# Islands as an Invasion Pathway for the Rusty Crayfish, *Orconectes rusticus*

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## Abstract

The invasive crayfish, *Orconectes rusticus*, was first discovered in Lake of the Woods, Ontario in 1964 and has since spread throughout many areas of the lake. Invasion fronts are generally identified along shorelines but islands would provide an opportunity for faster invasion to opposite shores. Lake of the Woods provides an excellent opportunity to determine if island colonization occurs. I investigated this hypothesis by sampling islands and adjacent shorelines throughout the northwest portion of Lake of the Woods. Most islands behind the identified invasion front in Ptarmigan Bay and all islands sampled throughout Corkscrew Channel and Clearwater Bay have been invaded by the rusty crayfish. Water depth and distance from mainland did not seem to prevent colonization. A second, previously unidentified invader, *Orconectes immunis*, did not colonize islands isolated by depths greater than 12 meters. It was also found that each species weakly preferred certain substrate types. Although this explains a small amount of the distribution of these species, *O rusticus* and *O. virilis*, which are habitat generalists, were still found on most substrate types. It is likely that invasion of Lake of the Woods by *O. rusticus* will continue with little deterrent.

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# Introduction

Canada is home to more than 1400 invasive species (Colautti *et al*., 2006). Most of these invaders have little impact, but some cause major changes in aquatic food webs and the habitats that they invade. These invaders have been called nuisance non-indigenous species (NIS) because they can cause major problems. In freshwater habitats introductions of non-indigenous species can be connected to sports fishing and ballast water discharge, but may also occur through aquarium release or aquaculture escapes (Dextrase and Mandrak, 2006). Nuisance introductions have included the sea lamprey (*Petromyzon marinus (Linneaus)*), the zebra mussel (*Dreissena polymorpha (Pallas)*), the round goby (*Neogobius melanostomus (Pallas))* and the rusty crayfish *(Orconectes rusticus (Girard*)). The projected cost for six aquatic invasive species in Canada is $343 million dollars per year (Colautti *et al*., 2006). Invasive species are the second most important factor causing declines of native freshwater fish in Canada (Dextrase and Mandrak, 2006). While some NIS have been successfully managed to some degree (sea lamprey, see Wappel, 2003) most are difficult to control once established in an ecosystem and may be impossible to eliminate, especially in open-water systems such as the Great Lakes. Even if controlled, maintenance can be very expensive (sea lamprey control costs ~$6 million annually (Colautti *et al*., 2006)). Prevention of further invasion is often a much more practical goal.

The following review aims to better understand a particularly worrisome invasive species, *Orconectes rusticus* (the rusty crayfish).

**Ecology of *Orconectes rusticus***

Crayfish are found throughout the world on all continents (excluding Antarctica) as both native and invasive species. These freshwater invertebrates inhabit both lotic and lentic waters and belong to several major families, Astacidae, Cambaridae (both found in the Northern Hemisphere) and Parastacidae (found in the Southern Hemisphere) (Fetzner and Crandall, 2002). Crayfish are generally nocturnal, using shelter during the day to avoid predators. They are omnivorous, but prefer animal protein in their diet as opposed to macrophytes or detrital materials (Momot, 1995). Because they are generally larger, more abundant and longer lived than most other invertebrates in a given ecosystem, they can greatly affect the systems they inhabit (Momot, 2004).

The rusty crayfish is native to the Ohio River Basin of the midwestern United States (Momot, 1997), encompassing portions of Ohio, Kentucky, Tennessee, Indiana and Illinois. It has spread throughout many areas in the United States as well as in Canada, and has successfully invaded these waters. The rusty crayfish has several easily identifiable features. Colouration is generally reddish-brown with a prominent rust-coloured spot on the lateral aspect of the carapace (Figure 1). The fingers of the chelae possess orange tips as well as conspicuous black bands (Hobbs and Jass, 1988). *Orconectes rusticus* was first found in Canadian waters in 1964 in Lake of the Woods, northwestern Ontario (Crocker and Barr, 1968). It is likely that this population was introduced through the dumping of bait buckets, as this location is such a great distance from the original range. Another population was discovered in 1985 at Pounsford Lake, Sibley Peninsula, Ontario, which seemed to have been established for some period of

Figure 1. Photograph showing the colouration and general appearance of the rusty crayfish, *Orconectes rusticus.* Notice the rust coloured spot on the lateral aspect of the carapace.

time. Several other populations were found over the next few years throughout northwestern Ontario including Lake Lenore, Wiswell Lake, Milkshake Lake, Pounsford Lake and the Pigeon River below Partridge Falls (Momot, 1992). The species has since spread further to inhabit many areas around Lake Superior and Lake Erie. While newly colonized areas tend to show relatively small abundances, population densities increase rapidly behind invasion fronts (Wilson *et al*., 2004).

It would seem that barriers to the movement of the rusty crayfish are much more effective in stream or river habitats. In these areas, beaver dams, hydro dams, flood control weirs and waterfalls can block, or at least slow movement rather effectively (Momot, 1997). Very shallow waters also seem to hinder mobility (El-Hashemy, 1999). In lake systems, however, there may not be many such barriers. The rusty crayfish prefers temperatures around 22$^{o}$C (Mundahl and Benton, 1990), which may discourage movement through deeper water where a temperature gradient exists, although movement may still occur in spring and fall during annual turnovers when the lake is isothermal.

The introduction of rusty crayfish into many water systems throughout Canada and the United States has resulted in a series of negative effects. These include reduction of macrophyte beds, decreased invertebrate and fish populations and eradication or displacement of native crayfish species (Wilson *et al*., 2004).

At one time crayfish were thought to be opportunistic feeders, taking advantage of any food source available to them including invertebrates, fish eggs, detritus, algae and macrophytes. This idea has been challenged by Momot (1995), who observed that crayfish destroy much vegetation while foraging for animal protein. Momot concluded that the rusty crayfish would consume macrophytes only when the supply of animal

protein had been exhausted. This phenomenon is often seen when crayfish are found in high densities (Lodge and Lorman, 1987; Chambers *et al*., 1990). When animal protein is no longer available, consumption of macrophytes and detritus will increase, leading to decreased macrophyte density and diversity (Lodge *et al*, 1994; Wilson *et al*, 2004; Lodge and Lorman, 1987). Unfortunately, macrophyte habitats are important spawning grounds for many fish as well as important sources of shelter to many organisms. As a result, their degradation can often lead to population declines across a food web.

In addition to degrading litoral habitat, crayfish feed on many invertebrate species leading to a decrease in many invertebrate populations. Charlebois and Lamberti (1996) observed declines in both abundance and species richness of Diptera, Ephemeroptera and Trichoptera in the presence of *O. rusticus*. Wilson *et al*. (2004) reported decreases in Odonata, Amphipoda and Trichoptera. Results from other studies, however, have been inconsistent (Lodge *et al*., 1994). It is likely that these decreases are due to a combination of predation and habitat destruction. Reduction of snail populations, which are important algivores, has also been observed (Charlebois and Lamberti 1996; Wilson *et al*. 2004) resulting in increased periphytic biomass (Lodge *et al*., 1994; Charlebois and Lamberti, 1996).

Fish populations are affected by the removal of macrophyte beds by crayfish, in part because they can be important spawning grounds and shelter areas for many fish species. They are also affected directly through crayfish consumption of fish eggs. For example, lake trout (*Salvelinus namaycush*) spawn on gravel substrates, which are a preferred crayfish habitat, and so eggs are often consumed during foraging (Jonas *et al*., 2005). Both bluegill (*Lepomis macrochirus (Rafinesque)*) and pumpkinseed sunfish

(*Lepomis gibbosus (Linnaeus)*) populations have declined in the presence of *O. rusticus*. Declines may have been caused by egg predation, decreased habitat or through competition for invertebrates as food (Wilson *et al*., 2004).

Crayfish native to lakes that have been invaded by *O. rusticus* often become displaced from their preferred habitat; their populations may be reduced or eliminated as a result of the behavioral and physical advantages the rusty crayfish possesses. The virile crayfish, *O. virilis*, is one species that has been negatively impacted by of the rusty crayfish. In situations where *O. rusticus* has invaded, *O. virilis* is in direct competition for food and shelter. Because of their aggressive nature, rusty crayfish will out-compete this native crayfish resulting in its lowered growth and increased predation rates (Hill and Lodge, 1999). *Orconectes rusticus* does not seem to express the same slowed growth rates in the presence of competition (Hill and Lodge, 1999). Because of this, *O. virilis* populations have been completely eliminated from several water bodies in Ontario including Lenore Lake, Pounsford Lake and portions of the Pigeon River (Momot, 1997).

The rusty crayfish is an extremely successful invader. *Orconectes rusticus* has higher metabolic and growth rates, more aggressive behavior and earlier egg deposition than native crayfish such as *O. virilis*. The rusty crayfish also shows copulation interference behavior during mating between other crayfish species (Garvey and Stein, 1993).

The life cycles of *O. virilis* and *O. rusticus* are very similar except for the time of egg deposition, which occurs earlier for *O. rusticus* than for *O. virilis*. Juveniles of *O. rusticus* also grow faster and exhibit more aggressive behavior than those of the virile crayfish (reviewed in Momot, 1997).

Size is often a good indicator of dominance and superiority in crayfish. This is especially true for chelae size. Large chelae are advantageous in agonistic encounters, defense against predators, and during reproduction (Garvey and Stein, 1993). These appendages require a large input of energy to grow, but are very beneficial. Large chelae allow for dominance over smaller crayfish, securing of females during copulation and interruption of copulation between other individuals. Large chelae also make crayfish less susceptible to fish predation, as fish tend to select for smaller crayfish. Even at equal sizes, *O. virilis* is more susceptible to fish predation than *O. rusticus* (Garvey *et al*., 1994). Where rusty crayfish tend to act aggressively towards approaching fish by raising their claws, virile crayfish show less aggression and increased swimming behavior, during which the use of chelae is not possible. In habitats with limited shelter such as sand and macrophyte substrates where *O. rusticus* would force *O. virilis* from covered areas, greater predation of *O. virilis* will occur. In highly cobbled areas with many opportunities for shelter, however, there is little predation on either species (Garvey *et al*., 1994).

The occurrence of agonistic encounters between crayfish is influenced by both intrinsic and extrinsic factors. These may include body and chela size, stage during molting, stage during reproduction, gender, hunger and the resource at stake. An individual assesses these factors to determine a course of action: approach, retaliation, intensification of agonistic behaviors or escape. Generally larger size, especially chela size, gives crayfish a competitive advantage over smaller individuals (Bergman and Moore, 2003). Dominance during an agonistic encounter provides the winner with heightened social status, which aids in the securing of resources, while the subordinate

individual may lose access to these resources, lowering its fitness. An agonistic encounter will generally begin when two crayfish come within two body lengths of each other. An approach will occur followed by increasing levels of aggression such as threat displays, chelae contact, and fighting, until one individual retreats (Bergman and Moore, 2003). Being a large, aggressive species, *O. rusticus* is often dominant over native species such as *O. virilis* and other invaders such as the northern clearwater crayfish, *Orconectes propinquus (Girard)*, which is also common in the Great Lakes region (Bergman and Moore, 2003; Garvey and Stein, 1993; Garvey *et al*., 1994). This dominance allows the rusty crayfish to secure the best shelter and feeding areas in locations at optimal temperatures for growth. Greatest rates of survival seem to be associated with temperatures near 22$^{o}$C, with highest survival occurring at a range of 20 to 25$^{o}$C, and optimum growth occurring around 27$^{o}$C. Temperatures below 20$^{o}$C are generally avoided when possible (Mundahl and Benton, 1990). Less aggressive individuals are forced to move into areas with unfavorable temperatures, where they may experience lower growth and higher mortality rates (Peck, 1985). Stocker and Huber (2001) showed that hungry crayfish acted in a much more aggressive manner than those that are satiated. Agonistic behaviors also have a longer duration in the presence of a food source than when food is absent. This was also true in the presence of other resources of high value such as shelter (Bergman and Moore, 2003).

Over winter, crayfish are generally inactive, with males in the form I (reproductive) stage of life possessing relatively large chelae and thin, functioning copulatory stylets. Sexually mature form I males become active in the spring, marking the beginning of the mating period (Crocker and Barr, 1968; Berrill and Arsenault, 1984).

Sexual activity begins when water temperature reaches approximately 4$^{o}$C. Shortly after, conspecific males begin exhibiting agonistic behavior to secure fecund females, and attempts to interrupt copulations are common (Berrill and Arsenault, 1984). Sperm from the males is stored in the female's seminal receptacle until egg extrusion occurs in late April when fertilization can take place. At this point females become much less conspicuous, going into hiding while extrusion occurs. It is thought that the time of egg extrusion may be linked to photoperiod and/or water temperature. With the removal of females from the environment, male agonistic behavior declines, with more energy focused towards foraging. Form I males will molt to non-reproductive form II throughout May. After molting males possess relatively small chelae and thickened, sclerotized copulatory stylets, which are not functional for mating (Crocker and Barr, 1968; Berrill and Arsenault, 1984). By late May eggs begin hatching and form I juveniles will attach to the pleopods of the mother until mid June when they become form III juveniles (Berrill and Aresenault, 1982). At this point juveniles are large enough to fend for themselves and will leave the mother, who undergoes a molting period. Males will undergo a second molt in late summer, regaining their form I characteristics for a period, during which reproduction will again take place (Hobbs and Jass, 1988). Sperm from these copulations is stored until spring for fertilization when egg extrusion occurs again. Male *O. rusticus* also produce a sperm plug which blocks the opening of the female's seminal receptacle preventing dilution of sperm as well as inhibiting other males from contributing to the sperm supply. It is thought, however, that the stiff, pointed copulatory stylets found on form I males may be used to remove sperm plugs from previous copulations (Berrill and Arsenault, 1984).

*Orconectes rusticus* has been shown to mate with congeners and interrupt mating between congeners. Several examples of possible hybridization have also been discovered. Hybridization may occur between *O. rusticus* and the spinycheek crayfish. *Orconectes limosus (Rafinesque)* (Smith, 1981), as well as with *O. propinquus* (Perry *et al*., 2001a; Perry *et al*., 2001b; Perry *et al*., 2002). No hybridization is known to occur among *O. rusticus* and *O. virilis* (Capelli and Capelli, 1980; Perry *et al*., 2002). Even if hybridization does not occur, interference of intraspecific mating among other species could still result in population declines.

**Objectives**

The objectives of my project were to determine if rusty crayfish use islands as an invasion pathway and whether water depth or the distance from mainland affected colonization of those islands. To test these possibilities areas throughout the northern portion of Lake of the Woods were surveyed to determine the distribution of the invading crayfish *O. rusticus*.

# Materials and Methods

## Study Area

The study area for my project was located in Lake of the Woods in northwestern Ontario. Portions of the lake extend into Manitoba as well as Minnesota, with two thirds located in Ontario. Lake of the Woods is part of the Winnipeg-Nelson River drainage system, which covers over 384,000 hectares. At the US/Canada border, Lake of the Woods is only 100km from Lake Superior, and at its southernmost point is only 100km from both the Mississippi and Red River-Nelson drainages. The lake drains northward, emptying into the Winnipeg River. Because of its close proximity to other water bodies and its popularity as a tourist destination, Lake of the Woods is at high risk of invasion and introduction of non-native species. As well, it may act a pathway for invasive species to other systems via the Winnipeg River.

The entire lake system is located on the Precambrian shield, but the areas covered by the lake are incredibly diverse physically, chemically and biologically. There are large variations in depth, productivity, alkalinity, total dissolved solids (TDS) and species composition throughout sections of the lake system. Because the area is so diverse, it can be separated into several major basins, as has been done by the Ontario Ministry of Natural Resources (Figure 2). The northern portion of the lake tends to be deeper and less productive than the southern portion. The northern portion also has a more rocky lake bottom and contains a much larger number of islands (T. Mosindy, OMNR, pers. comm.).

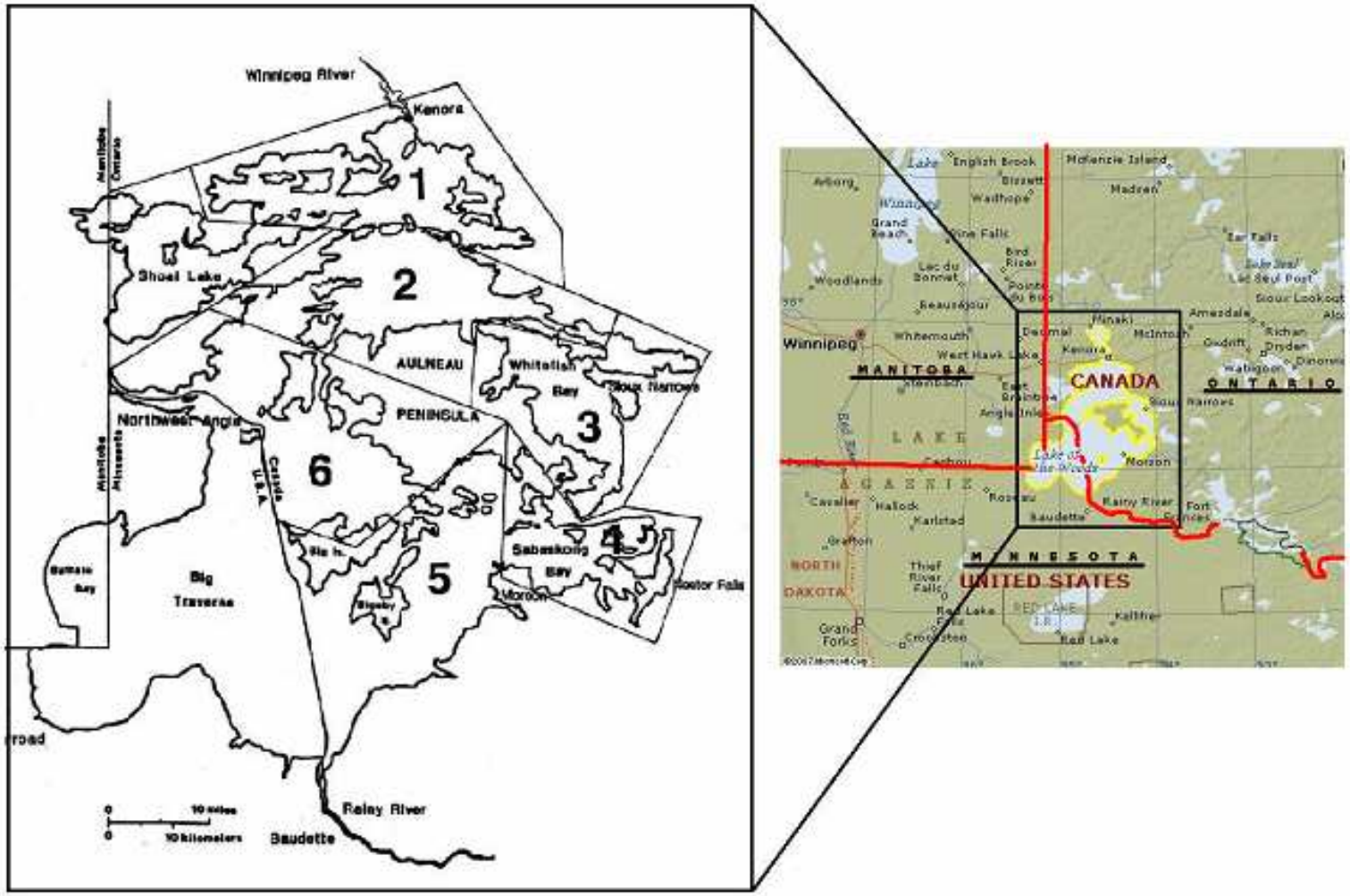


**Figure 2.** Map showing the study area. Lake of the Woods region covers areas in Ontario, Manitoba and Minnesota (right) and is partitioned into seven separate sectors by the Ontario Ministry of Natural Resources (left). Sampling took place in Sector 1 in the northern portion of the lake.

**Sampling Sites**

Sampling was carried out in Sector 1 of the Lake of the Woods area, as designated by the Ontario Ministry of Natural Resources (Figure 2). The total sampling covered only a small portion of this area but was still large (~62,000 m of shoreline). The sampling area consisted of shorelines within Clearwater Bay, Corkscrew Channel and Ptarmigan Bay (Figure 3), all located around 49°N, 94°W. Rusty crayfish were known to have invaded from the Kenora area, located northeast of the study site, and was known to have moved west, but its distribution in the study area was unknown.

**Sampling Methods**

Sampling was based on a protocol developed by the Ontario Ministry of the Environment at the Dorset Environmental Science Center (Somers, Keith per. comm.). Minnow traps were modified to have trap openings of approximately 3.5 cm to allow for capture of larger crayfish. Traps were baited with wet, fish flavored cat food, which was placed in plastic film canisters that had been perforated several times with a hole punch. Traps were arranged along traplines, each containing a set of six traps. Traps were attached to the line with three meters of rope between each trap. The first trap of each trapline was anchored near shore at a minimum depth of 0.5 meters, and the remaining traps were deployed from the boat perpendicular to shore. Each trapline was designated as an individual site. The shoreline was divided approximately into 500m sections, in which three sites were located. When possible, sites within each 500 meter section were chosen from different substrate types; namely rock, macrophyte and detritus, to capture as much of the habitat diversity as possible.

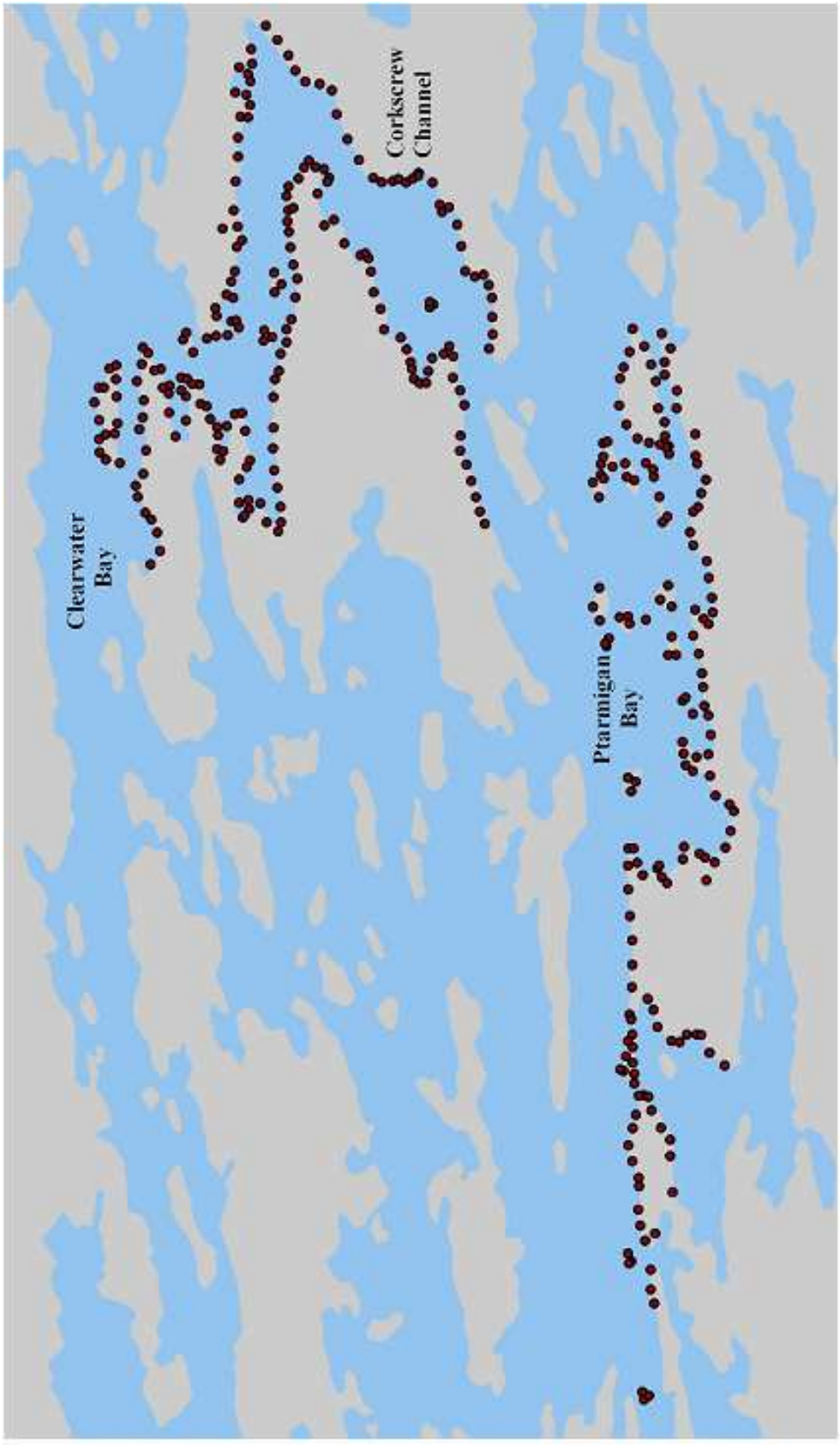


Figure 3. Map of the sampling area. Each dot represents one trapline (consisting of six traps). Trapping was carried out in areas of Clearwater Bay, Corkscrew Channel and Ptarmigan Bay

Sampling took place from mid June to early September, between known molting and reproductive periods. A total of 9 to 12 traplines were set each day, left overnight and retrieved approximately 19 - 25 hours later. Catches from each trap were counted, identified to species and expressed as a catch per unit effort (CUE) per trap per night. Crayfish were released at the site of capture after identification was complete. Depth was recorded for the first and last traps at all sites; the middle depth of the trapline was also recorded for the majority of sites. The depths of the remaining traps were estimated using linear interpolation of first and last trap depths (as well as mid depths when available).

Minnow traps were chosen for this project because they are inexpensive, easy to operate, effective and were used in the protocol developed by the Dorset Environmental Science Center. Minnow traps are known for having a bias towards larger, more aggressive individuals, which are often males (Dorn *et al.* 2005). Also, because *O. rusticus* is the largest and most aggressive of the three species, they are likely to be caught if present. Because this study did not deal with either sex distributions or absolute densities, this was not a large concern and would not affect the testing of my hypotheses. Data were also collected at each site for surface water temperature as well as substrate type and macrophyte presence or absence. Because of water turbidity the type of substrate was not visible at all depths, so the visible substrate was attributed to all traps at a site. A total of ~62,000m was sampled, including the shorelines of 27 islands and ~27,500 m of mainland shoreline.

Sampling took place between mid June and late August based on several details of the life history of the rusty crayfish. Firstly, most adult crayfish undergo molting

periods during the spring and fall. As well, females deposit eggs in early spring during which they are often less active and are caught in traps much less often (Somers and Green, 1993). Secondly, crayfish tend to be more active at higher environmental temperatures (Somers and Green, 1993) so sampling during summer months when water temperatures were at their highest was appropriate.

**Species Identification**

Three crayfish species were identified within the sample area: the native species *O. virilis* (the virile crayfish), the focal invading species *O. rusticus* (the rusty crayfish) and a second invasive species *O. immunis* (the papershell crayfish), which was previously unknown in the study area. Crayfish were identified using body colouration as well as several well known taxonomic features of the chelae. *Orconectes virilis* possesses a brown coloured carapace. Chelae are generally blue in colour, with orange tips and chelae fingers do not show separation when closed (Figure 4). *Orconectes rusticus* has a red to brown colouration, with a distinct rust coloured spot located on the lateral aspect of the carapace (Figure 1). Chelae of this species possess orange chelae tips, with adjacent black bands (Figure 4). A clear separation of the chelae fingers is seen when in a closed position. *Orconectes immunis* has a green to brown coloured carapace with mottled pigmentation. Chelae also possess this mottled colouration, and a distinct notch can be seen at the base of the chelae fingers (Figure 4).

Figure 4. Identifiable features of the chelae on the three sampled species *Orconectes virilis* (left), *Orconectes rusticus* (middle) and *Orconectes immunis* (right). Note the degree of separation between the chelae fingers of each species.

**Data Analysis**

The main results of this project were qualitative (presence or absence of the invasive *O. rusticus*). Most data, such as depth distributions, were analyzed using descriptive statistics such as mean and standard deviation.

Multivariate analysis was performed on both substrate type and species distributions. The type of substrate was broken down into five categories: large rock (rocks above 8cm in diameter and bedrock), small rock (gravel and sand), inorganic (silt and clay), organic (detritus) or manmade (concrete and asphalt used in cottage areas). Substrate and species distribution data were subjected to a redundancy analysis (RDA), which is a type of detrended correspondence analysis (DCA), using the Canoco data analysis program. This method calculates the correlation between species and environmental variables, such as substrate.

Spearman's Rank Correlation Analysis was used to explore the relationship between the numbers of each species caught at each trapline.

# Results

During the months of June through August 2006, 2256 traps were retrieved from the sample area in northwestern Ontario (though data were lost from several due to the separation or loss of traps during retrieval). The sampled shoreline totaled ~ 63 km and yielded a total of 9,833 crayfish. All islands sampled throughout Clearwater Bay and Corkscrew Channel had been invaded by the rusty crayfish as had most islands in the Ptarmigan Bay sample area. An invasion front was identified in Ptarmigan Bay near Copper Island. Two islands were identified within close range of this front, on which no rusty crayfish were trapped (Figure 5). Trapping continued westward through Ptarmigan Bay for approximately 8km of shoreline with no further occurrence of *O. rusticus*.

## Effect of Depth and Distance

Islands varied substantially in terms of distance from mainland and surrounding water depth. Island to mainland distances ranged from approximately 40m to 1100m. Because it is know that *O. rusticus* does in fact use islands as a pathway for invasion in this particular area, the largest distance traveled can be measured as the distance from one shore to the nearest invaded shore, which, at its longest measure, was approximately 420m. The water depths between shorelines of an island and adjacent mainland were determined by the use of a bathymetric map (intervals of 10 feet). The greatest depth was approximately 40 feet (~12 meters) while the shallowest crossing point was approximately 5 feet (~1.5 meters). For both *O. rusticus* and O. *immunis,* the average catch per unit effort (CUE) tended to decrease with increasing depth, though this trend was not seen in the native species, *O. virilis*, which seemed to be evenly distributed

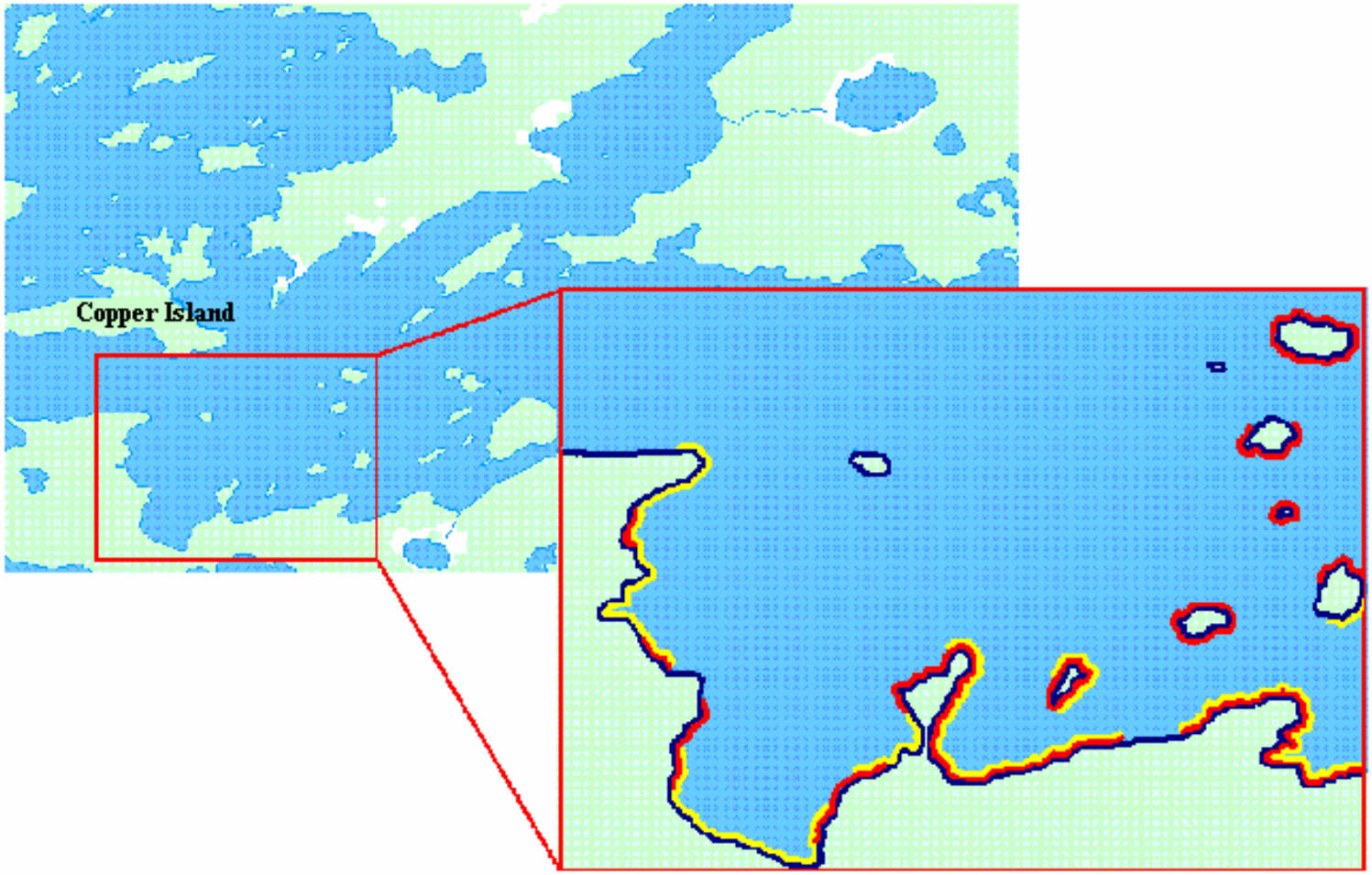


Figure 5. Map showing the invasion front of the rusty crayfish, identified in Ptarmigan Bay, Lake of the Woods. Species distributions are colour coded for O. virilis (blue), O. rusticus (red) and O. immunis (yellow). No rusty crayfish were caught on the two islands outlined only in blue. No further O. rusticus individuals were found west of this front in Ptarmigan Bay

throughout the trapped depths (Figure 6). Despite the decreasing CUE with depth the majority of sampled islands had been invaded by *O. rusticus*. The two islands that did not result in *O. rusticus* capture were close to the invasion front and no deeper or farther from mainland than the other invaded islands, so it is likely that time has been the only barrier to their colonization.

Unlike *O. rusticus*, water depth may be a barrier to island colonization in *O. immunis*. This species was not collected from any islands that were isolated by depths greater than 12m. This inhibition does not seem to be related to distance from mainland, as other islands that were found in shallower waters and located at similar distances, were still colonized (Figure 7). Islands to the east of the figure were all connected by depths of approximately 3m and were all colonized to some extent by *O. immunis*. Several islands located further west (located within boxes in Figure 7) were isolated by depths of over 12m and did not seem to be colonized. Because both sets of islands are found at a similar range of distances from the mainland, it is unlikely that distance affects colonization.

Average CUEs for *O. virilis* in areas of *O. rusticus* invasion versus areas beyond the identified invasion were compared (Figure 8). The general trend of depth distributions in both areas is very similar. Despite this, CUEs were much larger when *O. rusticus* was absent than when it was present. Spearman's Rank Correlation Analysis

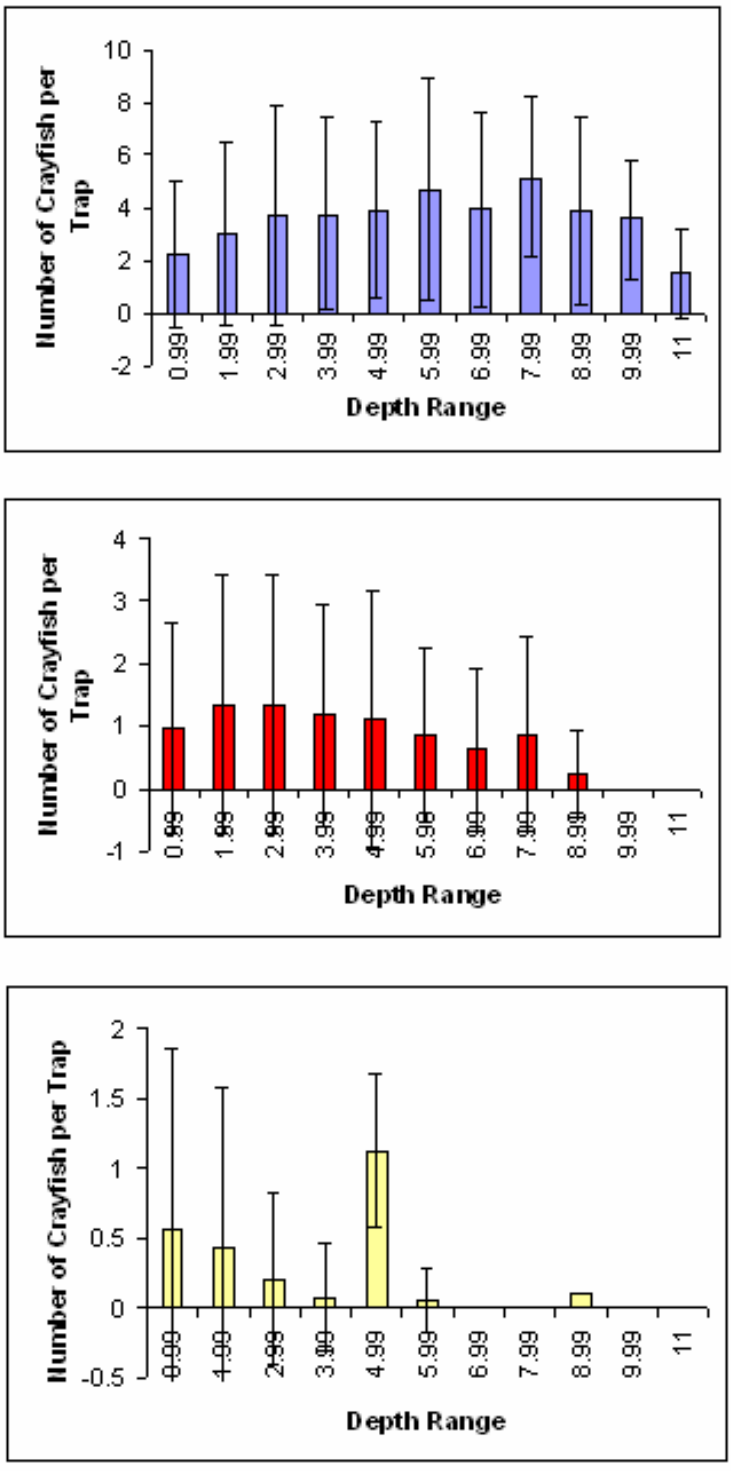


Figure 6. Depth distribution of the average CUE of O. virilis (top), O. rusticus (middle) and O. immunis (bottom). Mean and standard deviation are shown for each estimate

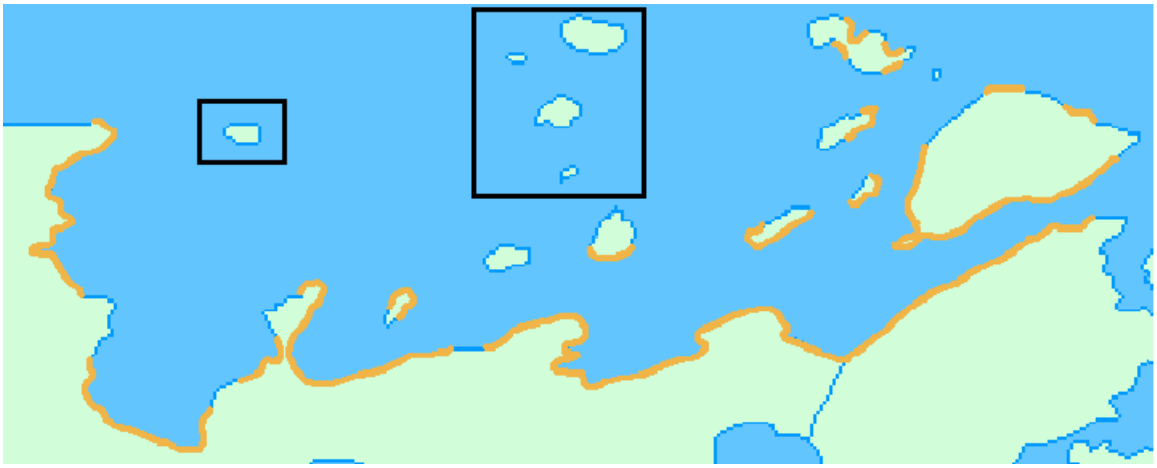

Figure 7. Distribution of *O. immunis* in Ptarmigan Bay. Distribution is indicated by orange colouration along the shoreline. Islands located within black boxes are isolated by water depths of at least 12m. No individuals were sampled on these islands. The group of islands in the east portion of the map are separated by water depths of approximately 3m and were all colonized to some extent.

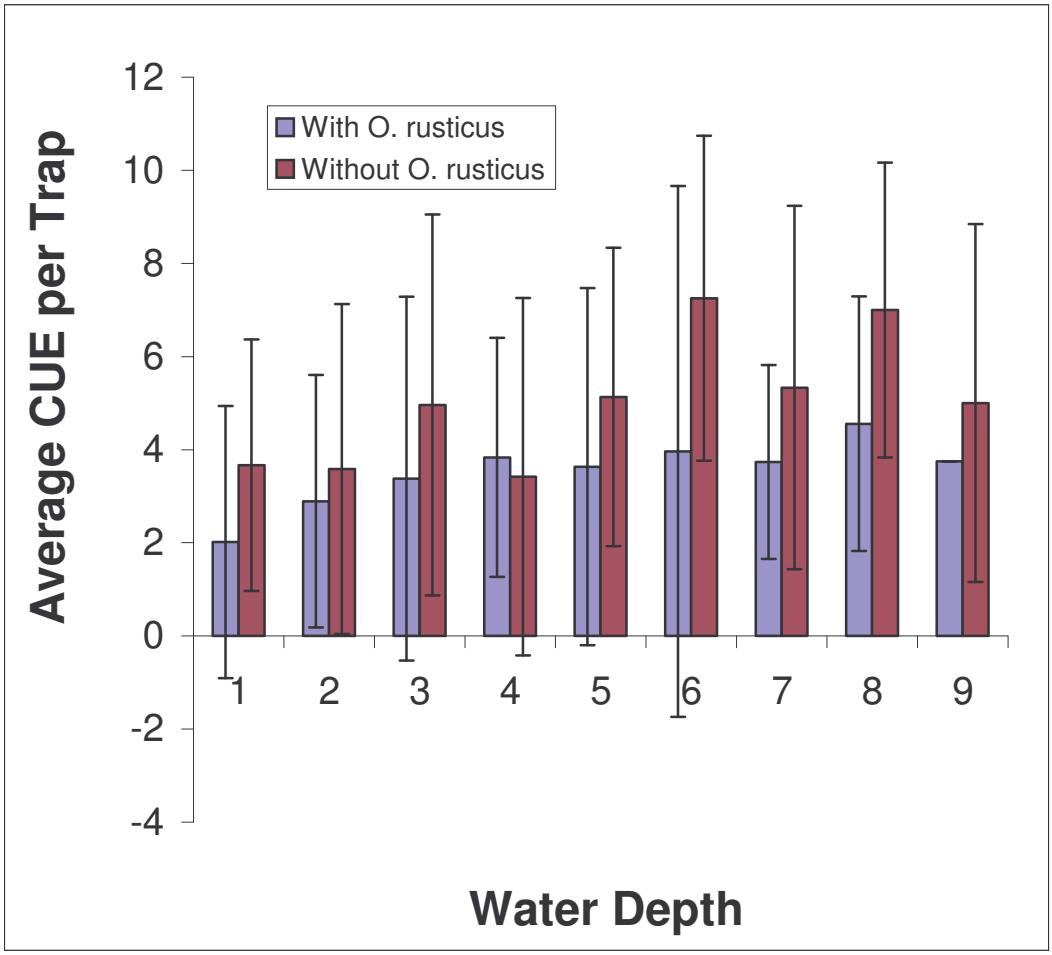


Figure 8. Average number of *O. virilis* individuals caught at a range of depths in the presence and absence of the invading species, *O. rusticus*. Mean and standard deviation are shown for each estimate

provided similar results; *O. rusticus* and *O. virilis* showed a weak negative correlation (-0.2.51, p=0.001). A negative correlation was also seen between *O. rusticus* and *O. immunis* (-0.133, p=0.018).

**Effect of Substrate**

Results from the RDA are displayed in an ordination plot (Figure 9). The variation in species distributions was explained, to a small degree, by the substrate types on which the crayfish were found. Despite the small amount of variation explained by these data, the results were significant ($p<0.05$ for both gradient axes). In this plot the two axes represent environmental gradients of substrate. The primary (X) axis represents the gradient between large rock/bedrock and organic substrates. This axis explained the majority (68.2%) of the species-environment relationship. The secondary (Y) axis, although explaining a relatively small proportion of the data variability (21.7%), still creates a gradient of substrate from small rock to organics. The analysis showed a weak correlation between each species and substrate preference (Figure 9). *Orconectes rusticus* was shown to be associated with large rock and bedrock substrates, while having a negative association with organic substrates such as detritus. This species showed no correlation with inorganic substrates, manmade or small rock substrates. *Orconectes virilis* displayed an association towards inorganic and small rock substrates and was negatively correlated with manmade substrates. *Orconectes immunis* was similarly associated with small rock and organic substrates.

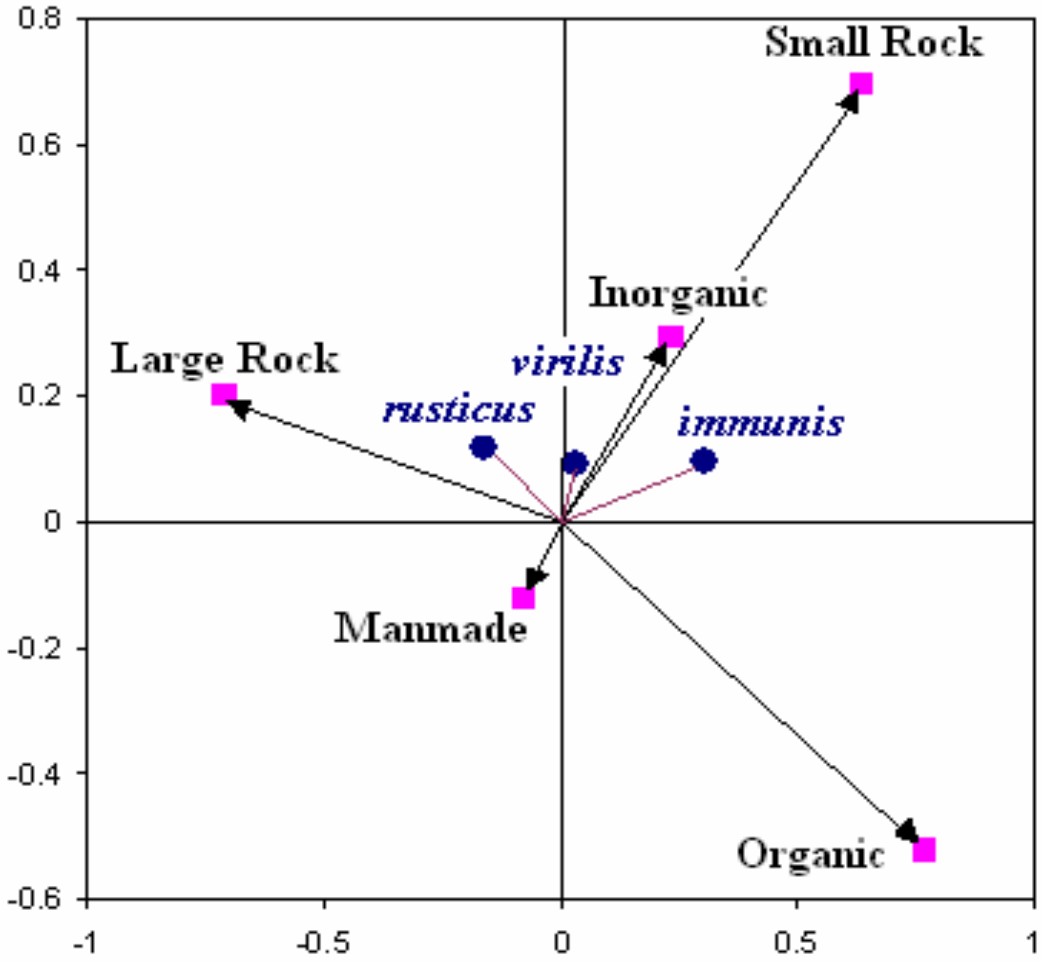


Figure 9. Ordination plot showing the correlation between crayfish species and substrate type. Vectors that are seen at close angles (near $0^{o}$) are highly correlated, those at large angles (near $180^{o}$) are negatively correlated and those at right angles (near $90^{o}$) show no correlation.

## Discussion

Islands did not seem to pose a barrier to colonization by *O. rusticus* in the study area of Lake of the Woods. Neither water depth nor distance from mainland seems to have prevented movement to islands in this area. Maximum depths crossed were greater than 12m, a depth that was matched in a study by Wilson *et al.* (2004), which looked at the movement of *O. rusticus* in Trout Lake, Wisconsin. This study reported the invasion of several islands in the southern basin of the lake, but did not address water depth or the location of these islands relative to shore. Pennak (1953) also commented that although *O. virilis* was often found in shallow waters, individuals had been found at depths of 104 feet (~32m). The rusty crayfish as well as the papershell crayfish became less abundant in deeper waters, while the distribution of virile crayfish seems to be independent of depth. A similar trend was seen by Somers and Stechey (1986), who witnessed a preference for shallow waters in the Appalachian crayfish, *Cambarus bartoni* (Fabricius), but not for *O. virilis* in Lake Opeongo, Ontario. It should be noted however that there were a small number of traps set at depths greater 7m. This may have resulted in average CUEs that are unrepresentative of the actual population at these depths.

The rusty crayfish has a preferred temperature of ~22$^{o}$C (Mundahl and Benton, 1990), which was generally exceeded above the thermocline in Lake of the Woods during much of the thermally stratified period during summer. The depth of the thermocline increased from approximately 4-6m in mid June to 10-12m at the end of August, and in the fall the thermocline degrades during the annual lake turnover. It may be that during periods when warm waters extend to greater depths, the rusty crayfish is able to move through these deeper waters and reach islands that would be isolated by deep, cool waters

at other times during the year. This was seen in females of *O. virilis* (Momot, 1967; Momot and Gowing, 1972) who moved into progressively deeper waters after their eggs had hatched. After this period, females become much less aggressive and intra-specific competition with males leads to their exclusion from optimal habitats (Bovbjerg and Stephens, 1974). Crocker and Barr (1968) also noted that crayfish would recede to deeper waters before the winter, and remain there until spring.

Because *O. rusticus* is dominant over *O. virilis*, the former often excludes the latter. This is true for shelter, substrate and temperature ranges as well. This may prevent *O. virilis* from keeping close to shore where temperatures would be ideal, resulting in the observed depth distribution. The papershell crayfish, *O. immunis*, does not compete with either species for habitat, as they are burrowers. Burrows are constructed on shore, out of clay-like substrates and extend down to the water table. Because these crayfish return to their burrows during periods of inactivity (e.g. during the day), it follows that they would remain closer to shore. This species is also capable of movement over land in relatively wet conditions (Cocker and Barr, 1968), which gives it an advantage for invasion.

The higher abundance of *O. virilis* in areas beyond the *O. rusticus* invasion front is quite obvious in the recorded data; however, this may be somewhat misleading. Minnow traps are biased towards catching larger, more aggressive crayfish, which would have been the rusty crayfish in most situations. This may lead to the capture of fewer individuals from the subordinate species, *O. virilis* and *O. immunis*. If this is the case, the observed differences may be due partly to the trapping procedure rather than a true difference in abundance. That being said, these data concur with the findings of many

other studies (Bouchard, 1978; Capelli, 1982; Garvey and Stein, 1993; Hill and Lodge 1994), which show that the rusty crayfish tends to negatively affect the densities of other crayfish species. Further analysis, using Spearman's Rank Correlation Analysis provided similar results, but as the same data were used for both analyses, they may both be biased by the trapping methods used.

The redundancy analysis explained a small proportion of the species distribution variability. The analysis showed that each species had a weak preference for specific substrate types. *O. rusticus* seemed to prefer large rock and bedrock substrates. This corresponded with *O. rusticus'* preference for habitats that provide good shelter from predators (Kershner and Lodge, 1995; Garvey *et al*., 1994). *O. virilis* abundance was correlated with small rocks and inorganic substrates, which corresponds to the fact that in the presence of *O. rusticus* where shelter is a limiting resource, they are excluded from shelter sites (Garvey *et al*., 1994; Hill and Lodge, 1994). *O. immunis* was also associated with small rock and inorganic substrates. This is consistent with the species requirement for soft substrates such as sand and clay for burrowing (Crawshaw, 1974).

Although these associations exist, they explain only a very small portion of the variability in the data set (~4% of total variation). This analysis may have had more statistical power had the substrate been identified for each separate trap. Because the lake bottom was not visible at all depths a generalized classification was used for each trapline, even though the substrate may not have been continuous along its entire length. Although *O. rusticus* and *O. virilis* exhibited preferences for substrate type, they were collected on most available substrates. It is therefore unlikely that the absence of preferred habitat would prevent invasion by *O. rusticus* from occurring. This may not be

the case for *O. immunis*, as it requires a limited range of substrates for burrowing. There may also be a barrier to island colonization for this species in terms of depth. *Orconectes immunis* was not sampled on islands isolated by depths of over 12m.

The rusty crayfish has been observed to have quite variable invasion rates. Wilson *et al*. (2004) found that *O. rusticus* moved through Trout Lake, Wisconsin at an average rate of 0.68 km/year. El-Hashemy (1999) studied the invasion of *O. rusticus* through several river systems and found that invasion rates were higher in a downstream direction (0.6 to 3.7 km/year) than upstream (0.5 to 2.8 km/year). Based on the results of this survey one can speculate that neither water depth or nor distance from the mainland prevent *O. rusticus* from colonizing islands in the study area, although depth may affect island colonization for *O. immunis*. One can also surmise that the two uncolonized islands, though currently free from *O. rusticus*, will likely become colonized as the invasion front progresses westward.

Without any apparent barriers to movement of *O. rusticus* in Lake of the Woods, it is unlikely that its further spread in the area can be prevented. Control of aquatic invasive organisms, such as crayfish, is extremely difficult given their habitat, behaviors and far reaching distributions. Many different control strategies have been employed in the past and although some are effective to a certain extent, none have been completely successful. Suggested control strategies have included toxins, trappings, increases in natural predator populations and the introduction of new predators.

Toxins have generally been rejected as a possible control measure. Although they are efficient, they are not species specific and are often harmful to other freshwater

organisms. A test of 19 different toxins showed that most were more harmful to fish than to the targeted crayfish (Bills and Marking, 1988).

Trapping has been attempted as a control measure as well providing an opportunity for commercial harvesting of crayfish. However, trapping tends to have a bias towards catching larger males, leaving the population with higher proportions of young and female crayfish (Bills and Marking 1988; Dorn *et al*., 2005). Therefore, this does not result in large crayfish population declines; and although it may suppress populations, it will not eliminate them.

Several fish species including yellow perch, rock bass, smallmouth bass and largemouth bass are predators of crayfish (Collins *et al*., 1983). Fish tend to pursue smaller-sized crayfish, generally less than 25 mm in length. In one instance increased populations of rock bass and smallmouth bass removed a large proportion of the biomass of the crayfish population (Hein *et al*., 2006). However, fish predation is not species specific and, as mentioned earlier, other crayfish species, such as *O. virilis*, can be more susceptible to fish predation even at comparable sizes. The invasive round goby is found throughout the Great Lakes including Lake Superior and Lake Erie where the rusty crayfish is also found. The round goby will prey on young of the year crayfish in preference to zebra mussels and other invertebrates. Predation rates decrease as size increases (from 65% at 4.9 mm to 13% at 12.7 mm). Gobies also acted aggressively towards crayfish, evicting them from shelters, which would increase the risk of predation from the gobies as well as larger fish such as bass (Davis *et al*., 1999).

Because invasive species can often be very difficult and costly to eradicate, prevention of their spread is the only realistic option. This can be done through public

education, restrictions on use and possession for bait purposes and restrictions on transport. Some European countries have put restrictions on the transport of live crayfish (Gherardi and Holdich, 1999). Several states in the U.S. have made the release of aquatic bait organisms illegal, but this restriction does not apply to organisms native to the state. Others states have banned the possession of live rusty crayfish completely (Lodge *et al*., 2000). The Manitoba Fisheries Act is preparing legislation to ban the possession of live crayfish use as bait. Currently Ontario regulations prevent the dumping of bait bucket species, including the rusty crayfish, into lakes other than the one from which they were taken. It is also illegal to bring crayfish into Ontario for the purpose of baiting. Although this prevents one pathway for introduction it still allows for transport of bait species across borders (both provincial and international) outside of Ontario. Introductions are also still possible through other routes such as aquarium release and the water garden trade. It is of utmost importance that the public become aware of this and other invasive species, so that they can prevent accidental introductions. Public education is probably the best way to prevent the spread of the rusty crayfish into new water bodies. By understanding the impact of these organisms we can hope to make an impact on those people who can prevent further spread.

Based on the apparent importance of depth distribution in my project, it would be useful to determine weather the depth distribution of *O. rusticus* varied seasonally. Similarly, it would also be interesting to see if changes in distribution were correlated with changes in temperature, especially with the depth of the thermocline Moreover, it would be worthwhile to look at the distributions of both sexes separately, as sex-linked differences in behavior have been seen in other crayfish species. Finally, islands that are

isolated by even deeper waters than those studied here could be sampled to see if greater depths could act as a barrier to movement, coupled with an assessment of whether lake mixing in the fall is a controlling factor.

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