

Final Report

## **Endoparasite impacts on rusty crayfish (*Orconectes rusticus*)**

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Start Date: April 15<sup>th</sup> 2011

End Date: April 15<sup>th</sup> 2012

### **Introduction**

Invasive rusty crayfish are a major driver of community composition in northern Wisconsin lakes where they extirpate native crayfish and reduce macrophyte, invertebrate, and fish populations (Capelli 1982, Lodge et al. 1994, Wilson et al. 2004). Crayfish population monitoring indicates that rusty crayfish remain at low densities in some lakes where they are introduced, but reach “outbreak” densities in other lakes. Understanding which factors are important in controlling crayfish density is essential for reducing the impacts of rusty crayfish. Feedbacks between abundances of fish predators, macrophytes, and crayfish may drive lake communities towards either high or low densities of crayfish (Roth et al. 2007). Intensive trapping combined with management of fish populations has been effective at reducing rusty crayfish populations (Hein et al. 2007). Parasites may also reduce rusty crayfish populations, but we have only recently begun to examine how parasites influence crayfish densities. Understanding parasite dynamics and how they alter interspecies relationships may provide alternative tools to managers or indicate lakes where particular management plans will be effective.

A series of closely related trematode parasites, *Microphallus spp.*, infect the hepatopancreas, or digestive organ, of rusty crayfish (*Orconectes rusticus*) and congeners (*O. propinquus* and *O. virilis*) in some northern Wisconsin lakes (Roesler 2009, Overstreet 2011). Crayfish are an intermediate host for *Microphallus spp.* and must be consumed by a predator for the parasites to complete their lifecycle. The identity of this predator is still unknown, but closely related trematodes can use a variety of definitive host predators including some species of fish and reptiles (Overstreet 1992). Roesler (2009) found that most lakes with low densities of rusty crayfish had *Microphallus sp.* present; whereas, *Microphallus sp.* was absent or detected at low levels in most lakes with high densities of rusty crayfish. These data suggest that *Microphallus spp.* could be affecting rusty crayfish populations, but little is known about how infection with these parasites alters rusty crayfish fitness. In addition, we hypothesized that high rusty crayfish abundance may reduce the abundance of the parasite via indirect mechanisms.

Previous research indicates that rusty crayfish can decrease snail populations through direct predation and reduction of macrophyte habitat in lakes (Weber and Lodge 1990, Lodge et al. 1994). Because snails from the family Hydrobiidae are a host of *Microphallus spp.* (Overstreet 2011), we expected that when rusty crayfish reach high densities, declines in host snail populations would cause the abundance of *Microphallus spp.* to decrease. Therefore, if *Microphallus spp.* have a negative impact on rusty crayfish fitness, these parasites may reinforce a state of low crayfish abundance in a lake, and high crayfish abundance may repress the parasites (Figure 1).

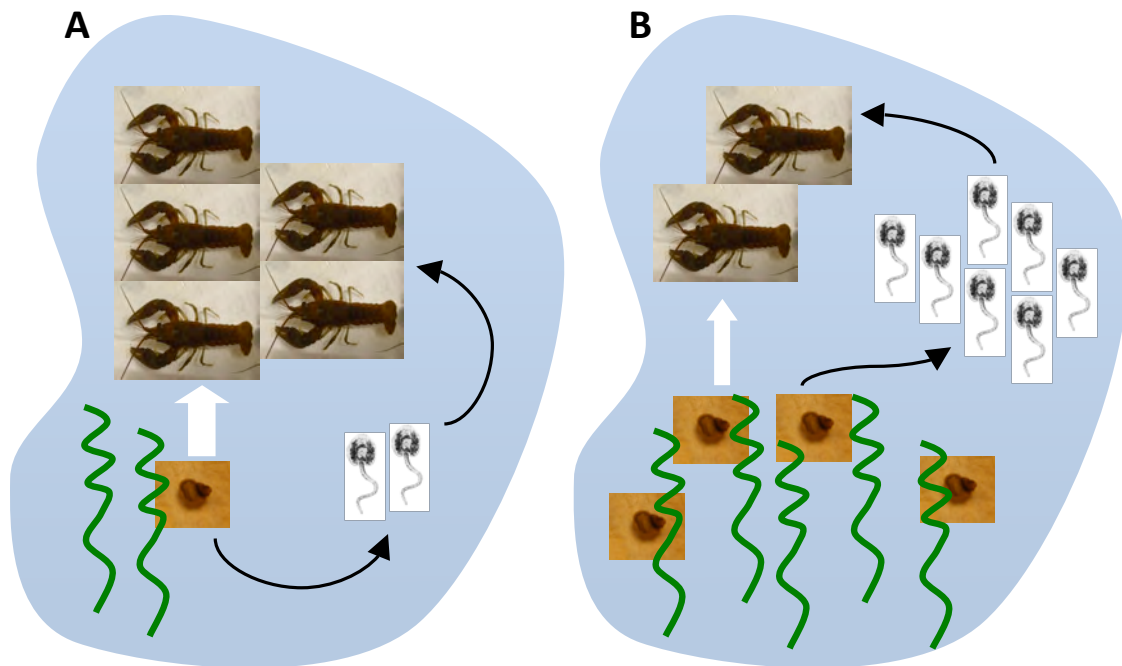


Figure 1. Hypothesized dynamics between rusty crayfish, macrophytes, snails, and *Microphallus spp.* in a lake with high crayfish abundance (A) and low crayfish abundance (B). Black arrows indicate movement of *Microphallus spp.* cercariae between snail and crayfish hosts. White arrows indicate trophic interactions between crayfish and both macrophytes and snails. Size of white arrows is reflective of the magnitude of impact that the crayfish population has on lower trophic levels.

In addition, because crayfish must be consumed by a predator for *Microphallus spp.* to complete their lifecycle, we hypothesized that *Microphallus spp.* may manipulate the behavior of crayfish to increase their vulnerability to predation. Behavioral manipulation by parasites is a common and complex phenomenon which can cause dramatic changes in host phenotype. Parasites that require multiple hosts to complete their lifecycle often manipulate intermediate hosts to increase their own transmission to higher trophic levels because this strategy is

evolutionarily advantageous (Combes 1991). For example, when infected with a trematode, crustacean amphipods swim to the water's surface where they are more likely to be consumed by birds (Lefevre et al. 2009). Crickets infected with a parasitic worm exhibit erratic behavior and leap into streams where the worms exit the body to reproduce (Sato et al. 2011), and tropical ants infected with a nematode mimic ripe fruit in their appearance and behavior so they are consumed by frugivorous birds (Yanoviak et al. 2008). While researchers have uncovered a number of examples of parasites that can manipulate their hosts to increase transmission, the ecological impacts of many of these interactions remain unexplored (Lefevre et al. 2009). However, we know from a few studies that manipulative parasites can have important impacts on the ecological community (e.g. Sato et al. 2011).

In the summer of 2010, a student in our lab, Kevin Towle, conducted research on how the *Microphallus* parasite affects the ability of northern clearwater crayfish to compete for shelter. The ability of crayfish to obtain shelter is essential for avoiding predation (Garvey et al. 1994, Soderback 1994), so we expected *Microphallus spp.* may alter this behavior to increase transmission to the definitive host predator. Towle found that northern clearwater crayfish with higher infection levels were less competitive for shelter than individuals with lower infection levels. Thus, infected northern clearwater crayfish may be more susceptible to predation. Because northern clearwater crayfish are closely related to rusty crayfish, we expected that *Microphallus spp.* would also alter rusty crayfish behavior to make them more vulnerable to predation.

In order to address these hypotheses, we conducted a field study examining crayfish infection levels in 15 lakes in Vilas and Oneida counties and examined how infection levels were related to crayfish abundance, crayfish population fluctuations between years, and hydrobiid snail abundance at different sites within these lakes. We also examined the impact of infection with *Microphallus spp.* on behavior and competitive ability in rusty crayfish.

## **Methods**

### *Field Survey*

Crayfish were collected from 15 northern Wisconsin lakes in the summer of 2010 using baited minnow traps. We also collected crayfish from Lake Ottawa in Michigan. The same trapping protocol (same number of traps in the same locations) has been used in many of these lakes for multiple years to assess changes in crayfish abundance over time. A more detailed description of trapping methods is available in Garvey et al. (2003). I chose lakes for crayfish collection that had been trapped at least two times (once per year) within the 5 years preceding crayfish collection in 2010. Many of these lakes had been trapped 3 or 4 times. I examined 40 – 100 crayfish in each lake at 5 – 15 different sites within each lake. More crayfish were

processed in those lakes where *Microphallus spp.* were rare to increase the likelihood of detecting the parasites if they were present.

Lakes that were sampled include eight lakes that are part of a multi-lake survey examining snail and macrophyte abundance and diversity in response to changes in rusty crayfish abundance (Ashley Baldrige, University of Notre Dame, unpublished data). In these lakes, snail abundance and diversity was assessed in 2011 using a substrate core at the same sites where crayfish were collected for crayfish and *Microphallus spp.* abundance in 2010. These data allowed us to examine the relationship between host snail abundance and crayfish infection levels.

In 2011, the eight multi-lake survey lakes and one additional lake from the *Microphallus spp.* abundance survey were trapped again for crayfish. Comparing trends in crayfish abundance between years allowed us to assess the importance of *Microphallus spp.* abundance on crayfish population trends. Data from the other seven lakes provide more information about the general prevalence and distribution of *Microphallus spp.* in northern Wisconsin. Crayfish trapping data from 2006 to 2011 was used to assess overall crayfish population trends in all 16 lakes.

#### *Methods for assessing infection level*

Crayfish were placed on ice in the field and later frozen for preservation of metacercariae. To count the number of *Microphallus spp.* metacercariae in the hepatopancreas (digestive organ) of each crayfish, samples were thawed and the hepatopancreas was removed through dissection. The hepatopancreas was then flattened between two glass slides and examined under a dissecting microscope. The top slide contained an 8mm<sup>2</sup> grid to allow for more accurate counts. Metacercariae are typically distributed uniformly throughout the hepatopancreas, which allowed accurate estimates to be obtained by sub-sampling. If crayfish were highly infected (> 1,000 metacercariae), metacercariae were only counted in half of the hepatopancreas. In a few very highly infected individuals, the hepatopancreas was sub-sampled by counting metacercariae in 3 gridded squares and visually estimating hepatopancreas area.

#### *Behavioral Experiments*

We collected rusty crayfish from locations with low infection levels in Big Lake (Cisco chain) and Lake Ottawa (MI) and experimentally infected half of these crayfish by exposing them to snails in the family hydrobiidae. Snails were collected from locations in High Lake and Plum Lake that contained highly infected rusty crayfish. Snails were contained in screened pouches with aquatic plants during crayfish infection to prevent crayfish from consuming snails, and aquaria received direct fluorescent light for 3 hours a day to induce shedding of cercariae.

Crayfish were initially exposed to 1,000 snails for a period of roughly one month. This did not result in desired infection levels, so snail number was increased to four to five thousand snails per aquarium and crayfish were exposed for an additional month. Control aquaria also contained screened pouches with aquatic plants (but no snails), and these crayfish were also exposed to direct fluorescent light for 3 hours a day. At the end of the infection experiment, experimentally infected crayfish had an average of 38.6 metacercariae per crayfish and control crayfish had an average of 0.6 metacercariae per crayfish. We also collected some crayfish in Plum Lake from a site where we had previously found very high infection levels and a site where most small crayfish were uninfected. These crayfish were also used in behavioral experiments to examine the impact of very high infection levels that we could not achieve with our experimental infection. I also conducted some preliminary behavioral experiments using northern clearwater crayfish (*O. propinquus*) and virile crayfish (*O. virilis*) which I collected from Plum Lake (MI) and Horse Head Lake.

We tested these crayfish for shelter use (crayfish alone with one shelter), shelter competition (two size and sex matched crayfish compete for one shelter), and food acquisition time (the amount of time before a crayfish obtains a section of earthworm placed in the bucket) in the lab at Notre Dame (Figure 2). For shelter use trials, an individual we expected to be infected was matched by size (within 1 mm) and sex with an individual we expected to be uninfected. Crayfish were dissected after experiments to confirm infection status. Each crayfish was placed in a bucket filled to 8 cm depth with aerated well water. Sand covered bottom of each bucket, and each crayfish was provided with a PVC pipe shelter. Crayfish were placed in the bucket in the evening and location of the crayfish (inside or outside the shelter) was recorded 5 times between 9:00 and 15:00 the following day with a minimum of 45 minutes between recordings.

For shelter competition, size and sex matched crayfish were placed together in one bucket with a single PVC pipe shelter. Crayfish were left to acclimate over night, and the location of each crayfish was recorded the following day using the same protocol described above. In the buckets that contained two crayfish, the crayfish that spent the most time in the shelter was recorded as the winner of the competition (in almost all trials only one crayfish spent time in the shelter).

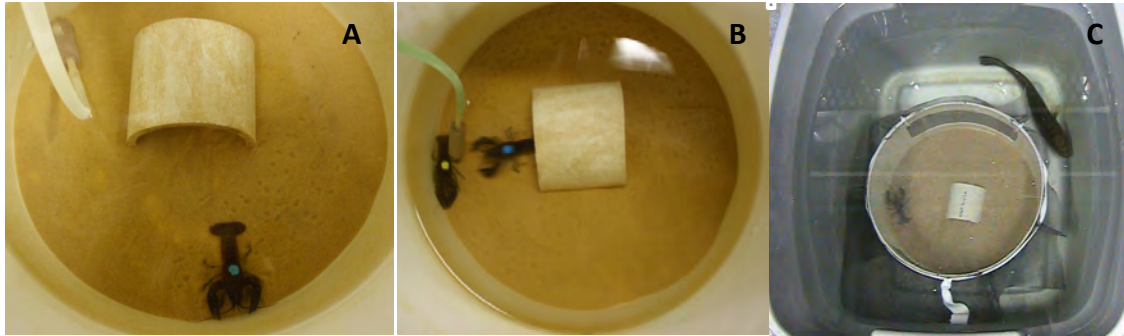


Figure 2. (A) Shelter use (single crayfish) arena. (B) Shelter competition arena. (C) Shelter use arena with a smallmouth bass in the surrounding tub to simulate a high risk environment.

Food acquisition trials were carried out by placing a section of earthworm in a bucket with a single crayfish and one shelter. We recorded the amount of time it took each crayfish to obtain the worm. Trials were terminated after one hour if the crayfish had not yet obtained the worm. If *Microphallus spp.* cause crayfish exhibit risky behavior and ignore predators, we expected infected crayfish to be quicker to approach the worm than uninfected crayfish in the presence of a predator.

To assess the impact of predators on behavior, shelter use and food acquisition were carried out in the presence or absence of a smallmouth bass (*Micropterus dolomieu*) to simulate high and low predation risk. Shelter competition was carried out only in the presence of a smallmouth bass. Smallmouth bass were placed within a larger tub surrounding the bucket and crayfish could visually and chemically detect the bass through screened openings in the side and top of the bucket (Figure 2). The screen prevented the bass from consuming the crayfish. Crayfish were dissected after all experiments to assess infection levels with *Microphallus spp.*

## Results

### Field Survey

Crayfish infection level had a significant negative relationship with the average *Microphallus spp.* count per crayfish at each site ( $F_{1,161} = 31.18$ ,  $P < 0.001$ ; Figure 3), indicating that sites with high infection levels have low crayfish abundance.

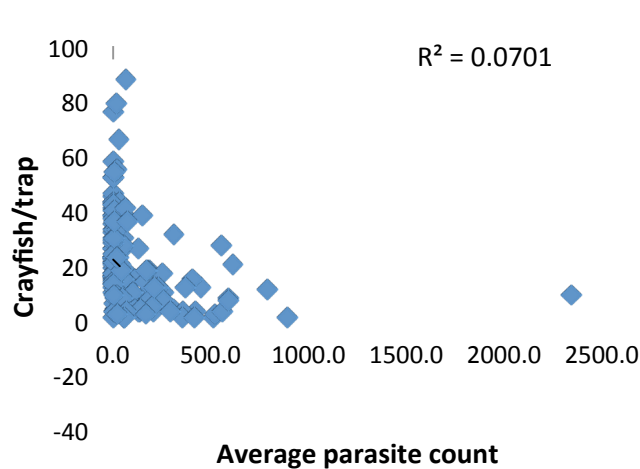


Figure 3. Relationship between the average *Microphallus spp.* count per crayfish at each site at the number of crayfish trapped at that site in 2010.

At the whole-lake scale, the negative relationship between crayfish population estimates and *Microphallus spp.* infection levels was non-significant ( $F_{1,14} = 0.86$ ,  $P = 0.3701$ ), indicating that infection levels did not predict crayfish abundance within an entire lake.

We did not find a significant relationship between hydrobiid snail density and infection levels at a site ( $F_{1,73} = 0.00$ ,  $P = 0.9664$ ). However, significantly higher *Microphallus spp.* counts were associated with sites where we detected hydrobiid snails ( $F_{1,73} = 8.78$ ,  $P = 0.0041$ ; Figure 4). These data indicate that while the presence of snails was important for the abundance of *Microphallus spp.* at a site, the abundance of snails was not a good predictor of infection levels.

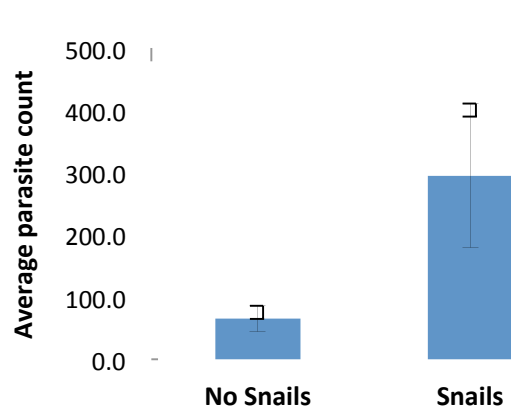


Figure 4. *Microphallus spp.* counts per crayfish ( $\pm$  SE) at sites where snails were or were not detected.

We found a trend indicating that infection level in 2010 had a negative relationship with the % change in crayfish abundance at a site between 2010 and 2011 ( $F_{1,98} = 2.88$ ,  $P = 0.0927$ ; Figure 5). This trend was not observed at the whole-lake level ( $F_{1,7} = 0.66$ ,  $P = 0.4437$ ). These data indicate that high infection levels at sites within lakes were associated with declines in crayfish abundance in those locations. However, higher infection levels did not necessarily lead to lakewide population reductions.

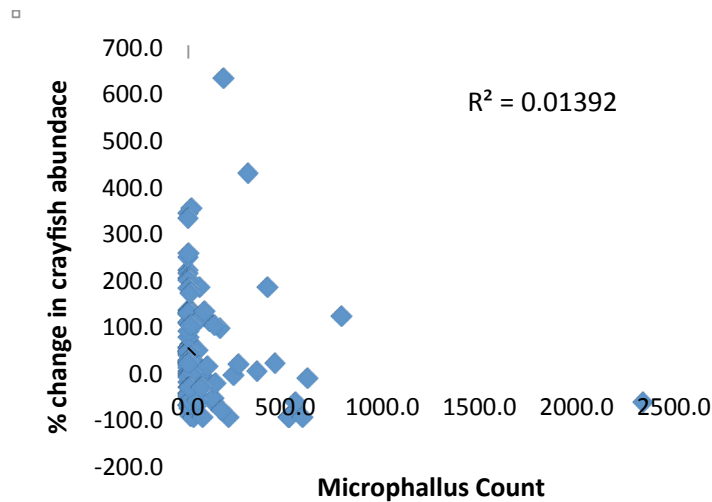


Figure 5. The relationship between *Microphallus spp.* counts per crayfish at a site and the percent change in crayfish abundance between 2010 and 2011.

We also used trapping data from the past six years (2006-2011) to determine if *Microphallus spp.* abundance in 2010 could predict crayfish population trajectories over longer time periods. We did not have data for all years in all lakes, but had at least three years of data for each lake. There was not a significant relationship between *Microphallus spp.* abundance and crayfish population trajectory ( $F_{1,14}=1.46$   $P = 0.2470$ ). However, Plum lake was the only lake with very high abundances of crayfish and *Microphallus spp.* included in our sample, and the crayfish population in this lake does show a clearly declining trend (Figure 6).



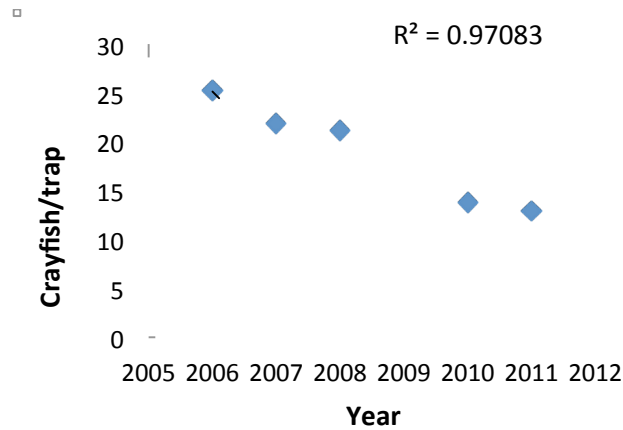


Figure 6. Average crayfish trap catches in Plum Lake over the past 6 years.

All analyses using *Microphallus spp.* counts at each site were  $\log_{10}$  transformed to meet assumptions of normality, but were back transformed in figures for ease of interpretation.

### *Behavioral Experiments*

#### *Rusty Crayfish*

There was no difference in shelter use (crayfish alone in a tank with one shelter) between infected and uninfected rusty crayfish, and no effect of predatory fish presence on shelter use, suggesting that infection does not alter the amount of time rusty crayfish spend in shelter when it is available and unoccupied.

There were differences in shelter competition, however, which were dependent upon infection level. Unexpectedly, rusty crayfish that were infected at low levels (< 50 parasites) were more likely to win shelter competition ( $\chi^2_{1,13} = 3.769$ ,  $P = 0.052$ ) when paired with uninfected individuals (Table 1). However, those that were infected at high levels (> 50 parasites) were more likely to lose shelter competition when paired with uninfected individuals ( $\chi^2_{1,18} = 5.556$ ,  $P = 0.018$ ; Table 1). Rusty crayfish that were infected at low levels also displayed aggressive behaviors more frequently than uninfected crayfish in the presence of conspecifics ( $t = 2.06$ ,  $P = 0.047$ ,  $d.f. = 32$ ).

Table 1. Number of infected and uninfected shelter competition winners when the infected crayfish in the match was infected at low levels (with less than 50 parasites) or high levels (with more than 50 parasites).

| INFECTION LEVEL       | UNINFECTED WINS | INFECTED WINS |
|-----------------------|-----------------|---------------|
| LOW (< 50 parasites)  | 3               | 10            |
| HIGH (> 50 parasites) | 14              | 4             |

Food acquisition trials revealed that rusty crayfish approached the worm more quickly when predatory fish were absent ( $F_{1,77} = 8.821$ ,  $P = 0.004$ ), but there was no difference in acquisition time between infected and uninfected crayfish, and no interaction between predator presence and infection level. These data indicate that infection with *Microphallus spp.* did not alter food acquisition behavior in rusty crayfish.

#### *Virile and Northern Clearwater Crayfish*

Northern clearwater crayfish were the only species in which there was a trend for reduced shelter use in infected individuals ( $F_{1,19} = 4.12$ ,  $P = 0.0567$ ). Few shelter competition experiments were completed for northern clearwater crayfish due to high mortality of the infected individuals we collected, and there was no significant difference in competitive ability between infected and uninfected individuals ( $\chi^2_{1,7} = 0.143$ ,  $P = 0.705$ ). Because research conducted in the summer of 2010 suggests that infected northern clearwater crayfish are less competitive for shelter, we expect that additional experiments would have revealed this trend. More virile crayfish that were infected at low levels than those infected at high levels won shelter competitions (all the virile crayfish we collected were infected to some extent); however, this result was not significant ( $\chi^2_{1,20} = 1.8$ ,  $P = 0.18$ ). These preliminary data indicate that infection has different effects on different crayfish species. Only rusty crayfish had increased aggression and competitive ability at low infection levels, whereas the data suggest that even low levels of infection may reduce the ability of northern clearwater crayfish to hide from predators.

#### **Discussion**

We found that high abundances of *Microphallus spp.* can reduce rusty crayfish populations in locations within lakes. Because infection levels are variable within lakes, some sites with low infection levels may continue to have high abundances of rusty crayfish while other sites experience declines. The lack of a clear relationship between *Microphallus spp.* abundance and crayfish abundance or crayfish population declines at the whole-lake level may

be caused by this variability in infection levels within a lake. It is also possible that a relationship between infection levels and lakewide crayfish population trends would be apparent if more lakes with very high parasite abundances were included in our analysis. We only had one lake with very high abundances of *Microphallus spp.* and high crayfish abundances, Plum Lake, and this lake does show a clear trend in crayfish population declines over the past six years. Lakes in this state should be rare, because our data suggest that high infection levels lead to declines in crayfish abundance. These data offer further support for previous research conducted by Roesler (2009) that suggests that very high infection levels in a lake can lead to lakewide rusty crayfish population declines.

We found *Microphallus spp.* to be widespread, and present in all of the lakes that we studied. Our data suggest that it is important to survey a number of sites within a lake when determining *Microphallus spp.* abundance, because abundances can be quite variable between locations in the same lake.

Contrary to our hypothesis, *Microphallus spp.* abundance was not explained well by densities of host hydrobiid snails, suggesting that the negative relationship between crayfish abundance and parasite abundance is likely due to impacts of *Microphallus spp.* on crayfish fitness. Our ability to detect hydrobiid snails at a site was associated with higher infection levels in crayfish at that site, so sites with very high densities of crayfish where snail abundance is dramatically reduced are likely to have lower abundances of *Microphallus spp.* for this reason, but *Microphallus spp.* abundance can be quite variable when hydrobiid snails are present. The data showing declines in crayfish populations between years are unlikely to be caused by variations in snail densities, because it takes many years for snail populations to recover following rusty crayfish declines (Ashley Baldrige, University of Notre Dame, unpublished data).

Results from behavioral experiments indicate that infection with *Microphallus spp.* is unlikely to have negative impacts on crayfish fitness when crayfish are infected at low levels (< 50 parasites). These crayfish were more aggressive and more competitive against uninfected individuals. Therefore, because they are better able to obtain shelter, they are likely less vulnerable to predation. We expect behavioral differences between infected and uninfected individuals are due to behavioral manipulation by *Microphallus spp.*, but these parasites may be more successful at increasing transmission to higher trophic levels in some crayfish species than in others.

Results from behavioral experiments also suggest that high levels of infection reduce rusty crayfish fitness. The lower competitive ability of these crayfish is indicative of reduced vigor in highly infected individuals. More parasites are present in larger crayfish because they are older and have had more time to be exposed to *Microphallus spp.* Decreased ability to

secure shelter would make larger crayfish that have accumulated more parasites more likely to be removed from the population by predators. Smaller individuals may be able to outcompete the more infected crayfish for shelter, but these crayfish will have lower reproductive output, which may cause population declines. In addition, reduced competitive ability in highly infected individuals likely means that these crayfish are weaker due to pathogenic effects of infection. Other trematode metacercariae have pathological effects on hepatopancreas tissue in other decapods (Robaldo et al. 1999). Infection, therefore, may have other negative effects on crayfish fitness in addition to altering vulnerability of highly infected crayfish to predation.

Overall, the data from the field study and behavioral experiments indicate that low to moderate infection with *Microphallus spp.* does not negatively impact rusty crayfish fitness or cause rusty crayfish population declines, but high abundances of *Microphallus spp.* can lead to reductions in rusty crayfish populations. While *Microphallus spp.* abundance can help managers predict population changes in lakes where parasite abundance is very high, the variation in the relationships we observed indicate that crayfish population trends are complex, especially at the whole-lake level, and many variables such as habitat, food availability, and predator abundance are likely also important. Therefore, all crayfish population trends cannot be explained by *Microphallus spp.* abundance. Our results indicate that predator populations could be especially important for decreasing crayfish abundance in lakes with high abundances of *Microphallus spp.*, and management of predator populations in those lakes may be especially effective.

Many lakes with low to moderate infection levels had very high rusty crayfish abundances. In lakes with low or moderate levels of infection, the parasites may favor rusty crayfish in competitive interactions with other crayfish species and could assist rusty crayfish in replacing these other crayfish. Because northern clearwater crayfish and virile crayfish do not have the same ecological impacts as rusty crayfish (reducing the abundance of macrophytes, macroinvertebrates, and fish), these findings could have major implications for the ecological community in many aquatic ecosystems in northern Wisconsin.

Our future research will focus on how these widespread parasites affect interactions between different crayfish species. When conducting preliminary experiments we collected different crayfish species from different lakes, so it is possible that they could have been infected with different species of *Microphallus* and that these species have different behavioral effects on crayfish. We will experimentally infect all crayfish species with the same snails in future research. In addition, future research will examine whether moderate infection levels can hasten crayfish species replacements in lakes. Understanding how infection levels impact the ability of rusty crayfish to reach high densities and replace other crayfish could allow managers to better predict whether the introduction of rusty crayfish into a lake is likely to

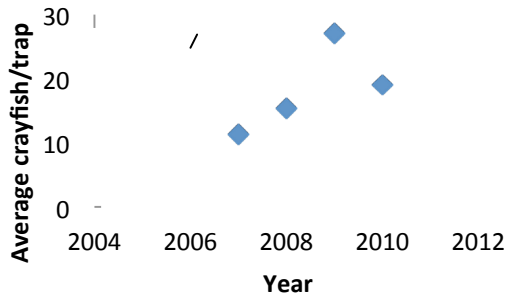
cause ecological and economic harm. Those lakes where harm is especially likely could be prioritized for measures that reduce the likelihood of introductions.

## Literature Cited

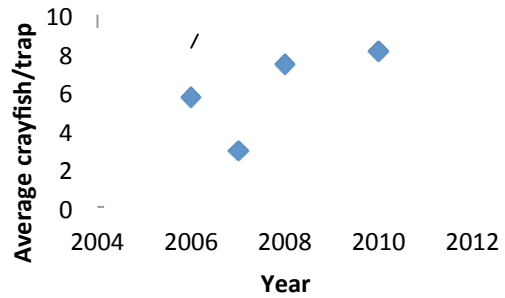
- Capelli, G. M. 1982. Displacement of northern Wisconsin crayfish by *Orconectes rusticus* (Girard). *Limnology and Oceanography* **27**:741-745.
- Combes, C. 1991. Ethological aspects of parasite transmission. *American Naturalist* **138**:866-880.
- Garvey, J. E., J. E. Rettig, R. A. Stein, D. M. Lodge, and S. P. Klosiewski. 2003. Scale-dependent associations among fish predation, littoral habitat, and distributions of crayfish species. *Ecology* **84**:3339-3348.
- Garvey, J. E., R. A. Stein, and H. M. Thomas. 1994. Assessing how fish predation and interspecific prey competition influence a crayfish assemblage. *Ecology* **75**:532-547.
- Hein, C. L., M. J. Vander Zanden, and J. J. Magnuson. 2007. Intensive trapping and increased fish predation cause massive population decline of an invasive crayfish. *Freshwater Biology* **52**:1134-1146.
- Lefevre, T., C. Lebarbenchon, M. Gauthier-Clerc, D. Misse, R. Poulin, and F. Thomas. 2009. The ecological significance of manipulative parasites. *Trends in Ecology & Evolution* **24**:41-48.
- Lodge, D. M., M. W. Kershner, J. E. Aloï, and A. P. Covich. 1994. Effects of an omnivorous crayfish (*Orconectes rusticus*) on a freshwater littoral food web. *Ecology* **75**:1265-1281.
- Overstreet, R. M. 2011. Microphallid parasites of Wisconsin crayfishes. Report for The Wisconsin Department of Natural Resources.
- Overstreet, R. M., R. W. Heard, and J.M. Lotz. 1992. *Microphallus fonti sp.n.* (Digenea: Microphallidae) from the red swamp crawfish in southern United States. *Memórias Instituto Oswaldo Cruz, Rio de Janeiro* **87** (Supplement 1):175-178.
- Robaldo, R. B., J. Monserrat, J. C. B. Cousin, and A. Bianchini. 1999. Effects of metacercariae (Digenea : Microphallidae) on the hepatopancreas of *Chasmagnathus granulata* (Decapoda : Grapsidae). *Diseases of Aquatic Organisms* **37**:153-157.
- Roesler, C. 2009. Distribution of a crayfish parasite, *Micropahllus sp.*, in northern Wisconsin lakes and apparent impacts on rusty crayfish populations. Report for the Wisconsin Department of Natural Resources.
- Roth, B. M., J. C. Tetzlaff, M. L. Alexander, and J. F. Kitchell. 2007. Reciprocal relationships between exotic rusty crayfish, macrophytes, and *Lepomis* species in northern Wisconsin lakes. *Ecosystems* **10**:74-85.
- Sato, T., K. Watanabe, M. Kanaiwa, Y. Niizuma, Y. Harada, and K. D. Lafferty. 2011. Nematomorph parasites drive energy flow through a riparian ecosystem. *Ecology* **92**:201-207.
- Soderback, B. 1994. Interactions among juveniles of 2 fresh-water crayfish species and a predatory fish. *Oecologia* **100**:229-235.
- Weber, L. M., and D. M. Lodge. 1990. Periphytic food and predatory crayfish - relative roles in determining snail distribution. *Oecologia* **82**:33-39.
- Wilson, K. A., J. J. Magnuson, D. M. Lodge, A. M. Hill, T. K. Kratz, W. L. Perry, and T. V. Willis. 2004. A long-term rusty crayfish (*Orconectes rusticus*) invasion: dispersal patterns and community change in a north temperate lake. *Canadian Journal of Fisheries and Aquatic Sciences* **61**:2255-2266.
- Yanoviak, S. P., M. Kaspari, R. Dudley, and G. Poinar. 2008. Parasite-induced fruit mimicry in a tropical canopy ant. *American Naturalist* **171**:536-544.

Appendix. Crayfish population trends in lakes sampled.

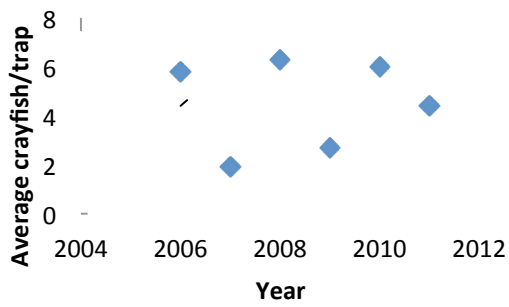
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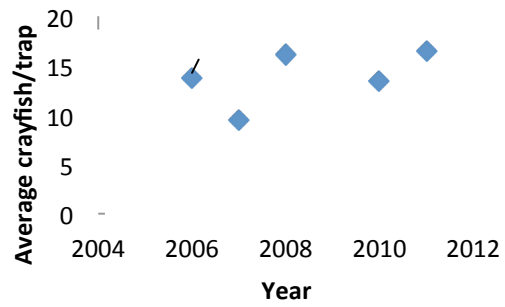
### Birch



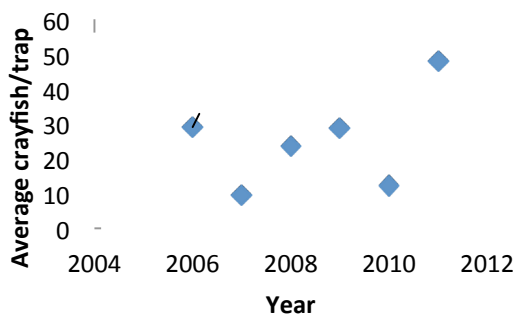
### High



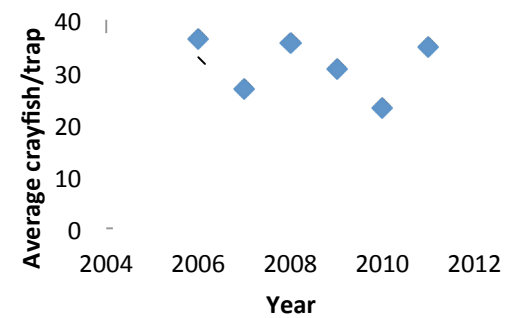
### Little John



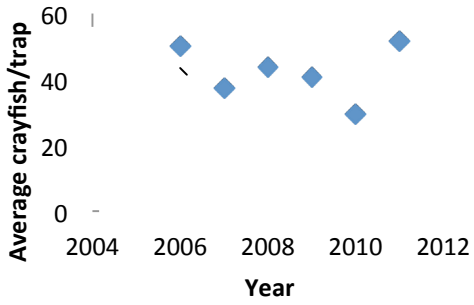
### Ottawa



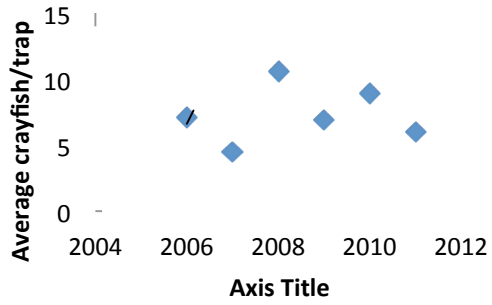
### Papoose



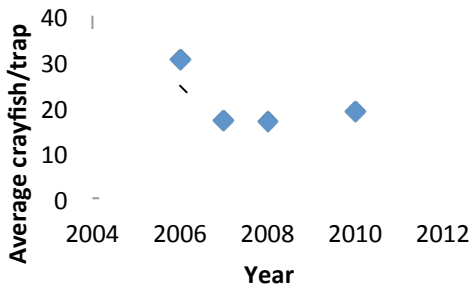
### Presque Isle



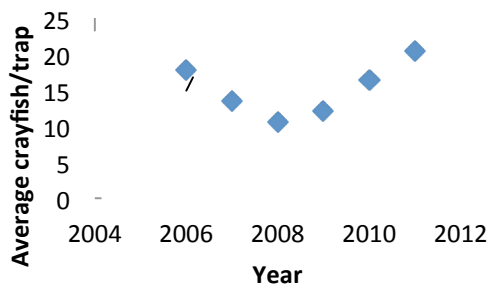
### Spider



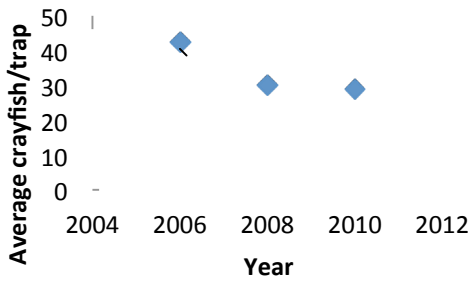
### South Turtle



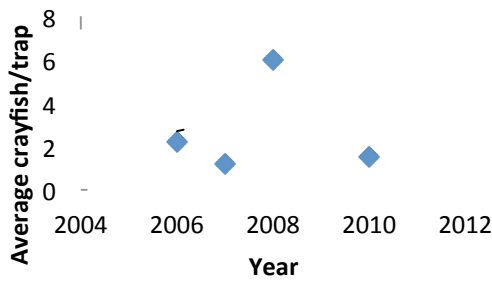
### Squirrel



### Star

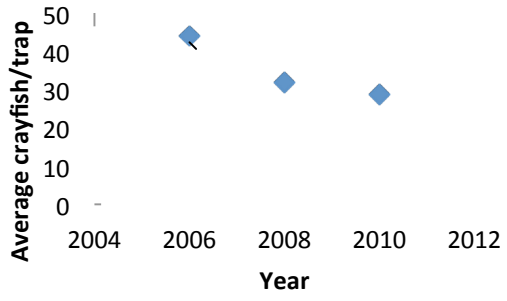


### Tamarack

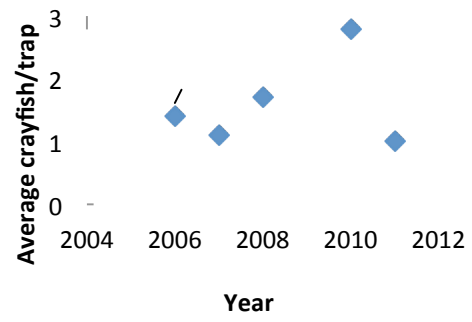




### Trout



### Van Vliet



### White Sand

