Does stream current modify crayfish impacts on a benthic community?

Todd Wellnitz, Drew Frase, Margaret Gapinski and Hayley Emerson Haggerty

Biology Department, University of Wisconsin - Eau Claire, Eau Claire, WI, USA

ABSTRACT
Non-native crayfish can have impacts on stream communities that are highly variable. A possible explanation for this variability is that crayfish are responding in a context-dependent manner to variation in environmental factors. Among the most critical environmental factors in streams is current velocity. Moving water defines lotic ecosystems and many benthic organisms, including crayfish, respond to its influence. To examine how current velocity affected the impacts of non-native Orconectes rusticus crayfish on benthic communities, we conducted a cage-enclosure experiment in a Wisconsin stream. We hypothesized that current velocities > 50 cm s\(^{-1}\) would decrease the effects that O. rusticus had on community composition (macroinvertebrate richness and numbers) and physical structure (sediment accumulation). Three cage enclosure treatments (open, closed crayfish and closed control) were grouped into eight replicate blocks divided equally among streambed regions of slow (< 50 cm s\(^{-1}\)) and fast (> 50 cm s\(^{-1}\)) current. Open cages allowed resident crayfish access, closed crayfish cages contained one O. rusticus, and closed controls had no crayfish. After three weeks, crayfish cages had lower macroinvertebrate abundance and richness and less sediment accumulation. Current velocity showed a positive relationship to macroinvertebrates in general, and a negative relationship to sediment build-up. The most common macroinvertebrates were hydropsychid caddisflies that responded to O. rusticus in a context-dependent manner such that cages containing crayfish had decreased hydropsychid numbers in fast current, but not in slow. Open cage treatments showed a similar pattern, suggesting that natural crayfish densities in the stream were also sufficient for lowering hydropsychid numbers in fast current. Our study demonstrates that current velocity may provide an important context for understanding the effects that O. rusticus have on benthic communities, not just in terms of what these crayfish do, but how the benthic communities respond to their presence.
Introduction

There is a considerable body of literature documenting the impacts crayfish, especially non-native crayfish, have on stream communities (see reviews by Phillips et al. 2009, Twardochleb et al. 2013). These impacts often have far-reaching consequences for stream structure and function and this had led many authors to classify crayfish as ecosystem engineers (Statzner et al. 2003, Hansen et al. 2013, Jackson et al. 2014), or alternatively, keystone consumers (Creed 1994, Lodge et al. 1994, Weinlander and Fureder 2016). As ecosystem engineers, crayfish foraging and burrowing can rearrange streambed substrates, affect bed topography, and influence gravel transport and sediment accumulation (Parkyn et al. 1997, Statzner et al. 2000, Statzner et al. 2003, Statzner and Sagnes 2008, Johnson et al. 2011, Albertson and Daniels 2016, 2018). As keystone consumers, omnivorous crayfish can have wide-ranging effects on lotic food webs by preying upon or competitively displacing benthic organisms (Charlebois and Lamberti 1996, Parkyn et al. 1997, Creed and Reed 2004, Bobeldyk and Lamberti 2010, Westhoff and Rabeni 2013) and by decoupling trophic cascades (Usio 2000, Jackson et al. 2014). Crayfish may also directly or indirectly affect the abundance of periphyton and algae (Hart 1992, Creed 1994, Moore et al. 2012), increase litter breakdown rates (Huryn and Wallace 1987, Schofield et al. 2001, Creed and Reed 2004, Zhang et al. 2004), and have negative effects on fish and amphibians (Dorn and Mittelbach 1999, Ilhêu et al. 2007).

The extent to which these impacts occur can vary among species and across habitats (Flinders and Magoulick 2003, Phillips et al. 2009, Larson and Olden 2010, Lodge et al. 2012, Jackson et al. 2014, Weinlander and Fureder 2016), and this is certainly true when comparing native and non-native species (Twardochleb et al. 2013, James et al. 2015). In their meta-analyses examining the ecological impacts of non-native crayfish on aquatic ecosystems worldwide, Twardochleb et al. (2013) found that non-natives generally had greater and more negative effects than did native species on stream communities. They also noted that non-natives had more variable effects on ecological parameters. Significantly, Twardochleb et al. (2013) found that differences among species were insufficient for explaining this variability and suggested that ‘extrinsic factors’ (e.g. available food resources) may be more important than species identity for determining disparities in ecological effects.

Another possible explanation for the observed discrepancies could be that crayfish in general, and non-native species in particular, are responding to variation in environmental factors (Flinders and Magoulick 2007, Jackson et al. 2017). Like many aquatic organisms, crayfish are subject to factors such as current velocity (Clark et al. 2008, Perry and Jones 2018), temperature (Gherardi et al. 2013, Johnson et al. 2014, Stoffels et al. 2016), substrate type (Adams and Marks 2016) and salinity (Bazer et al. 2016), among others. These factors all have the potential to affect crayfish physiology, behavior and performance (Dunson and Travis 1991), and this can have consequences for the ecological roles that crayfish play (Wellnitz and Poff 2001). For example, the ability of crayfish to effectively prey on benthic macroinvertebrates is partially dependent on their ability to navigate streambeds, and streambeds are subject to a wide range of flows and current velocities. It is easy to imagine that slower velocities would allow for greater manoeuvrability and more effective predation, whereas faster velocities might constrain movement and decrease predation. This being the case, crayfish impacts on benthic invertebrates could be considered ‘context-dependent’, and this may help explain the variable effects crayfish have on the stream communities and ecosystems.

Stream current velocity is a particularly important environmental factor because moving water defines lotic ecosystems and many, if not most, stream organisms respond to its
influence (Statzner et al. 1988, Hart and Finelli 1999). Current velocity can influence the distribution and abundance of benthic organisms (Hart 1992, Passy 2001, Dewson et al. 2007a, b), the interactions that occur between them (Hansen et al. 1991, Kuhara et al. 2000, Opsahl et al. 2003), and the functional contributions that they make to stream ecosystem functioning (Hintz and Wellnitz 2013, Poff et al. 2003). For crayfish in particular, current has been shown to be a key environmental variable for predicting their occurrence and habitat use in streams (Brooks et al. 2005, Flinders and Magoullick 2007, Magoullick et al. 2017). Current constrains crayfish movement, can affect feeding and positioning on streambeds (Maude and Williams 1983, Clark et al. 2008, Perry and Jones 2018), and may modify their impacts on benthic communities. For example, Hart (1992) and Creed (1994) demonstrated that fast current velocities > 50 cm s\(^{-1}\) limit the ability of native crayfish to remove filamentous Cladophora algae from the streambed. They showed Cladophora was in competition with epilithic diatoms for space, and regions of the streambed having fast current had fewer epilithic diatoms as compared to those having current < 50 cm s\(^{-1}\). This shift in algal dominance led to there being fewer sessile grazers that feed on diatoms. Thus, by modifying crayfish foraging on either side of this 50 cm s\(^{-1}\) threshold, current velocity affected the impact crayfish had on the physical and trophic structure of the benthic community.

To examine how different ranges of current velocity might affect the ecological performance of a non-native crayfish in a Wisconsin stream, we conducted a cage enclosure experiment. The species used was the invasive rusty crayfish, Orconectes rusticus, and our goal was to determine how current velocity affected its impact on benthic assemblages, using 50 cm s\(^{-1}\) as a cutoff between fast and slow current. We chose this velocity because other studies have shown crayfish foraging activity and food acquisition is depressed at current > 50 cm s\(^{-1}\) (Hart 1992, Creed 1994, Perry and Jones 2018). Rather than elucidate precise mechanisms by which current and O. rusticus exerted their effects, our goal here was to ascertain patterns in the macroinvertebrate response. To assess how current velocity influenced the ability of O. rusticus to structure the environment, we measured sediment accumulation, a frequently cited aspect of habitat modification by crayfish (Parkyn et al. 1997, Statzner and Sagnes 2008, Albertson and Daniels 2016). For both macroinvertebrates and sediment, we hypothesized that O. rusticus effects would be significantly less in fast current > 50 cm s\(^{-1}\).

**Methods**

**Focal organism**

The rusty crayfish, Orconectes rusticus (Girard, 1852), is native to the Ohio River basin and has been undergoing a northern range expansion into the Great Lakes region since the 1970s (Phillips et al. 2009). Much of this expansion has likely occurred through the bait trade and recreational fishing (Kilian et al. 2012, Arcella et al. 2014), and the spread of this invasive crayfish has significantly reduced native crayfish diversity and altered habitats in Wisconsin lakes and streams (Capelli 1982, Bobeldyk and Lamberti 2008, Olden et al. 2006). Rusty crayfish have been the focus of intensive management and control efforts because of their ecosystem-level impacts and persistence once established (Nilsson et al. 2012, Hansen et al. 2013). Orconectes rusticus has been shown to outcompete native crayfish, reduce macroinvertebrate and macrophyte abundances (Olden et al. 2006), and cause shifts in native fish populations (Wilson et al. 2004).
**Study site**

Lowes Creek is a third-order trout stream in Eau Claire County, Wisconsin, USA. The stream drains an agricultural watershed and flows 19 km north before joining the Chippewa River near the city of Eau Claire. Lowes Creek has a riparian buffer of mixed hardwood-conifer forest and passes through a forested corridor of parkland and dispersed residential development as it nears the city. Summer discharge ranges around 0.5 m$^3$ s$^{-1}$ and the average stream temperature during the August 2014 study period was 21°C. The Lowes Creek streambed is composed mostly of sand (51%), but there are areas of bedrock (19%), gravel (13%), and silt/clay (11%), and occasional patches of cobble/rubble (4%) and detritus (2%) (Spaeth et al. 2004).

Historically, native virile crayfish, *Orconectes virilis*, inhabited Lowes Creek, but *O. rusticus* was the only crayfish species encountered during our study. Daytime *O. rusticus* densities (determined with a 1-m$^2$ quadrat sampler; DiStefano et al. 2003) averaged 2.3 individuals m$^{-2}$ ($n = 12$). This is a relatively low density for *O. rusticus*-invaded streams (e.g. Charlebois and Lamberti 1996); however, *O. rusticus* forage primarily at night (Bergman and Moore 2003) so this daytime estimate likely under-represents actual stream densities.

Lowes Creek contains a diverse fish assemblage comprised of 27 species that include brook and brown trout (*Salvelinus fontinalis* and *Salmo trutta*, respectively), and gamefish such as small mouth bass (*Micropterus dolomieu*). A 2000 electro-shocking survey conducted by the Wisconsin Department of Natural Resources showed the dominant fish species, comprising 60% of the catch, were white suckers (*Catostomus commersonii*), mottled sculpin (*Cottus bairdii*), American brook lamprey (*Lethenteron appendix*), and brassy minnows (*Hybognathus hankinsoni*).

Our study reach (44° 46' 14" N, 91° 29' 33" W) was approximately 60 m in length and chosen because it was relatively wide (14–20 m) and shallow (0.2–0.4 m), and because the streambed was composed almost entirely sandstone bedrock. The bedrock provided stable substrate for fastening experimental cages and the section’s width and depth made it relatively easy to find streambed locations that differed in current velocity, but were similar in depth. We assessed the variability in current across the study reach with a Marsh McBirney Flo-Mate 2000 and found current velocity ranged from 3 to 102 cm s$^{-1}$ and averaged 44 cm s$^{-1}$ ($n = 24$).

**Study design**

Our experiment employed a 3 $\times$ 2 factorial design for cage and current velocity treatments, respectively. Cage treatments were open, closed crayfish and closed control. Open cages were open at both ends to allow resident crayfish access; closed crayfish cages (hereafter, simply ‘crayfish’) contained a single *O. rusticus* crayfish and had mesh covering both ends to prevent their escape; closed control cages also had mesh over both ends but no crayfish. Current velocity treatments were maintained within two ranges, 20-30 cm s$^{-1}$ and 50-70 cm s$^{-1}$, hereafter referred to as ‘slow’ and ‘fast’ current.

The cylindrical cages measured 45 $\times$ 15 cm (length $\times$ diameter) and were constructed of polyethylene ‘hardware cloth’ having 20 mm mesh held together with nylon cable ties (Figure 1). Each cage contained 1.75 L of landscaping gravel that covered the bottom to a depth of 5 cm. The gravel size was 3.8 $\pm$ 1.8 cm (mean $\pm$ SD) and was chosen because it was sufficiently large to not be displaced by fast current treatment, but was small enough to provide ample interstitial refugia for macroinvertebrates.
The three cage enclosure treatments (open, crayfish and closed control) were grouped into eight replicate blocks that were divided equally among regions of slow and fast current. The order of treatments within a block was randomized. The three cage treatments were held together by attaching them to a slotted steel bar staked to the streambed (Figure 1). Locations of fast and slow current were found by walking the study section and measuring current velocity with the Marsh McBirney Flo-Mate 2000. Once a location was identified, the block was held in place on the streambed and the current velocities inside each cage were determined with a MiniWater20 Micro velocity probe (Schiltknecht Messtechnik AG, Zürich). This probe was small enough to insert through the hardware cloth mesh so that measurements could be taken inside cages just above the gravel substrate. Current velocity measurements were taken near the upstream, middle and downstream ends of each cage. The average near-bed current at each position was recorded for 6 s using the Schiltknecht meter ‘rep’ function. If the current velocity within a cage was outside the desired treatment range, the positioning of the cage or the block was adjusted until the appropriate current range was established. After final adjustments, the block was fixed in place by securing its slotted steel bar to the streambed with steel spikes. The cage blocks were left in place for 1 week before adding crayfish. This was done so that macro-invertebrates could begin colonizing the gravel substrates, the stability of within-cage current velocities could be assessed, and to ensure that excessive sand build-up did not occur in cages.

The experiment began on 5 August 2014 and ran three weeks. Eight large *O. rusticus* crayfish (CL = 25–28 mm) were hand-collected from Lowes Creeks and introduced into each crayfish cage treatment. This was done by opening a gap in the hardware cloth, slipping the crayfish through the gap, then closing it with cable ties. During the experiment, the cages were inspected every-other day to assess crayfish condition, measure within-cage current velocities, and remove accumulated debris from cage surfaces to prevent clogging.

Although our crayfish treatments contained only one individual per cage, the effective density was 14.8 individuals m$^{-2}$ because of the small cage area (0.0675 m$^2$). This density...
exceeded the 2.3 individuals m$^{-2}$ found in Lowes Creek at the time of the experiment, but was within the range reported for other O. rusticus-invaded streams (Momot et al., 1978; Charlebois and Lamberti, 1996; Kuhlmann and Hazelton, 2007), and was below that used in similar cage studies (e.g. 24 crayfish m$^{-2}$, Albertson and Daniels, 2016). The discrepancy between experimental and natural crayfish densities was acceptable because our study was designed to examine how current velocity influenced O. rusticus impacts generally rather than just in Lowes Creek.

At the end of three weeks the cages were sampled for macroinvertebrates, organic matter and sediment. Sampling was accomplished by detaching the cage from the block array, lifting it from the streambed and transferring it into a 12 L plastic tub. The cage contents were emptied into the tub and organisms clinging to the hardware cloth mesh were removed with forceps and also put into the tub. These contents were then transferred to a 3.8 L Ziploc bag and were preserved by adding 75% ethanol. Crayfish then were put into a separate container to be euthanized; a practice mandated by the state of Wisconsin for invasive crayfish.

In the laboratory, Ziploc bag contents were emptied into white enamel sorting trays. Gravel was removed, rinsed with a wash bottle, and macroinvertebrates and coarse particulate organic matter (CPOM) were removed from the trays with forceps. Macroinvertebrates were counted after being identified using Bouchard (2004). Once macroinvertebrates and CPOM were removed, the remaining sediment was rinsed from the tray and filtered through glass fiber filters. CPOM and sediment samples were dried at 60°C overnight to determine dry weights.

**Data analysis**

To determine the effects of current velocity and cage treatments and their interaction on macroinvertebrate numbers, we used the General Linear Model function in JMP 8.0.1 (SAS Institute Inc., 2009). Models used a Poisson distribution to fit variables and a log link function to create linear models. We used a full model that included main factor effects (i.e., current and cage treatment) and the interaction between them. Chi-squared ($\chi^2$) probabilities ascertained significance levels of individual factors and interactions. Pairwise tests were done with Kruskal–Wallis post hoc tests to determine which cage treatments were different. The same analysis was used to examine the effects of current and cage treatments on CPOM and sediments.

**Results**

Crayfish and current velocity treatments were successfully maintained over the course of the experiment. No crayfish mortality was observed and no resident crayfish were found or seen in either treatment or control cages during regular, daytime observations. Current within cages varied over the course of the experiment, but slow and fast current velocity treatments were maintained within their experimental ranges ($t = -14.51$, $p < 0.0001$). Slow current ranged 25–31 cm s$^{-1}$ and fast current ranged 52–73 cm s$^{-1}$. The average difference between current measured at the beginning and the end of the experiment was $8 \pm 4$ (SD) cm s$^{-1}$.

Macroinvertebrate numbers responded to both current and cage treatments (Table 1), such that total numbers increased with current (Figure 2) and decreased in crayfish cages (Figure 3(a)). Macroinvertebrate richness, by comparison, responded only to cage treatments and was lowest in crayfish cages ($\chi^2 = 10.90$, df = 2, 23,
A total of 22 taxa were found in cages, of which eight (in decreasing order of abundance) were common: net-spinning caddisflies (Hydropsychidae, 51%), crane fly larvae (Tipulidae, 13%), midges (Chironomidae, 22%), mayflies (Batidae and Hepatgeniidae, 8%), microcaddisflies (Hydroptilidae, 2%), annelid worms (2%), snipe fly larvae (Athericidae, 1%), and blackflies (Simulium spp., 1%). The thirteen other taxa made up <1% of all macroinvertebrates.

Net-spinning caddisflies (Hydropsychidae) were the most abundant macroinvertebrate and the only taxonomic group to respond to both current and cage treatments and the interaction between these factors (Table 1). Across current velocities, hydropsychid...
numbers were highest in the closed control cages and lowest in crayfish and open cage treatments (Figure 3(b)). The current X cage interaction resulted from hydropsychid numbers increasing as current velocity increased in the closed cage treatment, but not in the open or crayfish cage treatments (Figure 4).

Craneflies (Tipulidae) were the only other taxon to show a response to experimental treatments (Table 1). Larval tipulids were most abundant in open cages (Figure 3(c)), and their distribution mirrored the pattern of CPOM accumulation. By the end of the experiment, CPOM in open cages was two orders of magnitude greater than that seen in other treatments (Figure 5(a)).

Sediment accumulation was greatest at slower velocities and lowest in crayfish cages (Table 2, Figure 5(b)). Gravel in crayfish cages looked ‘cleaner’ across the range of current velocity, but the difference was most distinct at slow velocities where differences between crayfish and non-crayfish cages were largest. The significant interaction between current and cage treatments resulted from cages with crayfish having less sediment than open cages at slow, but not fast current. Sediment accumulation did not differ between open and closed cage treatments.
Current velocity and *O. rusticus* crayfish had divergent effects on macroinvertebrate assemblages in cages. Overall, macroinvertebrate numbers increased with current velocity and decreased in the presence of *O. rusticus*. Macroinvertebrate richness, by contrast, was affected only by *O. rusticus* and decreased. We had hypothesized that crayfish impacts would be modified by current, and while this did not occur for macroinvertebrates in general, there was an interaction between current velocity and cage treatments for the most common macroinvertebrate, hydropsychid caddisflies.

Hydropsychids showed a context-dependent response to *O. rusticus* such that hydropsychid numbers were reduced in fast current, but not in slow. This result met our expectation of finding current-mediated effects, but it ran counter to our hypothesis that *O. rusticus* impacts would decrease as current velocity increased. It is noteworthy that hydropsychid numbers were already quite low in slow current, so it would have been

**Figure 5.** The mean g weight ± SE for CPOM (A) and sediment (B) in cage treatments after 21 d in Lowes Creek. Note CPOM data has been log-transformed. Closed cages excluded crayfish, crayfish cages had one *O. rusticus*, and open cages allowed resident crayfish to enter and leave freely. Cage treatments that differed significantly are indicated by an asterix (Kruskal–Wallis, *p* < 0.05).

**Table 2.** Results of the GLMs used to test cage treatment and current velocity effects on CPOM and sediment accumulation in cages.

| Parameter | Source       | DF | $\chi^2$ | P-value |
|-----------|--------------|----|----------|---------|
| **CPOM**  | Cage         | 2  | 10.15    | 0.006   |
| $\chi^2$ = 13.22, df = 5 | Current | 1  | 2.17     | 0.14    |
| $p = 0.021$ | Cage*Current | 2  | 2.58     | 0.27    |
| **Sediment** | Cage         | 2  | 29.67    | <0.0001 |
| $\chi^2 = 38.31$, df = 5 | Current | 1  | 12.89    | 0.0003  |
| $p < 0.0001$ | Cage*Current | 2  | 13.85    | 0.001   |

**Discussion**

Current velocity and *O. rusticus* crayfish had divergent effects on macroinvertebrate assemblages in cages. Overall, macroinvertebrate numbers increased with current velocity and decreased in the presence of *O. rusticus*. Macroinvertebrate richness, by contrast, was affected only by *O. rusticus* and decreased. We had hypothesized that crayfish impacts would be modified by current, and while this did not occur for macroinvertebrates in general, there was an interaction between current velocity and cage treatments for the most common macroinvertebrate, hydropsychid caddisflies.

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difficult for *O. rusticus* to have an effect there. Consequently, our result may not so much have been a case of *O. rusticus* having an impact on hydropsychids in fast over slow current, but rather, *O. rusticus* having an impact on hydropsychids where they were abundant. The context-dependent interaction we observed, therefore, may have been driven more by hydropsychid responses to current than current-mediated *O. rusticus* impacts on these caddisflies. The observed response hydropsychids showed to current velocity and crayfish may stem from their feeding ecology.

Hydropsychid larvae are filter-feeders that live in fixed retreats (i.e. immovable cases attached to substrates) and capture drifting food particles with silken nets oriented perpendicular to flow (Wiggins 1996). Constructed of sand grains, tiny stones and plant material held together with silk, these retreats are thought to serve two functions: to provide hydropsychids with stable scaffolding for supporting their food-capturing nets, and to serve as refugia from predators (Fuller and Rand 1990, Holomuzki and Van Loan 2002, Fairchild and Holomuzki 2005). Food capture rates in hydropsychid nets often correlate positively with current velocity (Georgian and Thorp 1992, Brooks and Haeusler 2016), so having stable support for feeding nets becomes critical at higher flows. In our experiment, this positive relationship between current velocity and food capture likely explains why hydropsychids became more abundant as current increased.

In terms of predator defense, fixed retreats afford some protection (Fuller and Rand 1990), but they also impose a sedentary lifestyle that may make hydropsychids vulnerable to crayfish. Weinlander and Fureder (2016), for example, showed that native and non-native crayfish in Austrian streams preyed more successfully on slow-moving and sessile invertebrates than those that were agile and fast-moving. Unlike filter-feeding Simulidae, which can reposition themselves on substrates with relative ease (Lacoursière 1992), hydropsychids cannot move away from or escape threats without vacating their retreats, which means sacrificing the energy and resources it took to construct the retreat, to say nothing of the lost feeding time incurred before another retreat can be built.

Predation is not the only way crayfish affect macroinvertebrates. Disturbance resulting from crayfish foraging can make substrates less habitable. *O. rusticus* foraging could potentially damage or dislodge hydropsychid retreats, causing the larvae to abandon them, and also stir up sediments that could foul capture nets or bury larvae (Runde and Hellenthal 2000). Crayfish are known bioturbators and their activity can increase streambed erosion (Statzner et al. 2000) and disturb fine sediments and gravels (Statzner et al. 2003, Johnson et al. 2011, Harvey et al. 2014, Albertson and Daniels 2016). Our data show that crayfish cages had less sediment than non-crayfish cages, which suggests that *O. rusticus* activity disturbed substrates, and we believe this deterred macroinvertebrate colonization in general, and hydropsychid establishment in particular. The difference in sediment accumulation between crayfish and non-crayfish cages was greatest at slow current velocities (Figure 5), which may partially explain why fewer hydropsychids were found at slow velocity, since greater mobilization of sediment may have led to more net clogging (Runde and Hellenthal 2000).

It should be noted that sediment removal by crayfish can also benefit benthic organisms. Albertson and Daniels (2016) conducted a similar cage-enclosure experiment with *O. rusticus* in a Pennsylvania stream, and like us, found *O. rusticus* decreased sediment accumulation on gravel. Unlike us, they found that this crayfish-mediated disturbance increased macroinvertebrate abundance. These authors attributed this positive effect to the way in which sediment removal improved macroinvertebrate habitat by clearing sediments from interstitial spaces between gravel substrates, a key habitat for many
macroinvertebrates (Bruno et al. 2012). That this did not occur in our experiment may have been due to the gravel size used. Whereas Albertson and Daniels (2016) used particle ranging between 5.6 and 31 mm, our gravel particles were larger (averaging 38 mm diameter) and more homogenous. This meant the interstitial spaces in our substrates were generally larger, since there were not smaller particles to fill gaps between larger particles. Because of this gravel size difference, we speculate that interstitial clogging by sediment was less a factor in our study than it was for Albertson and Daniels (2016). In the present study, we suspect the beneficial effects of sediment removal by *O. rusticus* were countermanded by the negative effects of *O. rusticus*-mediated disturbance.

When comparing hydropsychid abundance across cage treatments it is interesting to note that numbers did not differ between crayfish and open cage treatments. When checking cages over the course of the experiment, we did not observe crayfish in the open cages; however, we checked them only during the day and *O. rusticus* forage primarily at night (Bergman and Moore 2003). There is evidence to suggest that naturally occurring *O. rusticus* did visit the open cages at night. While the total numbers of macroinvertebrates were greater in open cages compared to crayfish cages, hydropsychid numbers in open and crayfish cages were similarly low. This would make sense if crayfish visitation to the cages was sporadic. Occasional disturbance and/or predation events could have been sufficient to keep hydropsychid densities low, whereas mobile species could reoccupy cages soon after the crayfish left so their numbers would be unaffected. It should be noted that ambient crayfish densities in Lowes Creek were > 6X lower than in crayfish cage treatments (2.3 vs. 14.8 individuals m$^{-2}$, respectively). Thus, if crayfish did sporadically visit open cages as we hypothesize, our data suggest that ambient crayfish densities were sufficient to reduce hydropsychid numbers.

Open cages were distinctive for another reason: they had significantly more CPOM and Tipulidae than any other treatment. CPOM biomass took the form of leaves, small twigs and detritus and was highly variable among the open cages. CPOM was more abundant in open cages because the treatment’s openings allowed drifting CPOM to enter and become entrapped inside. CPOM provides additional habitat and food resources for macroinvertebrates in general and shredders in particular (Cummins and Klug 1979), and this probably accounted for tipulid shredders being 5X more abundant in open cages.

Our study demonstrates that current velocity can provide an important context for understanding crayfish impacts on benthic stream communities. That crayfish can reduce the abundance of benthic organisms on streambeds is well documented (Twardochleb et al. 2013), but for some taxa, such as the hydropsychids, this may only occur within certain ranges of flow. We had hypothesized that *O. rusticus* impacts would be less at higher current velocities, but found the opposite to be true for hydropsychid caddisflies. And the impact *O. rusticus* had on hydropsychids appeared to be driven more by the caddisfly’s response to current than current-mediated *O. rusticus* effects. We did not examine underlying mechanisms, yet it is likely that multiple factors contributed to the patterns found. The hydropsychid response may have involved such factors as current-mediated food capture rates, sediment accumulation, and vulnerability to crayfish predation and/or disturbance. This study provides evidence that current velocity-dependent species impacts and responses may have relevance for assessing the influence of invasive species like *O. rusticus*. It remains to be seen if *O. rusticus* effects differ from those of native crayfish across the gradient of stream current.

**Disclosure statement**

No potential conflict of interest was reported by the authors.
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Notes on contributors

Dr. Todd Wellnitz is a professor of biology at the University of Wisconsin – Eau Claire where he teaches courses in field biology, aquatic ecology and invertebrate zoology. He studies how current and flow structure stream communities and the impact that humans have on wilderness areas.

Drew Frase studied chemistry and biology at the University of Wisconsin – Eau Claire and is currently a research assistant in the Program in Gene Expression and Regulation at the Wistar Institute’s Center for Chemical Biology and Translational Medicine.

Margaret Gapinski is a high school teacher at Rufus King International Baccalaureate High School in the Milwaukee Public School District. She teaches Biology and Environmental Health with a focus on environmental toxins and water quality.

Hayley Emerson Haggerty studied Ecology, Evolutionary Biology and Psychology at the University of Wisconsin – Eau Claire.

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