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# 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

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(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 cravfish, contributing to recent trends in Great Lakes cravfish 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 m<sup>2</sup>, 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 guarters of the mesocosms as "open" or "cobble" habitat. Cobble habitat guarters 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 m<sup>2</sup> of cobble habitat in each mesocosm. The stocked mussel biomass represented an approximate density of 3225 individuals/m<sup>2</sup> (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/m<sup>2</sup> (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/ $m^2$ ) and high density mesocosms with 16 crayfish (8 crayfish/ $m^2$ ), 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/m<sup>2</sup> 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

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