Rusty Crayfish

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In the field of Invasion Ecology, there is a core question when looking at invasive species: will it cause harm to the ecosystem? That question has many answers depending on the invasive species. For some invasive species, they pose no threat at all or no longer pose a threat. For others, they pose an active threat and will continue to spread to new areas. For the rusty crayfish, *Orconectes rusticus*, that answer is a bit unique. The rusty crayfish (*Orconectes rusticus*) presents a huge danger to native biodiversity in areas where it quickly passes through due to its predation of many organisms and interbreeding with native congeners. However, because its transport is limited to human vectors and its spread is limited by abiotic and biotic factors, if humans stop using the rusty crayfish for biocontrol of macrophytes and as live bait for fishing, it will no longer be introduced to any new areas.

Understanding the four stages of invasion for a specific invader is imperative in order to understand the invader. This idea is well documented with rusty crayfish. The rusty crayfish is a crustacean native to the Ohio River Basin and its tributaries (Hein et al., 2007). However, the rusty crayfish has invaded not only nearby states such as Wisconsin, but also far away areas such as Ontario and Oregon (Hein et. al., 2007; Sorenson et. al., 2012). The reason the rusty crayfish has invaded multiple places in the US and Canada is its two methods of movement; human-mediated jump dispersal for transport followed by natural movement through streams for spread.

The spread of rusty crayfish to new areas due to human-mediated jump dispersal is primarily due to its past use as live bait for fishing as well as its use for macrophyte control (Hein et al. 2007). During the 1970s, fishermen in northern Wisconsin used rusty crayfish when fishing in lakes (Byron & Wilson 2001). Additionally, its use in controlling macrophyte populations in lakes as well as being a popular aquarium pet have caused its spread (Hein et al. 2007). Furthermore, the higher the human use of a lake is, the more likely the lake is to be invaded by rusty crayfish (Puth & Allen 2005). Although the exact reasons vary, the transport of the rusty crayfish is entirely dependent on humans as a vector.

Once the rusty crayfish is transported to a new area, it easily establishes itself and begins to spread (Byron & Wilson, 2001). It quickly spreads to bodies of water near its original entry point (Puth & Allen, 2005). It does so easily due to its varied diet and large range of acceptable environmental conditions (Byron & Wilson, 2001). The spread is affected by many factors, including the availability of cobble substrates to live on, the abundance of food such as macrophytes and invertebrates, and the prevalence of predators in the body of water (Byron & Wilson, 2001). The rusty crayfish has spread the fastest in Oregon, the farthest area it has been transported to (Sorenson et. al., 2012). During the first five years of invasion in Oregon, the rusty cravfish doubled its range; in Wisconsin, it took twenty years for the rusty crayfish to spread throughout a single body of water (Puth & Allen, 2005, Sorenson et. al., 2012). Although the cause of the rapid spread could be for a variety of reasons, the most likely cause is a lack of predation and competition as there are no native crayfish in the invaded river (Sorenson et al. 2012). Regardless of the factors that affect spread, the rusty crayfish cannot invade new areas naturally; a human vector is required.

Understanding the transport and spread methods of the rusty crayfish helps to understand why areas, both close to and far from its native range, are considered invaded. The rusty crayfish has never migrated out of the Ohio River Basin since the populations evolved in that area and there is no evidence that native populations are migrating now (Puth & Allen, 2005). Any new area that the rusty crayfish is found in, even areas extremely close, such as Wisconsin and Michigan, is due to being transported by humans (Puth & Allen, 2005). Every area outside of the Ohio River Basin the rusty crayfish populations inhabit are, at the least, connected to bodies of water that have high levels of human use (Hein et. al., 2007). Once they are transported to a new area, they easily establish due to their versatility and lack of predators; they then begin to spread throughout that body of water and throughout connected bodies of water (Byron & Wilson, 2001). The spread of the rusty crayfish is dependent not only on the availability of substrates and food sources but also on the prevalence of predators and competitors (Byron & Wilson, 2001).

Regardless, the areas the rusty crayfish is considered to be invading are the bodies of water that the rusty crayfish was transported to by humans and subsequently spread from. If the rusty crayfish was never transported to certain bodies of water, it would never migrate there naturally. The rusty crayfish is a great example of how one stage of invasion is affected by previous stages.

Although the first three stages of an invasion are important to understanding the invader, the impact stage of invasion is more important because it includes all the effects on the invaded ecosystem. For the rusty crayfish, the impacts are the result of its behavior (McCarthy et. al., 2006). Although this behavior is similar to native crayfish, the rusty crayfish can escape predators faster and has fewer predators than any other native crayfish (Kuhlmann, 2008). As a result, the rusty crayfish not only outcompetes other native crayfish but also extensively preys on species that are accustomed to the more passive and slower native crayfish (McCarthy et al., 2006). The impacts of the rusty crayfish on new environments include the direct and indirect effects of decreases in local populations and hybridization with native crayfish species.

In bodies of water the rusty crayfish is introduced to, many native populations of fish, benthic invertebrates, and native crayfish decline dramatically (McCarthy et al., 2006). The rusty crayfish is a generalist omnivore and eats a variety of organisms, from invertebrates to algae to small fish and even piscivore eggs (Kreps et al., 2016). This feeding behavior is consistent with almost every other crayfish species (Renai & Gherardi, 2004). However, compared to native crayfish, the rusty crayfish grows faster, has a larger body and pincers, and is less susceptible to predation even as a juvenile (Perry et al., 2001). As a result, the rusty crayfish is a better predator than native crayfish and preys on organisms at a higher rate than native crayfish (Perry et al., 2001; Kreps et al., 2016).

Native crayfish in areas invaded by the rusty crayfish are already directly hindered by the reduced population of their prey; the indirect effects of prey population reduction hinder them even further (Kreps et al., 2016). By feeding on a variety of invertebrates, the rusty crayfish damages the micro food web of invertebrates in lakes, further reducing the population of invertebrates (McCarthy et al., 2006). On a larger scale, the reduced populations of small fish and invertebrates forces the larger piscivore fish to rely more on other food sources, mainly native crayfish (Kreps et al., 2016). The increased predation by the piscivores along with reduced prey populations caused by the rusty crayfish cause native crayfish population to decline further.

Even though native crayfish already have less to eat, are outcompeted for available food, and are at risk of increased predation, the rusty crayfish further threatens their populations by hybridizing with native crayfish (Perry et al., 2001). The rusty crayfish is much more aggressive than clearwater crayfish during mating (Kuhlmann, 2008). Additionally, the rusty crayfish is very similar to the clearwater crayfish and produce fertile, fit offspring (Kuhlmann, 2008; Perry et al., 2001). As a result, male rusty crayfish mate with female clearwater crayfish; rusty crayfish mate more often than male clearwater crayfish; rusty crayfish mate more often than male clearwater crayfish; fewer pure clearwater and rusty crayfish (Perry et al., 2001). Due to this, fewer pure clearwater crayfish eggs are produced each mating season (Perry et al., 2001). Since the rusty crayfish is more aggressive in mating than many native crayfish, any native crayfish species that has the ability to mate with the rusty crayfish and produce fertile, fit offspring is at risk of disappearing and being replaced by a hybrid.

These behaviors are the reason for the rusty crayfish's huge impact on the ecosystems it invades. The behaviors of the rusty crayfish are not significantly different than native crayfish but instead are simply "more" than that of native crayfish. The rusty crayfish is bigger, stronger, faster, and more aggressive than native crayfish (Kuhlmann, 2008). This allows the rusty crayfish to be a more efficient predator than native crayfish (Kuhlmann, 2008). The species normally preyed on by native crayfish are not prepared to deal with a more aggressive crayfish and their populations decline (McCarthy et al., 2006). This leads to food webs being drastically altered on small and large scales (McCarthy et al., 2006). Additionally, the already suffering natives are at risk of being replaced by hybrids because the rusty crayfish outcompetes natives in mating as well (Perry et al., 2001). The rusty crayfish poses a significant threat to native crayfish populations due to their ability to outcompete and eventually either slowly reduce their population to nothing or replace them with a hybrid of rusty and native crayfish.

Many invaders, regardless of how bad for the native ecosystem, are limited in what they can do by various factors. These limiting factors, along with certain control measures, can dramatically decrease an invader's effects on the ecosystem. Despite the damage that the rusty crayfish causes, it is limited by multiple factors, too. The rusty crayfish's effects on invaded ecosystems are limited by where it spreads, which is limited by waterway connections, calcium concentration, and the presence of *Lepomis* species.

Due to their dependence on calcium for their exoskeletons, rusty crayfish are hindered in bodies of water with low calcium concentration (Edwards et al., 2013). All crustaceans need calcium during molting to harden their exoskeletons (Edwards et al., 2013). Crustaceans have the highest calcium demand for animals and crayfish have the highest calcium demand of any crustacean (Edwards et al., 2015). The rusty crayfish is currently expanding north into areas with much lower dissolved calcium concentrations than their native bodies of water (Edwards et al., 2013). With less calcium dissolved in the water, the rusty crayfish incorporates less of it into its carapace, making its body softer and more easily preyed upon (Edwards et al., 2015). Therefore, the rusty crayfish is limited in the range it can invade due to its dependence on calcium to sufficiently harden its exoskeleton.

Although calcium dependence is a better limiting agent for the spread of rusty crayfish, the presence of *Lepomis*, or sunfish such as pumpkinseed and bluegill, in lakes results in rusty crayfish only achieving low population abundance in a wide range of environments (Teztlaff et al., 2011; Roth et al., 2007). *Lepomis* species keep rusty crayfish population levels low by readily consuming juveniles (Roth et al., 2007). Their effectiveness is due mainly to their high population abundance compared to larger and more common predators of crayfish, such as yellow perch or rock bass (Teztlaff et al., 2011). In fact, bluegill and pumpkinseed are better at reducing crayfish populations than common crayfish predators (Teztlaff et al., 2011). Due to their skilled hunting of juvenile crayfish, *Lepomis* species effectively lower populations of rusty crayfish in bodies of water where both crayfish and *Lepomis* species are present.

Despite the biotic and abiotic factors that limit where rusty crayfish leave an impact, the real reason the rusty crayfish is not a future threat is because humans are its vector (Byron & Wilson, 2001). The rusty crayfish has never spread outside of the Ohio River Basin naturally; the only reason the rusty crayfish is an invasive species is its use as live bait and its use as macrophyte control (Hein et al., 2007). Therefore, government regulation preventing the use of rusty crayfish for anything that might cause it to be transported to new areas should eliminate its threat to new areas.

The rusty crayfish presents a huge threat to native biodiversity that it is established in. In bodies of water where the rusty crayfish occurs, they threaten the populations of benthic invertebrates, small fish, and native crayfish (Kreps et al., 2016). The rusty crayfish also threatens to wipe out native crayfish in bodies of water or replace it with a hybrid of the native crayfish and the rusty crayfish (Perry et al., 2001). However, with the right regulations, no other areas should be affected. Without human vectors, the rusty crayfish cannot spread to new areas (Hein et al., 2007). Additionally, the rusty crayfish only achieves low population abundances in bodies of water with low calcium concentrations or high *Lepomis* population abundances (Edwards et al., 2013; Teztlaff et al., 2011). Therefore, the rusty crayfish is a huge problem, but only in the areas it has already invaded.

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