty crayfish than in control treatments. If rusty crayfish shift macroinvertebrate communities by increasing their abundance, these effects may cascade to other trophic levels. For example, the direct effects of crayfish on biofilm may be minimal (Bobeldyk and Lamberti 2008, Magoulick 2014), but indirect effects on biofilm biomass in response to shifts in the invertebrate grazer community that result from crayfish activity have been suggested (Charlebois and Lamberti 1996). Future researchers might investigate links among crayfish, fine sediment, grazers, and biofilm productivity.

Rusty crayfish can outcompete and eliminate native crayfish species (Hill and Lodge 1999, Wilson et al. 2004), and the consequences of native biodiversity loss for ecosystem functioning are wide reaching (Hooper et al. 2005). Several behaviors probably drive competition between invasive rusty crayfish and native crayfish. For example, crayfish often display aggressive, territorial behaviors as they compete for food or protect young (Capelli and Munjal 1982), and rusty crayfish are known to be more efficient predators of fish eggs than their native counterparts (Sargent et al. 2013). Except for limitations imposed by streams and lakes with low pH or low Ca, rusty crayfish have been moving rapidly throughout the midwestern and northeastern USA, and native crayfish have been declining as a result (Olden et al. 2006). In PA, shifts in crayfish species distributions associated with rusty crayfish invasion have been documented, but the mechanisms driving these shifts and the physical constraints on rusty crayfish invasion (e.g., substrate size, pH) have yet to be identified (Lieb et al. 2011). In a 2003–2006 survey in northern PA, the historically numerically dominant *Orconectes limosus* constituted only 2.4% of the crayfish assemblage, whereas *O. rusticus* was the most commonly collected crayfish and constituted 37% of the assemblage. In southern PA sites where *O. rusticus* has not yet invaded, *O. limosus* constituted 52% of the crayfish assemblage during the same survey. Although *O. limosus*, which is native to our study system, can also alter gravel-bed topography (Statzner et al. 2000, 2003), we hypothesize that the larger body mass, faster growth rate, and higher density achieved by the rusty crayfish, which has been documented in other systems with multiple species of crayfish present (Hill and Lodge 1999, Wilson et al. 2004), may make it a more effective engineer of stream substrate (Albertson and Allen 2015), producing increased rates and depths of substrate disturbance, increased baseflow fine-sediment transport rates, and decreased embeddedness of gravels. Direct comparisons between rusty crayfish and the abundant and widely distributed mid-Atlantic native spiny

cheek (*Orconectes limosus*) and Appalachian Brook crayfish (*Cambarus bartonii*) are an important next step for research.

Our cage enclosures isolated the effects of crayfish and excluded other relatively large organisms known to disrupt benthic substrates. Fish, in particular, are important substrate engineers that were excluded from our cages but can influence grain-size distributions and entrainment by building redds for eggs or by foraging for food (Flecker 1996, Moore et al. 2004, Hassan et al. 2008). Statzner and Sagnes (2008) found that crayfish and fish both influence gravel transport and bed surface characteristics when alone, but their effects when together in polyculture were less than expected given their effects in monoculture. The joint influence of multiple coexisting and interacting animals is relatively understudied. As a growing body of research highlights the importance of species traits and mechanistic abilities in regulating the magnitude of ecosystem engineering effects on physical habitat conditions, understanding the relative effect of native vs invasive species, body size, mechanistic activity (e.g., burrowing vs foraging), and competitive fitness will be important directions for future research (Hughes and Stachowicz 2004, Albertson et al. 2014, Allen et al. 2014).

The relative roles of competitive dominance and environmental degradation in controlling the effects of invasive crayfish also deserve further attention (MacDougall and Turkington 2005, Light and Marchetti 2007). Many streams in the northeastern USA are impaired (Bernhardt et al. 2005), and most invasions are occurring in already highly disturbed ecosystems (Hobbs and Huenneke 1992, Strayer 2010, Früh et al. 2012). The positive, indirect influence that we detected of crayfish on macroinvertebrates, possibly mediated by a reduction in fine sediment in the substrate, was unexpected but highlights the need for a better understanding of invasive species in impaired systems (Ricciardi 2001, Tablado et al. 2010). Invasive species may be beneficial in some impaired ecosystems, but the small sample size of our study does not allow us to make management recommendations. Future work might address whether crayfish engineers help ameliorate habitat degradation associated with high fine-sediment loads in urbanized streams. Some researchers have suggested that habitat degradation combined with species invasion is a more likely driver of ecological change than are invasive dominants alone (Didham et al. 2005). Given the large amount of funding that is allocated to river restoration, including removal of invasive crayfish (Gherardi et al. 2013, Rogowski et al. 2013), a better understanding of invasions may help improve restoration designs that have been only minimally successful (Stranko et al. 2012, Smucker and Detenbeck 2014). In freshwater ecosystems, both species invasion and increased sediment loads because of land-use change have been identified as significant impairment

factors (Richter et al. 1997), and future investigators should consider crayfish invasion, crayfish removal, and ecosystem function in the context of many streams' modern, impaired status.

Authors of a growing number of synthesis papers have emphasized the strong effect that biology can have on physical habitat conditions in streams (Jones 2012, Statzner 2012). Rusty crayfish engineering effects provide further evidence that biology can alter substrate dynamics. The importance of invasive ecosystem engineers is recognized (Crooks 2002). However, the role of *O. rusticus* engineers in structuring benthic substrate dynamics is poorly documented but may play a critical role in guiding the management of degraded, sediment-impaired streams where these crayfish are invasive. Including invasive species across stream impairment gradients will be an important next step in studies that incorporate the complexity of ecological dynamics into models of sediment transport.

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., B. J. Cardinale, and L. S. Sklar. 2014. Species interactions generate non-additive increases in sediment stability in laboratory streams. PloS ONE 9:e103417.

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

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

Bernhardt, E. S., M. A. Palmer, J. Allan, G. Alexander, K. Barnas, S. Brooks, J. Carr, S. Clayton, C. Dahm, J. Follstad-Shah, D. Galat, S. Gloss, P. Goodwin, D. Hart, B. Hassett, R. Jenkinson, S. Katz, G. M. Kondolf, P. S. Lake, R. Lave, J. L. Meyer, T. K. O'Donnell, L. Pagano, B. Powell, and E. Sudduth. 2005. Synthesizing U.S. river restoration efforts. Science 308: 636–637.

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

Buffington, J. M., and D. R. Montgomery. 1999. Effects of hydraulic roughness on surface textures of gravel-bed rivers. Water Resources Research 35:3507–3521.

Capelli, G. M., and B. L. Munjal. 1982. Aggressive interactions and resource competition in relation to species displacement among crayfish of the genus *Orconectes.* Journal of Crustacean Biology 2:486–492.

Carling, P., A. Kelsey, and M. Glaister. 1992. Effect of bed roughness, particle shape and orientation on initial motion criteria. Pages 23–29 *in* P. Billi, R. Hey, C. Thorne, and P. Tacconi (editors). Dynamics of gravel-bed rivers. John Wiley and Sons, Chichester, UK.

Charlebois, P., and G. Lamberti. 1996. Invading crayfish in a Michigan stream: direct and indirect effects on periphyton and macroinvertebrates. Journal of the North American Benthological Society 15:551–563.

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

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.

Crooks, J. A. 2002. Characterizing ecosystem-level consequences of biological invasions: the role of ecosystem engineers. Oikos 97:153–166.

Curran, J. C., and P. R. Wilcock. 2005. Effect of sand supply on transport rates in a gravel-bed channel. Journal of Hydraulic Engineering 131:961–967.

Didham, R. K., J. M. Tylianakis, M. A. Hutchison, R. M. Ewers, and N. J. Gemmell. 2005. Are invasive species the drivers of ecological change? Trends in Ecology and Evolution 20: 470–474.

Dietrich, W., J. Kirchner, H. Ikeda, and F. Iseya. 1989. Sediment supply and the development of the coarse surface-layer in gravel-bedded rivers. Nature 340:215–217.

Flecker, A. 1996. Ecosystem engineering by a dominant detritivore in a diverse tropical ecosystem. Ecology 77:1845–1854.

Früh, D., S. Stoll, and P. Haase. 2012. Physicochemical and morphological degradation of stream and river habitats increases invasion risk. Biological Invasions 14:2243–2253.

Gherardi, F., L. Aquiloni, J. Diéguez-Uribeondo, and E. Tricarico. 2013. Managing invasive crayfish: is there hope? Aquatic Sciences 73:185–200.

Gozlan, R. E., J. R. Britton, I. Cowx, and G. H. Copp. 2010. Current knowledge on nonnative freshwater fish introductions. Journal of Fish Biology 76:751–786.

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

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.

Hassan, M. A., A. S. Gottesfeld, D. R. Montgomery, J. F. Tunnicliffe, G. K. C. Clarke, G. Wynn, H. Jones-Cox, R. Poirier, E. MacIsaac, H. Herunter, and S. J. Macdonald. 2008. Salmon-driven bed load transport and bed morphology in mountain streams. Geophysical Research Letters 35:L04405.

Hauer, F. R., and G. A. Lamberti. 2007. Methods in stream ecology. Elsevier, Burlington, Massachusetts.

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

Hobbs, R. J., and L. F. Huenneke. 1992. Disturbance, diversity, and invasion: implications for conservation. Conservation Biology 6:324–337.

Hooper, D. U., F. S. Chapin, J. J. Ewel, A. Hector, P. Inchausti, S. Lavorel, J. H. Lawton, D. M. Lodge, M. Loreau, S. Naeem, B. Schmid, H. Setala, A. J. Symstad, J. Vandermeer, and D. A. Wardle. 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. Ecological Monographs 75:3–35.

Hughes, A. R., and J. J. Stachowicz. 2004. Genetic diversity enhances the resistance of a seagrass ecosystem to disturbance. Proceedings of the National Academy of Sciences of the United States of America 101:8998–9002.

Jackson, J. 2009. Understanding stream conditions: lessons from an 11-year study of macroinvertebrates in eastern Pennsylvania's Schuylkill River watershed, with a focus on exceptional-value and high-quality streams. Stroud Water Resource Center, Avondale, Pennsylvania. (Available from: http://www.stroud center.org/schuylkill/Schuylkill_Summary.pdf)

Jenkins, M. 2003. Prospects for biodiversity. Science 302:1175–1177.

Johnson, M., S. 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.

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. Oikos 69:373–386.

Kershner, M. W., and D. M. Lodge. 1995. Effects of littoral habitat and fish predation on the distribution of an exotic crayfish, *Orconectes rusticus*. Journal of the North American Benthological Society 14:414–422.

Koehn, J. D. 2004. Carp (*Cyprinus carpio*) as a powerful invader in Australian waterways. Freshwater Biology 49:882–894.

Kuhlmann, M., and P. 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.

Lawler, D. M., G. E. Petts, I. D. L. Foster, and S. Harper. 2006. Turbidity dynamics during spring storm events in an urban headwater river system: the Upper Tame, West Midlands, UK. Science of the Total Environment 360:109–126.

Lieb, D., R. Bouchard, and R. Carline. 2011. Crayfish fauna of southeastern Pennsylvania: distributions, ecology, and changes over the last century. Journal of Crustacean Biology 31:166–178.

Light, T., and M. P. Marchetti. 2007. Distinguishing between invasions and habitat changes as drivers of diversity loss among California's freshwater fishes. Conservation Biology 21:434–446.

Lisle, T., and S. Hilton. 1999. Fine bed material in pools of natural gravel bed channels. Water Resources Research 35:1291–1304.

Lodge, D. M., A. D. 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.

Lodge, D. M., M. Kershner, J. Aloi, and A. P. Covich. 1994. Effects of an omnivorous crayfish (*Orconectes rusticus*) on a freshwater food web. Ecology 75:1265–1281.

Lodge, D. M., T. K. Kratz, and G. M. Capelli. 1986. Long-term dynamics of three crayfish species in Trout Lake, Wisconsin. Canadian Journal of Fisheries and Aquatic Sciences 43:993–998.

Lodge, D. M., C. Taylor, D. Holdich, and J. Skurdal. 2000. Non-indigenous crayfishes threaten North American freshwater biodiversity: lessons from Europe. Fisheries 25(8):7–19.

MacDougall, A. S., and R. Turkington. 2005. Are invasive species the drivers or passengers of change in degraded ecosystems? Ecology 86:42–55.

MacIsaac, H. 1996. Potential abiotic and biotic impacts of zebra mussels on the inland waters of North America. American Zoologist 36:287–299.

Magoulick, D. D. 2014. Impacts of drought and crayfish invasion on stream ecosystem structure and function. River Research and Applications 30:1309–1317.

Merritt, R. W., K. W. Cummins, and M. B. Berg. 2008. An introduction to the aquatic insects of North America. 4th edition. Kendall/Hunt, Dubuque, Iowa.

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.

Montgomery, D., J. Buffington, N. Peterson, D. Schuett-Hames, and T. Quinn. 1996. Stream-bed scour, egg burial depths, and the influence of salmonid spawning on bed surface mobility and embryo survival. Canadian Journal of Fisheries and Aquatic Sciences 53:1061–1070.

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

Moore, J. W., D. E. Schindler, and M. D. Scheuerell. 2004. Disturbance of freshwater habitats by anadromous salmon in Alaska. Oecologia (Berlin) 139:298–308.

Olden, J., J. McCarthy, J. Maxted, W. Fetzer, and M. Vander Zanden. 2006. The rapid spread of rusty crayfish (*Orconectes rusticus*) with observations on native crayfish declines in Wisconsin (U.S.A.) over the past 130 years. Biological Invasions 8:1621–1628.

Parkyn, S., C. Rabeni, and K. Collier. 1997. Effects of crayfish (*Paranephrops planifrons*: Parastacidae) on in-stream processes and benthic faunas: a density manipulation experiment. New Zealand Journal of Marine and Freshwater Research 31:685–692.

Pimentel, D., R. Zuniga, and D. Morrison. 2005. Update on the environmental and economic costs associated with alien-invasive species in the United States. Ecological Economics 52:273–288.

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

Reinhardt, L., D. Jerolmack, B. J. Cardinale, V. Vanacker, and J. Wright. 2010. Dynamic interactions of life and its landscape: feedbacks at the interface of geomorphology and ecology. Earth Surface Processes and Landforms 35:78–101.

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.

Ricciardi, A. 2001. Facilitative interactions among aquatic invaders: is an "invasional meltdown" occurring in the Great Lakes? Canadian Journal of Fisheries and Aquatic Sciences 58:2513–2525.

Ricciardi, A., and J. Rasmussen. 1999. Extinction rates of North American freshwater fauna. Conservation Biology 13:1220–1222.

Richards, C., and K. Bacon. 1994. Influence of fine sediment on macroinvertebrate colonization of surface and hyporheic stream substrates. Great Basin Naturalist 54:106–113.

Richter B., D. Braun, M. Mendelson, and L. Master. 1997. Threats to imperiled freshwater fauna. Conservation Biology 11:1081–1093.

Rogowski, D. L., S. Sitko, and S. A. Bonar. 2013. Optimising control of invasive crayfish using life-history information. Freshwater Biology 58:1279–1291.

Roth, B., and J. Kitchell. 2005. The role of size-selective predation in the displacement of *Orconectes* crayfishes following rusty crayfish invasion. Crustaceana 78:297–310.

Roth, B., J. Tetzlaff, M. Alexander, and J. Kitchell. 2007. Reciprocal relationships between exotic rusty crayfish, macrophytes, and *Lepomis* species in northern Wisconsin Lakes. Ecosystems 10:74–85.

Sargent, L. W., J. W. Morse, and A. K. Baldridge. 2013. Invasive crayfish *Orconectes rusticus* (Decapoda, Cambaridae) is a more effective predator of substrate nesting fish eggs than native crayfish (*O. virilis*). Crustaceana 86:387–402.

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(Supplement s2):1–7.

Smucker, N. J., and N. E. Detenbeck. 2014. Meta-analysis of lost ecosystem attributes in urban streams and the effectiveness of out-of-channel management practices. Restoration Ecology 22:741–748.

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

Statzner, B., E. Fiévet, J. 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.

Stranko, S. A., R. H. Hilderbrand, and M. A. Palmer. 2012. Comparing the fish and benthic macroinvertebrate diversity of restored urban streams to reference streams. Restoration Ecology 20:747–755.

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

Suttle, K. B., M. E. Power, J. M. Levine, and C. McNeely. 2004. How fine sediment in riverbeds impairs growth and survival of juvenile salmonids. Ecological Applications 14:969–974.

Tablado, Z., J. L. Tella, J. A. Sánchez-Zapata, and F. Hiraldo. 2010. The paradox of the long-term positive effects of a North American crayfish on a European community of predators. Conservation Biology 24:1230–1238.

Taylor, C. A., M. L. Warren, J. F. Fitzpatrick, H. H. Hobbs, R. F. Jezerinac, W. L. Pflieger, and H. W. Robinson. 1996. Conservation status of crayfishes of the United States and Canada. Fisheries 21(4):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.

VFNHP and PFBCCP (Valley Forge National Historic Park and Pennsylvania Fish and Boat Commission of the Commonwealth of Pennsylvania). 2004. Valley Creek Restoration Plan. Valley Forge National Historic Park, Valley Forge, Pennsylvania, and Pennsylvania Fish and Boat Commission of the Commonwealth of Pennsylvania, Belleforte, Pennsylvania. (Available from: http://fishandboat.com/images /exec/env_ser/valleycreek/final.pdf)

Vitousek, P. M., C. M. D'Antonio, L. L. Loope, M. Rejmanek, and R. Westbrooks. 1997. Introduced species: a significant component of human-caused global change. New Zealand Journal of Ecology 21:1–16.

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.

Wood, P. J. 1997. Biological effects of fine sediment in the lotic environment. Environmental Management 21:203–217.

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