



Invasive dreissenid mussels benefit invasive crayfish but not native crayfish in the Laurentian Great Lakes



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ABSTRACT

Invasive ecosystem engineers, such as dreissenid mussels, may facilitate subsequent invaders. Despite their potential ecological importance, interactions between dreissenid mussels and crayfish in the Laurentian Great Lakes have received little research attention. Invasive rusty crayfish (*Orconectes rusticus*) have recently spread within the Great Lakes, and we hypothesized that food resources provided by invasive dreissenid mussels may have enhanced this spread. Dreissenid mussels may also benefit native crayfish such as the virile crayfish (*O. virilis*), but the distribution of virile species has not increased in the Great Lakes in recent years. We tested the interactive effects of dreissenid mussels and crayfish density on the growth, survival and activity of sympatric rusty and virile crayfish using a mesocosm experiment. We found that dreissenid mussels increased growth and activity of rusty crayfish while high crayfish densities negatively affected rusty crayfish growth. Dreissenid mussels did not affect growth or activity of virile crayfish, but high crayfish densities negatively affected their survival. The different responses of rusty and virile crayfish to mussels may be due to a greater ability of invasive crayfish to exploit mussel-associated food resources and/or to behavioral interactions between these species in sympatry. Our results suggest that dreissenid mussels may facilitate the establishment, spread, and potential impacts of invasive crayfish where these taxa co-occur.

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Introduction

Despite efforts to curtail introductions of nonindigenous species (e.g., Leung et al., 2002), biological invasions are becoming increasingly prevalent (Crowl et al., 2008; Grigorovich et al., 2003; Mack et al., 2000). The accelerating frequency of biological invasions is the result of numerous phenomena such as unprecedented global connectivity due to travel and trade (Crowl et al., 2008), ongoing habitat disturbances and modifications (Didham et al., 2005), and climate change (Rahel and Olden, 2008; Stachowicz et al., 2002). Here, we focus on the possible role that established invasive species might play in the increasing incidences and impacts of biological invasions by both directly and indirectly facilitating subsequent invaders (DeVanna et al., 2011; Ricciardi, 2001; Simberloff, 2006). For example, invasive centrarchid fish indirectly facilitate the establishment of invasive bullfrogs (*Rana catesbeiana*) by reducing abundances of predatory dragonfly nymphs that prey on tadpoles (Adams et al., 2003). Similarly, invasive plants are capable of modifying ecosystems in ways that promote subsequent plant invasions while hindering growth of native plants by altering soil composition

(Callaway and Aschehoug, 2000; Jordan et al., 2007). Understanding when and why invasive facilitations occur and what these mean for recipient ecosystems is an important step towards reducing the impacts of biological invasions.

The invasion of dreissenid mussels (zebra mussel, *Dreissena polymorpha*, and quagga mussel, *D. rostriformis bugensis*) from the Ponto-Caspian region to freshwater lakes and rivers worldwide has led to notable examples of facilitation between invasive species (DeVanna et al., 2011; Higgins and Vander Zanden, 2010; Madenjian et al., 2015). Due to their high abundances and filter feeding, dreissenid mussels restructure aquatic ecosystems by redirecting pelagic primary productivity to the benthos (Hecky et al., 2004; Higgins and Vander Zanden, 2010). These bottom-up ecosystem changes negatively affect several native species including unionid mussels and pelagic fish (Ricciardi et al., 1998; Strayer et al., 2004), while benefitting a number of associated benthic invaders (Higgins and Vander Zanden, 2010; Ricciardi, 2001). In the Laurentian Great Lakes, dreissenid mussels have facilitated several benthic invasive species like the round goby (*Neogobius melanostomus*) and amphipod (*Echinogammarus ischnus*), which use dreissenid beds as habitat and feed directly on these mussels or organisms associated with increased benthic productivity (Ricciardi and MacIsaac, 2000; Vanderploeg et al., 2002). Importantly, some invasive species that have benefitted from dreissenid invasions have also

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had negative impacts on native species. For example, invasive round gobies consume salmonid eggs and displace native sculpins and darters (Fitzsimons et al., 2006; Lauer et al., 2004). Mussel-mediated changes in the Laurentian Great Lakes have not exclusively benefited invasive species, as evidenced by increases in the biomass and density of some native species (DeVanna et al., 2011); however, Great Lakes food webs are now dominated by benthic invaders associated with mussels (Bunnell et al., 2014; Ricciardi and MacIsaac, 2000), suggesting that these species have been favored by the introduction of dreissenids. Although mussel-mediated facilitations of invaders have been relatively well-studied, there remains a lack of knowledge on the effects that dreissenid mussels have on certain ecologically-important taxa, including larger benthic invertebrates such as crayfish (Higgins and Vander Zanden, 2010).

Crayfish occupy the same benthic habitats as mussels and consume mussels as well as macroinvertebrates and algae that inhabit mussel beds (Perry et al., 1995; Stewart et al., 1998). Because of their polytrophic interactions, crayfish can strongly influence the abundance and distribution of other organisms as well as the flow of energy across trophic levels (Reynolds et al., 2013; Twardochleb et al., 2013). Crayfish also function as ecosystem engineers by accelerating leaf-litter breakdown through shredding activity and by altering the spatial distribution of sediment (Alp et al., 2016; Creed and Reed, 2004). The pivotal role of crayfish in freshwater ecosystems, in turn, causes a breadth of impacts in ecosystems where they are invasive (Karatayev et al., 2009; Lodge et al., 2012). In North America, for instance, the rusty crayfish (*Orconectes rusticus*) has been introduced outside of its native range of the Ohio River Drainage through pathways including live bait releases by anglers (Lodge et al., 2000; Olden et al., 2006). The invasion of the rusty crayfish has been well-studied in many inland lakes and rivers (e.g., Olden et al., 2011), where it has had negative impacts on native crayfish, macrophytes, macroinvertebrates, and fish (Wilson et al., 2004). The rusty crayfish has also invaded all five of the Laurentian Great Lakes (Peters et al., 2014) although its impacts in these lakes remain largely unknown (but see Jonas et al., 2005; Stewart et al., 1998). The spread of rusty crayfish in the Great Lakes in recent decades, which has coincided with the establishment and spread of dreissenid mussels, suggests that this crayfish is thriving in this increasingly invaded ecosystem (Madenjian et al., 2015; Peters et al., 2014). Conversely, preliminary research suggests that native Great Lakes crayfish may have been displaced, at least in some instances, by invasive rusty crayfish over this same time interval (Peters et al., 2014).

We therefore hypothesized that invasive dreissenid mussels would enhance the ecological performance of invasive rusty crayfish but not native crayfish, contributing to recent trends in Great Lakes crayfish distribution (Peters et al., 2014). To test this hypothesis, we assessed performance (as measured by growth, survival, and activity) in the presence and absence of dreissenid mussels of the invasive rusty crayfish and the Great Lakes-native virile crayfish (*O. virilis*). In order to simulate an ongoing invasion of rusty crayfish in a habitat occupied by virile crayfish, we ran our experiments with these crayfish species in sympatry and used two separate crayfish density treatments to represent a gradient of densities for these species that have been documented in the Great Lakes (Jonas et al., 2005). We chose to use virile crayfish because this crayfish species is native to all five Great Lakes (Peters et al., 2014) and because interactions between invasive rusty crayfish and native virile crayfish have been well-studied in other systems (e.g., Hayes et al., 2009; Lodge et al., 1986), giving us a knowledge base to build upon. Because both crayfish and dreissenid mussels function as ecosystem engineers, they can have large, widespread impacts when invasive (Higgins and Vander Zanden, 2010; Reynolds et al., 2013; Twardochleb et al., 2013; Fryxell et al., 2016). Despite this, previous research has not evaluated potential interactions, such as facilitations, between dreissenid mussels and native and invasive crayfish. Our study attempted to fill this knowledge gap, and to determine if invasive rusty crayfish might benefit more from dreissenid mussels than native crayfish when these

crayfish are in sympatry, thereby potentially favoring the increased spread and impacts of rusty crayfish in the Great Lakes.

Methods

We conducted an experiment at the Central Michigan University Biological Station mesocosm facility on Beaver Island, MI (45.7423° – 85.5097°) in which we factorially manipulated the presence of dreissenid mussels and the density of native and invasive crayfish. We designed our experiment to assess performance, as measured by growth, survival, and activity levels, of sympatric invasive rusty crayfish and native virile crayfish under these different treatments.

Mesocosm setup

The facility in which we conducted this experiment consists of 12, 800 l cylindrical mesocosms (surface area: 1.98 m², diameter: 127 cm, depth: 66 cm). Each mesocosm was individually connected to an autonomously filling tank that provided a constant flow-through of water directly from Lake Michigan, allowing us to closely replicate natural conditions of this lake where all three of our focal species (i.e., dreissenid mussels, rusty crayfish, and virile crayfish) currently occur. Prior to the start of the experiment, we covered the bottom of mesocosms with a 2.5 cm layer of 2.5–5 cm diameter gravel, and then designated alternating quarters of the mesocosms as “open” or “cobble” habitat. Cobble habitat quarters received an additional 15 cm deep layer of approximately 15–25 cm diameter rock. Previous research has found that our focal crayfish species prefer cobble over open habitats, most likely to avoid predation (Hill and Lodge, 1994); we provided both cobble and open habitats to reflect natural variation in substrate. In an effort to replicate natural conditions in our mesocosms, we obtained all substrate directly from Lake Michigan.

On 12 July 2015, we obtained dreissenid mussels (predominantly quagga mussels, which have widely displaced zebra mussels in the Great Lakes [Madenjian et al., 2015]) from Lake Michigan. We randomly assigned half of the mesocosms ($n = 6$) to a mussel treatment and stocked each of these with approximately 3 kg of mussels. While collecting dreissenid mussels, we observed that they were present in the interstitial spaces between cobbles and boulders, but not on exposed gravel. We therefore placed our mussels evenly on the 1 m² of cobble habitat in each mesocosm. The stocked mussel biomass represented an approximate density of 3225 individuals/m² (based on an average weight of 0.93 g/mussel determined by weighing a subset of 30 mussels), well within natural Great Lakes densities of 10 to 100,000 individuals/m² (Madenjian et al., 2015). Because we observed non-mussel macroinvertebrates inhabiting the interstitial spaces between mussels, we rinsed the equivalent mass of mussels in a bucket to remove attached macroinvertebrates and evenly inoculated the non-mussel tanks with these organisms.

Density can influence crayfish activity and foraging behavior (Jonas et al., 2005; Pintor and Kerby, 2009); therefore, we evenly divided our mesocosms into low and high crayfish density treatments. We stocked low density mesocosms with 6 crayfish (3 crayfish/m²) and high density mesocosms with 16 crayfish (8 crayfish/m²), densities that are within the range that has been observed in the Great Lakes (Jonas et al., 2005 report a mean density of 7.9 rusty crayfish/m² in the Great Lakes). In both cases, the crayfish stocked consisted of an equal number of rusty and virile crayfish. We hand-collected rusty crayfish ($n = 66$) in Grand Traverse Bay in Lake Michigan (44.9039° – 85.4181°) on 13 July 2015. Mean \pm SE carapace lengths of rusty crayfish were 31.59 \pm 0.48 mm and weights were 9.31 \pm 0.42 g at the start of the experiment. We caught virile crayfish ($n = 66$) in Saint James Harbor on Beaver Island in Lake Michigan (45.7472° – 85.5179°) on 15 and 16 July 2015 with minnow traps baited with canned cat food. Mean \pm SE carapace lengths of virile crayfish were 41.09 \pm 1.17 mm and weights were 19.77 \pm 1.62 g at the start of the experiment. We used only male

crayfish of both species to avoid potential differences in survival, growth, or foraging related to sex. Male crayfish of the family Cambaridae cycle between a reproductively active form I and inactive form II stage; all rusty crayfish used in our experiment were initially form II, whereas 10 virile crayfish were form I and 56 were form II at the start of our experiment. We did not investigate effects of the small number of form I crayfish at the beginning of the experiment as this was a phenological artifact of the previously documented (e.g., Hamr, 2010) synchronous molt of Cambarid crayfish from form II to form I which occurs during mid to late summer.

After weighing and measuring each crayfish, we marked it with a unique identifier consisting of a pleura clip and a hole punched into one of its uropods or its telson sensu Guan (1997), which permitted us to track growth and survival of individual crayfish. We then stocked crayfish into the mesocosms. There was no significant difference in initial weight or carapace length of rusty crayfish (one-way ANOVA; weight, $F_{11,54} = 0.07$, $p = 1.0$; carapace length, $F_{11,54} = 0.1$, $p = 1.0$) or virile crayfish (one-way ANOVA; weight, $F_{11,54} = 0.12$, $p = 1.0$; carapace length, $F_{11,54} = 0.44$, $p = 0.93$) among mesocosms. However, virile crayfish were significantly larger than rusty crayfish (2-sample t -test; weight, $t_{107,01} = -13.02$, $p < 0.01$; carapace length, $t_{128,56} = -13.83$, $p < 0.01$).

Data collection

We ran the experiment for a total of 28 days, from 16 July 2015 to 13 August 2015. We maintained a 12:12 h day to night lighting schedule and monitored the mesocosms for temperature and pH on a daily basis (mean \pm SE temperature, 20.13 ± 0.17 °C; mean \pm SE pH, 8.22 ± 0.03). In order to replicate natural conditions, crayfish could consume invertebrates (including the dreissenid mussels) and algae within mesocosms, but we did not provide additional food.

On the penultimate day of the experiment, we used an underwater camera (GoPro, Inc., San Mateo, California) to film crayfish activity. We filmed each mesocosm in random order for 15 min during daylight hours (12 h40 to 16 h03). For each video, we recorded the amount of time that crayfish of each species were visible on both the cobble and open habitats. We considered a crayfish to be visible when its entire body was out of shelter and on one habitat. For each mesocosm, we divided the amount of time by the number of crayfish that survived in order to determine species-specific per capita activity.

At the conclusion of the experiment, we weighed and measured all surviving crayfish. We considered any missing crayfish to have died during the experiment. We calculated growth of surviving crayfish as the difference between the final and initial blotted wet mass. We also recovered the mussels from each mesocosm and calculated the change in mussel biomass (initial blotted wet mass - final blotted wet mass). We found reductions in mussel biomass in all mesocosms (mean \pm SE, 190.2 ± 68.5 g), which we attribute in part to consumption by crayfish, a phenomenon that we directly observed during the experiment. Reductions in mussel biomass did not differ significantly between low and high crayfish density treatments (two-sample t -test, $t_{3,979} = -0.74$, $p = 0.50$).

Algal and macroinvertebrate biomass

Previous studies have found that dreissenid mussels can indirectly benefit crayfish by increasing the biomass of non-mussel macroinvertebrates and algae (Auer et al., 2010; Mayer et al., 2002). We therefore measured macroinvertebrate and algal biomass in our mesocosms to determine if these variables were affected by our treatments. We quantified relative abundance of macroinvertebrates by using a d-net on the final day of the experiment, sampling the substrate of each mesocosm for 20 s around the outside wall and 10 s around the inside standpipe. We preserved these samples in 70% ethanol for later analysis. We sorted and identified macroinvertebrates to class (e.g., Oligochaeta), order

(e.g., Amphipoda, Ephemeroptera, Isopoda, Trichoptera), or family (e.g., Chironomidae, Tipulidae) then used length-weight regressions to determine total dry weight of macroinvertebrates we collected from each mesocosm (Benke et al., 1999; Miyasaka et al., 2008). In order to quantify algal biomass, we placed four, 4.85 cm² clay tiles on the bottom of each mesocosm (two tiles per gravel segment; four total per mesocosm) on the first day of the experiment. We removed these tiles on the final day of the experiment and froze them in plastic bags for later analysis. We used 95% ethanol to extract chlorophyll directly from clay tiles and standard fluorometric methods to measure chlorophyll *a* (Wetzel and Likens, 1981).

Statistical analyses

Although virile crayfish routinely attain larger maximum sizes than rusty crayfish (Garvey and Stein, 1994), our use of different methods to collect each crayfish species likely resulted in larger average size of virile than rusty crayfish because traps are biased towards larger, aggressive males (Chucholl, 2011; Dorn et al., 2005; Larson, 2016). Because younger, smaller crayfish may grow faster than older, larger crayfish (Momot, 1978), we first explored whether the initial size mismatch between our two focal species seemingly affected their observed patterns of growth by creating and comparing a series of general linear mixed effects models at the individual crayfish level. Specifically, we created a base model where crayfish growth by weight was the response to predictors that included mussel presence/absence, crayfish density, and their interaction as fixed factors and mesocosm as a random factor. We then created three additional iterations of the base model by adding the following fixed factors: (1) crayfish species, (2) initial weight, and (3) crayfish species + initial weight. We used Akaike's Information Criterion corrected for small sample sizes (AICc) to compare the four models and to determine which one was the best supported (i.e., lowest AICc value; Burnham and Anderson, 2002). Models within two AIC values of each other were considered equivalent. We used this AICc analysis to evaluate whether initial weight explained growth of crayfish as well as or better than species when all else was equal (other fixed and random factors) to inform subsequent analyses conducted at the mesocosm level (i.e., only one measurement per mesocosm) that are more easily interpreted.

We next used separate models to examine the effects of mussels and crayfish density on each crayfish species; we could alternatively have included crayfish species as a factor, but because our replication was at the mesocosm level, doing so would have artificially inflated our replication. We designed our experiment to be analyzed with parametric statistics, but used non-parametric statistics in cases when our data did not meet the assumptions and could not be transformed (e.g., normality and homoscedasticity). We chose to analyze crayfish growth as the mean change in crayfish mass rather than length because crayfish length only increases incrementally through molts and we cannot be sure that all our crayfish molted and therefore had an opportunity to increase their length during the experiment. Mass, on the other hand, increases continuously, and was a better performance measure for an experiment of this length. To analyze growth, we first ran a paired t -test to determine if there was a significant difference between species across density and mussel treatments. We also ran separate two-way ANOVAs for each species on a mesocosm level in order to determine the effects of mussels, crayfish density, and their interaction on growth. For survival, we tested for a difference between species across crayfish density and mussel treatments using a paired Wilcoxon signed rank test. We then ran separate generalized linear models using the binomial distribution for each crayfish species to determine the effects of mussels, crayfish density, and their interaction on survival. For activity (mean seconds spent in the open), we used paired Wilcoxon signed rank tests to look for a difference between species across crayfish density and mussel treatments. We then analyzed total and habitat-specific (i.e., cobble and open) activity for both species using Kruskal-Wallis

tests to determine the effects of mussels and crayfish density, and adjusted rank transform tests (Leys and Schumann, 2010) to determine the effect of their interaction. For algal biomass, we used Kruskal-Wallis tests for the effects of mussels and crayfish density, and an adjusted rank transform test to examine the effect of their interaction. For macroinvertebrate biomass, we used a two-way ANOVA in order to test for the effects of mussels, crayfish density, and their interaction. We performed analyses using the AICcmodavg (Mazerolle, 2016), lme4 (Bates et al., 2015) and sft packages (Houpt et al., 2014) in R (R Core Team, 2014) and made graphs using the ggplot2 package (Wickham, 2009).

Results

AICc model comparison

Our AICc comparison revealed that the best supported general linear mixed-effects model was the base model that included crayfish species, rather than the models that included either initial weight only or species and initial weight together, neither of which were within two AICc values of the top model (Table 1). We therefore concluded that, although our sampling methods resulted in a mismatch in the initial size of our crayfish between species, crayfish growth was influenced more by crayfish species rather than differences between species in initial size. Consequently, we proceeded to mesocosm level analyses that did not include initial weight or size as a predictor.

Growth

Mean \pm SE growth was 2.62 ± 0.19 g for rusty crayfish and 1.24 ± 2.31 g for virile crayfish. Rusty crayfish grew significantly more than virile crayfish across density and mussel treatments ($t_{11} = 4.51, p < 0.01$). We found a positive effect of mussels and a negative effect of crayfish density on rusty crayfish growth (Table 2, Fig. 1). No other treatment effects were significant for rusty crayfish, and no significant treatment effects were found for virile crayfish.

Survival

Rusty crayfish experienced little mortality, with 61 of the original 66 (92%) crayfish surviving the entire length of the experiment. Conversely, only 45 out of the initial 66 (68%) virile crayfish survived the full length of the experiment. Rusty crayfish survived significantly more than virile crayfish across crayfish density and mussel treatments ($V = 21, p = 0.04$). We found a negative effect of crayfish density on virile crayfish survival (Table 3, Fig. 2). No other treatment effects were significant for virile crayfish, and no significant treatment effects were found for rusty crayfish.

Activity

The mean \pm SE per capita time that rusty crayfish were active out of shelter was 36.23 ± 15.99 s for cobble habitat, 51.2 ± 29.44 s for open habitat, and 87.43 ± 37.07 s for cobble and open habitat combined (Fig. 3a and c). The mean \pm SE per capita time that virile crayfish were active out of shelter was 6.60 ± 3.55 s for cobble, 14.8 ± 8.76 s for open, and 21.39 ± 11.64 s for cobble and open habitat combined

Table 2

ANOVA results of mussel presence, crayfish density and mussel presence * crayfish density on growth of rusty and virile crayfish. Significant effects denoted by asterisks.

Species	Factor	$F_{1,8}$	p
Rusty	Mussel presence	11.08	0.01*
	Crayfish density	16.81	0.003*
	Mussel presence * crayfish density	0.32	0.59
Virile	Mussel presence	2.57	0.15
	Crayfish density	1.16	0.24
	Mussel presence * crayfish density	0.23	0.64

(Fig. 3b and d). There were no significant differences between species in total activity out of shelter ($V = 12, p = 0.13$), nor in activity in cobble ($V = 9, p = 0.12$) or open ($V = 11, p = 0.36$) habitats across crayfish density and mussel treatments. We found a positive effect of mussels on rusty crayfish activity in the cobble habitat (Table 4). No other treatment effects were significant for rusty crayfish, and no significant treatment effects were found for virile crayfish.

Algal and macroinvertebrate biomass

Mean \pm SE chlorophyll *a* concentration in our mesocosms was 0.003 ± 0.0004 mg/cm². Chlorophyll *a* concentrations were positively affected by mussels ($\chi^2_1 = 5.03, p = 0.02$) but not by crayfish density ($\chi^2_1 = 0.03, p = 0.87$), but there was a significant interaction between these two factors ($MIC < 0.01, p < 0.01$; Fig. 4a), preventing the interpretation of either variable independently of the other. For instance, within the mussel treatment, there were higher chlorophyll *a* concentrations in tanks with low crayfish density, but within the non-mussel treatment, there were higher chlorophyll *a* concentrations in tanks with high crayfish density. Mean \pm SE macroinvertebrate biomass was 6.88 ± 1.52 mg per mesocosm. Macroinvertebrate biomass was not affected by mussels ($F_{1,8} = 0.03, p = 0.87$) or crayfish density ($F_{1,8} = 1.72, p = 0.23$), and there was no significant interaction between these two factors ($F_{1,8} = 0.5, p = 0.5$; Fig. 4b).

Discussion

Given the large potential contribution of facilitative interactions between co-occurring invasive species to the global increase in the incidence and impacts of biological invasions (DeVanna et al., 2011; Ricciardi, 2001; Simberloff, 2006), we sought to evaluate interactions between invasive dreissenid mussels and both native and invasive crayfish within the Laurentian Great Lakes system. In our study, we found greater performance of invasive crayfish in the presence of invasive dreissenid mussels, but no difference in native crayfish performance between mussel treatments. Our results suggest that in sympatry, rusty crayfish may be able to better exploit the resources provided by dreissenid mussels than native crayfish, a phenomenon that may have contributed to their recent spread in the Great Lakes as well as to corresponding declines of native crayfish (Peters et al., 2014).

During our experiment, invasive rusty crayfish exhibited increased growth in the presence of dreissenid mussels, likely in response to additional food resources provided by mussels. Indeed, rusty crayfish were significantly more active on cobble habitats (on which we placed mussels) when mussels were present than absent, and we witnessed

Table 1
General linear mixed effects model comparison of crayfish growth. The base model includes the fixed effects of mussel presence, crayfish density and their interaction, as well as the random effect of mesocosm. Models differ by the addition of the fixed effects crayfish species, initial weight, and crayfish species + initial weight, respectively, and are shown in order of increasing AICc value.

Model	df	AICc	Δ AICc	AICc weight	Cumulative AICc weight	Restricted log likelihood
Base + species	7	415.43	0.00	0.97	0.97	-200.14
Base + species + initial weight	8	422.65	7.22	0.03	1.00	-202.58
Base + initial weight	7	428.07	12.64	0.00	1.00	-206.46
Base	6	431.10	15.67	0.00	1.00	-209.13

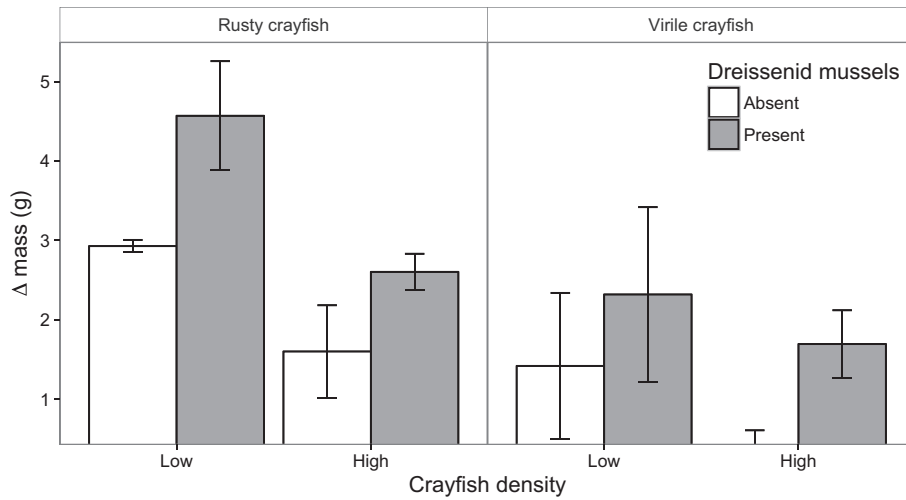


Fig. 1. Mean ± SE growth (g) of rusty and virile crayfish across dreissenid mussel presence/absence and crayfish density treatments. See Table 2 for hypothesis test results.

feeding behavior by rusty crayfish on cobble (but not in open habitats) both in our activity videos and during regular monitoring throughout the experiment. Rusty crayfish likely benefited from the presence of mussels both directly, by consuming mussels, and indirectly, by consuming mussel-associated organisms such as macroinvertebrates and algae. Although we did not find increased macroinvertebrate biomass in the presence of mussels (which might be expected given the short duration of our experiment relative to invertebrate generation times), we did find increased algal biomass, suggesting that mussel-associated algae may have subsidized the diets of rusty crayfish. Our analyses also revealed an interaction between mussels and crayfish density on algal biomass. In the absence of mussels, algal biomass was higher in mesocosms with the high crayfish density treatment, whereas the opposite was true when mussels were present. Algal biomass in mesocosms with the high crayfish density, mussel-absent treatments may have been enhanced by nutrient excretion from crayfish (Fritschie and Olden, 2016). Alternatively, it may be that there was less grazing in the high crayfish density treatment because there was greater crayfish mortality, and crayfish may have been consuming other crayfish instead of algae. We observed dead crayfish that appeared to have been partially consumed on several occasions throughout the course of the experiment, and predation (or cannibalism) within or between crayfish species is common (Figler et al., 1999; Nakata and Goshima, 2006). Future experiments would be required to distinguish between these hypotheses, but our data suggest that mussels may alter the relationship between crayfish density and algal biomass.

In contrast to rusty crayfish, virile crayfish exhibited no perceivable response to mussels, and grew less than rusty crayfish across mussel and crayfish density treatments. Previous studies have shown that virile crayfish consume dreissenid mussels (Perry et al., 1995). Therefore, the growth discrepancy between our two species is likely a result of differential abilities to compete for and exploit mussels and mussel-

associated food resources in sympatry. This finding is corroborated by previous studies that have found that invasive rusty crayfish are better able to exploit food resources than both conspecifics from their native range and native congeners, leading to increased growth (Pintor and Sih, 2009; Sargent and Lodge, 2014). The heightened ability of invasive crayfish to exploit food resources might have arisen as a result of selection for r-selected life history traits in response to low conspecific densities during the invasion process (Burton et al., 2010; Sargent and Lodge, 2014). In our study, the predisposition of invasive rusty crayfish to exploit abundant food resources may thus have prevented virile crayfish from obtaining sufficient sustenance.

Another objective of our experiment was to determine if crayfish density might influence the potential facilitative effects of dreissenid mussels on crayfish. We found that rusty crayfish grew significantly less in the high crayfish density treatment, regardless of the presence or absence of mussels. Within crayfish density treatments, however, rusty crayfish growth was consistently higher in the presence of dreissenids. Interestingly, rusty crayfish growth was nearly equal between high crayfish density, mussel-present treatments and low crayfish density, mussel-absent treatments, suggesting that the presence of mussels can offset the negative effects of high densities on rusty crayfish growth and survival, likely by providing additional food resources. The relatively limited growth of virile crayfish was not influenced by crayfish density; however, virile crayfish experienced heightened mortality at high densities. Although we cannot provide a definitive conclusion regarding the relatively poor survival of virile crayfish (i.e., we had insufficient mesocosms to examine rusty and virile crayfish in allopatry), numerous other studies have assessed potential mechanisms and consequences of competition between virile and rusty crayfish. Capelli and Munjal (1982) and Hill and Lodge (1999) both found that invasive rusty crayfish are competitively dominant over virile crayfish. This competitive advantage translates to increased growth and survival of rusty crayfish (e.g., Hill et al., 1993) in the short term and species replacements in the long term (e.g., Lodge et al., 1986). Specifically, virile crayfish growth declines when rusty crayfish are present because rusty crayfish win contests for food (Hill and Lodge, 1999). In addition, rusty crayfish displace virile crayfish from shelter, increasing their vulnerability to predation (Garvey and Stein, 1994), including potentially from other crayfish (Nakata and Goshima, 2006). Lastly, Brown et al. (1995) ran an experiment in which they assessed growth and survival of virile crayfish in monospecific experimental pools and found that virile crayfish survival decreased with increased density. However, even at the lowest density treatment in Brown et al. (1995)'s experiment (13 crayfish/m²), the mean virile crayfish survival rate (90%) was notably higher than ours was (68%), suggesting that low survival of our virile

Table 3
Generalized Linear Model results of mussel presence, crayfish density and mussel presence * crayfish density on survival of rusty and virile crayfish. Significant effects denoted by asterisks.

Species	Factor	Z ₁₁	p
Rusty	Mussel presence	0.002	0.99
	Crayfish density	0.003	0.99
	Mussel presence * crayfish density	0.000	0.99
Virile	Mussel presence	-2.282	0.78
	Crayfish density	2.335	0.02*
	Mussel presence * crayfish density	0.004	0.99

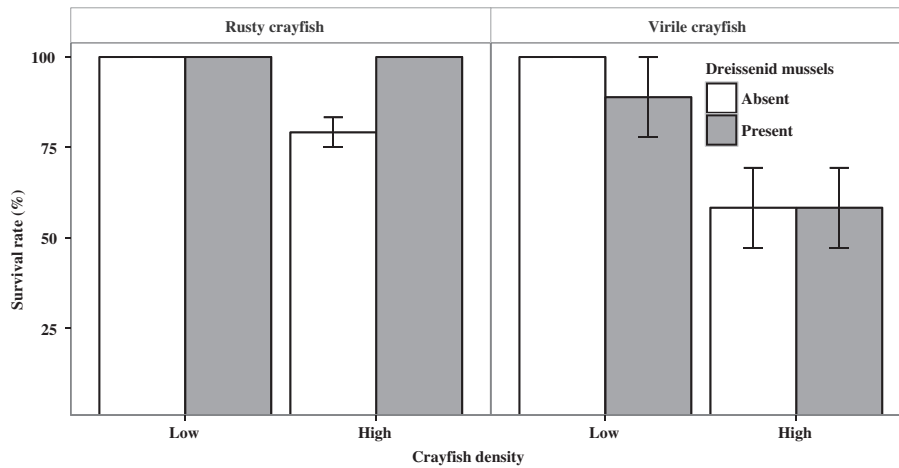


Fig. 2. Mean ± SE survival rate (%) of rusty and virile crayfish across dreissenid mussel presence/absence and crayfish density treatments. See Table 3 for hypothesis test results.

crayfish was driven by factors other than high density alone. We therefore conclude that the decreased survival of virile crayfish in our high crayfish density treatments was likely driven by competition with invasive rusty crayfish.

One possible limitation of our study was the initial mismatch in size between our two crayfish species. Previous studies have shown that the rate of somatic growth of crayfish decreases as size increases (Momot, 1978), so it is reasonable to expect that larger crayfish should grow more slowly than smaller ones. However, our most supported model of crayfish growth used only species identity and not initial size, suggesting that our results were driven by inherent differences between rusty and virile crayfish rather than between crayfish age or size classes. Further, size is important in determining the outcomes of agonistic encounters in crayfish, with larger individuals almost invariably exhibiting dominance over smaller ones (Bergman and Moore, 2003; Glon et al., 2016). In our experiment, virile crayfish were significantly larger than rusty crayfish and yet were outperformed by the latter, contradicting expectations of how size should affect competitive interactions

between crayfish. Accordingly, while we cannot rule out the potential influence of the initial crayfish size mismatch on our results, we believe our observed effects were more attributable to species identity than initial size.

Strong, ecosystem-wide impacts of dreissenid mussels in the Great Lakes and other ecosystems have been documented (e.g., Bunnell et al., 2014), and include facilitations of numerous benthic invasive species (Higgins and Vander Zanden, 2010; Ricciardi, 2001). The recent spread of rusty crayfish in the Great Lakes has coincided with the introduction and spread of invasive dreissenid mussels (Madenjian et al., 2015; Peters et al., 2014). Over the same time period, the distribution of native Great Lakes crayfish has declined (Peters et al., 2014). Our observation of improved rusty crayfish performance in the presence of dreissenid mussels suggests that the spread of these crayfish may have been facilitated by dreissenid mussels. Likewise, our observation of poor performance by virile crayfish, especially in high crayfish density treatments, suggests that the increased abundance of rusty crayfish in the Great Lakes may in turn have negatively affected native crayfish. The negative

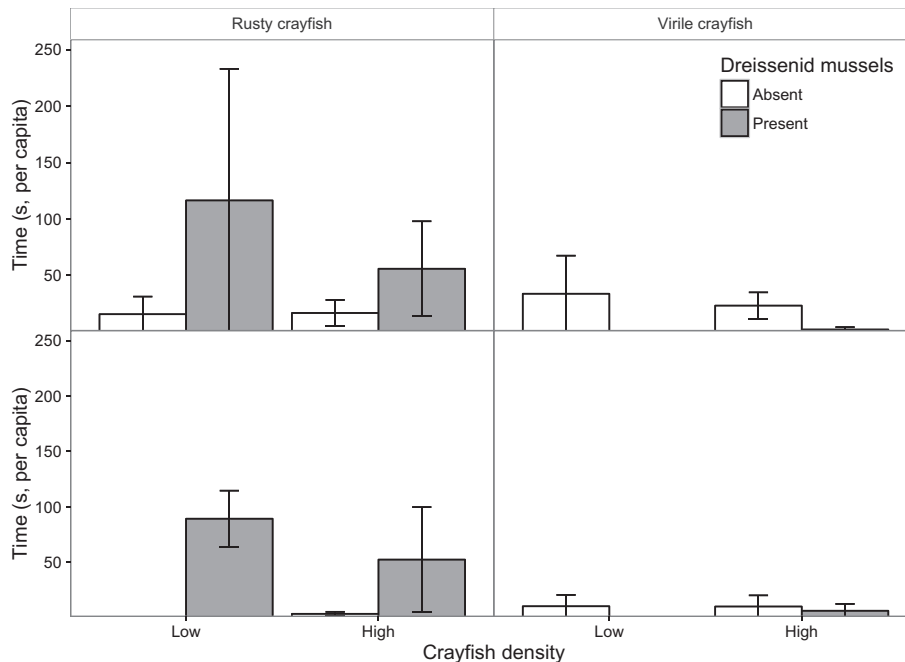


Fig. 3. Mean ± SE per capita time spent on open (top row) and cobble (bottom row) habitat by rusty and virile crayfish across dreissenid mussel presence/absence and crayfish density treatments. See Table 4 for hypothesis test results.

Table 4

Kruskal-Wallis and adjusted rank transform test results of mussel presence, crayfish density and their interaction on total and habitat-specific per capita activity of rusty and virile crayfish. Individual treatment effects evaluated using Kruskal-Wallis tests (χ^2_1); interactions evaluated using adjusted rank transform test (MIC, mean interaction contrasts). Significant effects denoted by asterisks.

Species	Habitat	Factor	χ^2_1 /MIC	p
Rusty	Total	Mussel presence	3.71	0.05
		Crayfish density	0.23	0.63
		Mussel presence * crayfish density	101.88	0.39
	Cobble	Mussel presence	6.80	0.01*
		Crayfish density	0.06	0.81
		Mussel presence * crayfish density	40.27	0.20
Open	Mussel presence	0.11	0.74	
	Crayfish density	1.30	0.25	
	Mussel presence * crayfish density	64.94	0.88	
Virile	Total	Mussel presence	2.04	0.15
		Crayfish density	0.74	0.39
		Mussel presence * crayfish density	-19.00	0.88
	Cobble	Mussel presence	0.71	0.4
		Crayfish density	0.18	0.67
		Mussel presence * crayfish density	-6.39	0.89
	Open	Mussel presence	2.04	0.15
		Crayfish density	0.74	0.39
		Mussel presence * crayfish density	-12.61	0.88

impacts of invasive rusty crayfish in the Great Lakes likely extends beyond other crayfish species. The continued spread of invasive rusty crayfish in the Great Lakes is likely to alter littoral benthic communities and ecosystem processes, as has been observed in other systems (Twardochleb et al., 2013). To date, the impacts of rusty crayfish on the Great Lakes have been minimally studied; however, negative effects on salmonid eggs, macroinvertebrates, and native crayfish have been documented (Jonas et al., 2005; Stewart et al., 1998). Future research focusing on the impacts of rusty crayfish in the Great Lakes may be important for understanding Great Lakes benthic littoral communities.

Our study provides evidence of the facilitation of an invasive ecosystem engineer by another (albeit under laboratory conditions), and is likely to have implications for areas outside of the Great Lakes. Both dreissenid mussels and numerous species of crayfish are widely invasive in freshwater ecosystems throughout the world. Specific instances where these organisms already overlap include France, Britain,

Germany, the Netherlands, and Poland (Molloy et al., 1997; Zu Ermgassen and Aldridge, 2011), and this list is likely to grow as the ranges of invasive crayfish and dreissenid mussels continue to expand (Drake and Bossenbroek, 2004; Morehouse and Tobler, 2013). Additional research is needed to determine the prevalence of dreissenid mussel-mediated facilitations such as the one in our study, with an emphasis on determining whether similar facilitative interactions occur in different systems and with other invasive species of crayfish or crustaceans in general. Further, although the negative ecosystem impacts of invasive dreissenid mussels and invasive crayfish have been studied independently of one another (e.g., Lodge et al., 2012; Madenjian et al., 2015; Twardochleb et al., 2013), research is needed to explore the combined impacts of these invasive taxa in areas where they co-occur. Sympatric invasive species can have complex, non-additive effects on ecosystems, leading to increases in biological invasions and their impacts (Ricciardi, 2001; Simberloff, 2006; Johnson et al., 2009). These impacts may be especially pronounced when the invasive species in question are ecosystem engineers, such as dreissenid mussels and crayfish, as these species alter species compositions and ecosystem processes (Creed and Reed, 2004; Havel et al., 2015; Richardson et al., 2000). This is also true in cases, such as ours, where native species are competitively inferior to invasive species and therefore may not benefit from facilitation when the invasive species is present.

Conclusion

One phenomenon that may be contributing to the global increase in the prevalence of biological invasions is facilitation between invasive species (DeVanna et al., 2011; Ricciardi, 2001; Simberloff, 2006). In our study, we found greater performance of invasive crayfish in the presence of invasive dreissenid mussels, but no difference in native crayfish performance between mussel treatments. This difference between native and invasive crayfish may be due to heightened ability of invasive crayfish to exploit mussel-associated food resources, a trait that might arise as a result of the invasion process (Burton et al., 2010; Sargent and Lodge, 2014). We suggest that interactions between dreissenid mussels and crayfish are likely important in nature and should be further explored, as both of these taxa are spreading to new locations throughout the world and have the potential to impact the ecosystems that they invade.

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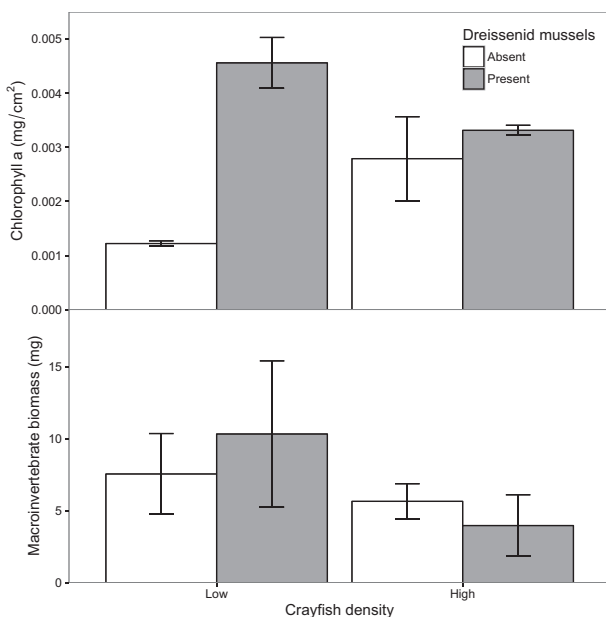


Fig. 4. Mean \pm SE chlorophyll a biomass (mg/cm^2 ; top) and macroinvertebrate biomass (mg ; bottom) across dreissenid mussel presence/absence and crayfish density treatments.

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