SCALING UP: LONG-TERM, LARGE-SCALE IMPACTS OF THE INVASION OF
LAKES BY THE INVASIVE RUSTY CRAYFISH (ORCONECTES RUSTICUS)

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by

Timothy A. Kreps

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David M. Lodge, Director

Graduate Program in Biological Sciences
Notre Dame, Indiana
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SCALING UP: LONG-TERM, LARGE-SCALE IMPACTS OF THE INVASION OF LAKES BY THE INVASIVE RUSTY CRAYFISH (*ORCONECTES RUSTICUS*)

Abstract

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The introduction of nonindigenous species is an increasing threat to global biodiversity and ecosystem function. The success of management efforts often relies on the study of the dynamics and impacts of previous invasions. Small-scale experiments of nonindigenous species provide valuable and timely information, but are limited in their ability to assess adequately the potential long-term effects of invasion at the whole-ecosystem level. Here, I build on previous smaller scale studies of the impacts of the invasive rusty crayfish *Orconectes rusticus* in order to assess the impacts and dynamics of the invasion at longer temporal scales, larger spatial scales, and more complex levels of ecological organization.

Using data from long-term monitoring, I evaluated trends in the crayfish community over three decades in lakes invaded by *O. rusticus*. Results showed that an earlier congeneric invader, *O. propinquus* is extirpated, while the native *O. virilis* tends to coexist by using a habitat refuge. Patterns of *O. rusticus* abundance were more variable than previously believed. Most lakes sustained high *O. rusticus* abundance through time, while a few exhibited a pattern of boom-and-bust. Long-term *O. rusticus* abundance appeared to be related to risk of fish predation, variation in lake benthic substrate, and crayfish resource limitation.
A long-term, whole-lake survey of snail and crayfish abundance showed that the magnitude of impact by *O. rusticus* can be great, differs across habitats, and that the full extent of impact on congeners and prey may not be evident until many years after initial colonization. Analysis of snail gut contents and a set of laboratory feeding experiments demonstrate that snails do not consume macrophytes, indicating that the primary effect of *O. rusticus* predation on snails is reduced grazing efficiency on periphyton. Samples from two lakes that experienced large declines in *O. rusticus* abundance indicated little ecosystem recovery.

Comparison of food webs in invaded and uninvaded lakes using stable isotopes provided evidence that *O. rusticus* decoupled littoral and pelagic food webs. The combined effect of reduced grazing efficiency and food web decoupling is likely to be reduced flow of energy to the top of the lake food web.
"Daddy, you don't like to play do you? Work, work, work. All you ever do is work."

-Andrew K. Kreps

This is dedicated to my wonderful family who has shown endless patience (above quote aside) and love. May my love for play never ever be questioned again.
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CHAPTER 1:

INTRODUCTION

1.1. Nonindigenous species

Anthropogenic alterations of natural ecosystems and human-assisted translocations of species outside of their native ranges have led to an increasing homogenization of the earth’s biota (Olden et al. 2004). Expansion of species’ ranges is a natural process, but species introductions are growing increasingly frequent as species are moved intentionally and unintentionally, aided by globalized human transportation and commerce (Office of Technology assessment 1993; Perrings et al. 2000).

The majority of non-indigenous species introductions do not cause problems. The Ten's Rule, proposed by Williamson (1996) estimates that only about 10% of nonindigenous species introduced to a new habitat establish viable populations, and only 10% of established species become a nuisance or invasive species. More recent estimates indicate that these numbers likely vary among taxa. Vertebrate introductions between North America and Europe have had rates of establishment and invasiveness estimated to be up to 50%, much higher than that of plants (~5%: Jeschke and Strayer 2005).

While not all introduced species become invasive, successful colonizers have caused significant ecological and economic damage. Invasive species introductions can lead to the decline of native species through multiple mechanisms including predation,
competition, hybridization with the native species, and alteration of the abiotic environment (Williamson 1996; Mack et al. 2000). Although some debate has arisen over the importance of nonindigenous species as a driver of global species extinctions (Gurevitch and Padilla 2004; Ricciardi 2004), most research has indicated that species introductions are one of the most important threats to global biodiversity (Vitousek et al. 1996; Mooney and Hobbs 2000; Sala et al. 2000; Clavero and Garcia-Berthou 2005). There is also increasing awareness that nonindigenous species can alter ecosystem processes (Mack et al. 2000) and may negatively impact many of the important ecosystem services upon which human society relies (Fischer et al. 2006). In total, the economic cost of nonindigenous species to the U.S. economy alone is over $120 billion annually (Pimentel et al. 2000).

1.2. Freshwater nonindigenous species

More than 40% of all fish species and approximately one third of all vertebrate species live exclusively in freshwater (Dudgeon et al. 2006; Williamson 1996). Considering that freshwater covers only about 0.8% of the earth’s surface (Gleick 1996), this makes freshwater ecosystems extremely species rich habitats. Throughout history, human populations have centered near sources of freshwater and used freshwater ecosystems intensively as a source of food and drinking water as well as for transportation, irrigation, waste disposal and a host of other economic activities. As a result, biodiversity is declining in freshwaters at a greater pace than in terrestrial ecosystems. For example, in the U.S., 14-18% of terrestrial vertebrate and butterfly
species have been designated as vulnerable, imperiled or extinct while such rates are much higher for fish (35-37%), crayfish (65%) and unionid mussel (67%) species (Master 1990; Richter et al. 1997). The primary threats to freshwater species include habitat change, overexploitation, pollution, flow modification and interactions with nonindigenous species (Richter et al. 1997; Dudgeon et al. 2006). In contrast to pollution, which has declined in many industrialized nations, species introductions have become an increasing concern (Richter et al. 1997), a trend which is likely to continue into the future (Sala et al. 2000).

1.3. Management of nonindigenous species

Unlike chemical pollution, which will generally abate over time when sources are removed, successful introductions of nonindigenous species tend to be irreversible without significant human management. Therefore, prevention is generally more feasible than control or eradication efforts after establishment (Simberloff 2003). Prevention efforts are also often more cost effective than controlling established populations or mitigating losses caused by the species (Lodge et al. 2006). It is impossible to prevent all species introductions, as resources are limited and many introductions can in many ways be beneficial (Knowler and Barbier 2005). Thus, many attempts have been made to predict which species pose the greatest threat and which biological communities are most likely to be invaded.

One of the earliest efforts to predict potential invaders was to attempt to identify species traits that aid in invasion success. For plants, traits such as continuous seed
production, total seed production, lack of specialized germination requirements and vegetative propagation have been suggested (Baker 1974; Williamson 1996). While for animals, it has been proposed that characteristics such as diet and habitat generalism, omnivory, and rapid growth and reproduction may play a role (Williamson 1996). A number of characteristics have also been suggested to explain which ecological communities are most easily invaded. For example, it has been proposed that habitats that are species rich or that lack vacant or underutilized niches are most resistant to invasion (Elton 1958; Williamson 1996). Another possibility is that habitats that have been disturbed by humans are more easily invaded as physical conditions, nutrient regimes, and ecological relationships within the community are altered (Olyarnik et al. 2009).

While broad generalizations about the traits of invaders and invaded communities may be helpful in understanding the underlying mechanisms of invasions, they have not proven to be particularly useful management tools. Exceptions to these types of generalizations are common (Williamson 1996; Mack et al. 2000), and interactions between the traits of species and habitats may be important in determining invasion success (Hamilton et al. 2005). In addition, different traits may be important at different stages of the invasion process (Kolar and Lodge 2001). Recent efforts have improved the accuracy of predictions by narrowing the taxonomic and spatial scope of the analyses (Kolar and Lodge 2002; Hamilton et al. 2005; Keller et al. 2007; Keller and Drake 2009).

Acknowledging that not all species introductions can be prevented, another important part of managing the spread of nonindigenous species is to prevent secondary spread once a species has been introduced to a new region (Vander Zanden and Olden
In this case, it is important to identify which habitats within the region are most susceptible to secondary spread, and which of these are most likely to be vulnerable to negative impact (Vander Zanden and Olden 2008). This type of approach is particularly applicable to species introductions in lakes because they are relatively isolated islands surrounded by terrestrial ecosystems, and introductions into individual lakes can be viewed as separate invasions. Lakes can differ greatly from each other in terms of physical and chemical characteristics as well as the biotic communities that they support, and therefore they are very likely to represent a wide range in vulnerability (Vander Zanden and Olden 2008). Comparisons of the habitats that have had previous successful and unsuccessful introductions can be used to identify characteristics that make habitats vulnerable to invasion by a particular species. This type of information can then inform risk assessment efforts and thus inform management as to how and where limited monies can be most effectively spent (Vander Zanden et al. 2004; Branstrator et al. 2006; Drake and Lodge 2006).

Once species have established within a system, the greatest hope for eradication is to identify the introduction early and eliminate the species quickly after introduction when populations are small, often using blunt force techniques (Simberloff 2003; Simberloff 2009). If this is not possible, there are several examples where human management efforts managed species continually below nuisance levels (Simberloff 2009). While the blunt force quick eradications often require more quick thinking and action than good population or community biology (Simberloff 2003), efforts to control invasive species at low levels do require a great deal more biological information (Simberloff 2009).
1.4. Assessing the impact of nonindigenous species: Importance of temporal and spatial scale

Effective management and policy decisions often require good biological data. As pointed out above (section 1.3), both the prediction of invasion success and management of established species often require the assessment of patterns seen in previous invasions. In addition, the magnitude of current or potential impact is needed to inform policy makers and to motivate action. The temporal and spatial scale at which invasive species research is conducted is of particular importance (Parker et al. 1999; Strayer et al. 2006). The majority of invasive species research consists of small-scale, short-term lab and field experiments (Parker et al. 1999). These experiments can be conducted quickly, thus informing rapid action, and can be very useful in identifying the potential magnitude and mechanisms of a species’ impact. However, small-scale experiments often cannot incorporate all relevant ecological variables. Field enclosure-exclosure experiments can provide early assessments of the impact of a nonindigenous species but they often suffer from cage-effects (Englund and Cooper 2003). For example, while enclosures may maintain known abundances of the species of interest, they may also exclude predators which can alter the target species behavior. Also, these types of experiments may be carried out in only a subset of the habitats actually available, thus not taking into account the true heterogeneity of the ecosystems being studied. These limitations lead to problems in scaling-up the results of small-scale experiments to the whole-ecosystem level (Carpenter 1996; Lodge et al. 1998b).

Similarly, the duration over which experiments are carried out is important. Short-term lab and field experiments or large-scale correlative studies can return results
relatively quickly, but these experiments generally are not able to examine changes in the effects of invasive species over time. Most studies of nonindigenous species are short-term and focus on the acute effects of introductions while the long-term or chronic effects may be very different (Strayer et al. 2006). Mechanisms that may lead to changes in the effects of a species over time include: (1) physical or genetic changes in the introduced species, (2) changes in the species composition of the invaded community, (3) changes in the physical or chemical characteristics of the invaded ecosystem, and (4) interaction between the introduced species and other controlling variables such as weather or disturbance (Strayer et al. 2006). Despite the likelihood that the impact of a species changes throughout the course of an invasion, time since invasion is often ignored in the study of invasive species impacts (Lodge et al. 1988).

The total impact that a nonindigenous species has on a receiving ecosystem is dependent on total area that is colonized, the abundance of the species, and the effect that each individual can have. Parker et al. (1999) combined these factors into a conceptual model for estimating nonindigenous species impact:

Equation 1:  \[ I = R \times A \times E \]

where \( I \) is the impact of the species, \( R \) is range size, \( A \) is abundance and \( E \) is the per capita or per biomass impact of the species. Such a conceptual model assists in comparing the impacts among species or within a species in different habitats. Considering the potential for changing impact through time, I suggest that each variable in this model should be considered a function of time:

Equation 2:  \[ I_t = R_t \times A_t \times E_t \]
therefore encouraging researchers to consider how each of these factors will vary through
the course of an invasion. In my research, using invasions by rusty crayfish (*Orconectes
rusticus*) as a case study, I focused on the long-term dynamics of invasions and their
impact, considering especially how abundance as a driver of impact changed over time.

1.5. The rusty crayfish *Orconectes rusticus*

The rusty crayfish (*Orconectes rusticus*) has spread from its native Ohio River
valley to lakes and streams in large areas of the eastern and midwestern United States and
Ontario (Hobbs et al. 1989; Lodge et al. 2000). Spread has occurred through human
transport (primarily the release of unused bait by anglers) as well as natural dispersal
through stream connections among lakes (Capelli and Magnuson 1983; Puth and Allen
2005). In Wisconsin, *O. rusticus* has spread throughout the state, with a particularly
high rate of occurrence in the Northern Highlands Lake-District (Olden et al. 2006)
where it has been most intensively studied. As it spreads, *O. rusticus* replaces both the
native *O. virilis* and a previous invader *O. propinquus* (Capelli 1982; Olsen et al. 1991;
Olden et al. 2006). While the three species are closely related, *O. rusticus* has a number
of advantages over its congeners including larger chelae (Garvey and Stein 1993), more
aggressive behavior (Capelli and Munjal 1982) and a higher growth rate and metabolism
(Lippson 1976). As a result, *O. rusticus* out-competes *O. virilis* and *O. propinquus* for
resources (Capelli and Munjal 1982) and is less susceptible to predation by fish
(Didonato and Lodge 1993; Garvey et al. 1994). As an omnivore, *O. rusticus* can have
negative effects on multiple components of the food web including macrophytes,
macroinvertebrates and fish (Olsen et al. 1991; Lodge et al. 1994; Wilson et al. 2004; McCarthy et al. 2006; Rosenthal et al. 2006; Roth et al. 2007). Impacts on snails, a preferred prey, can be particularly strong (Lodge et al. 1994; Lodge et al. 1998a; Wilson et al. 2004; McCarthy et al. 2006).

While the impacts of rusty crayfish introductions in lakes have been relatively well studied, most studies have been small-scale and short-term (for exceptions see Wilson et al. 2004; McCarthy et al. 2006; Rosenthal et al. 2006) and therefore, there is a need to examine large-scale impact over longer durations. Field surveys and pool experiments have shown that at the local scale, multiple substrates (cobble, sand, muck and macrophyte) may affect the impact of crayfish on the food web (Hill and Lodge 1994; Kershner and Lodge 1995). However, only the influence of cobble has been tested at the whole-lake level (Capelli and Magnuson 1983; Garvey et al. 2003). Also, the effects on the individual components of the food web (e.g. macrophytes and macroinvertebrates) have been studied, but little is known about how these combine to alter energy flow through the food web. Finally, almost all research has focused on the important initial impact of invasion (e.g. Lodge et al. 1994), and almost nothing is known about how the impacts may change over time.

In order to better evaluate any long-term changes in the impacts caused by *O. rusticus*, I consider the interactions of *O. rusticus* with factors of the lake ecosystems that may alter its abundance (Figure 1.1).
Figure 1.1. Interactions between rusty crayfish and the factors that affect crayfish abundance. Overlapping ovals represent organisms that may have multiple roles. For example, macrophytes serve as habitat, as well as food for crayfish. Also, large fish may prey on crayfish while crayfish may consume fish eggs and fry. Arrows points in both directions because a specific factor may affect the abundance of rusty crayfish, but rusty crayfish may also alter the factor (macrophytes provide predation refuge for \textit{O. rusticus} while \textit{O. rusticus} can also reduce the abundance of macrophytes).

**Rusty crayfish \leftrightarrow \textbf{Habitat}:** The primary habitats for \textit{O. rusticus} are vegetated substrates (usually sand and organic-rich sediments referred to as muck) and cobble which provide refuge from fish predation (Garvey et al. 1994; Kershner and Lodge 1995). At the same time, macrophytes are food for the crayfish; thus crayfish consumption can alter the abundance of one portion of its habitat (Lodge et al. 1994).

**Rusty crayfish \leftrightarrow \textbf{Food resources}:** Although little evidence about food limitation of crayfish exists, the abundance of food resources may alter crayfish size and population size (Lodge and Hill 1994). Considering the large declines seen in macrophytes and macroinvertebrates (Lodge et al. 1994; Wilson et al. 2004; McCarthy et al. 2006), it is also likely that \textit{O. rusticus} significantly reduces the availability of its own food resources.
Rusty crayfish ↔ Predators: Abundant predators (e.g. rock bass *Ambloplites rupestris*, largemouth bass *Micropterus salmoides*, smallmouth bass *Micropterus dolomieu*, and yellow perch *Perca flavescens*) consume crayfish and may be able to depress *O. rusticus* populations (Kershner and Lodge 1995; Garvey et al. 2003). Consumption of abundant crayfish may be a positive for the predator as it may improve growth, survival and/or reproduction. At the same time, predation by *O. rusticus* on fish eggs (Dorn and Mittelbach 2004), and the reduction of fish food (macroinvertebrates) and habitat/nursery areas may negatively affect predators.

In terms of the modified model of invasive species impact (Equation 2) each factor may now be examined in light of our knowledge of the *O. rusticus* invasion. Range (*R_t*) is likely to increase over time as the species spreads and increases within each lake. No range contraction has yet been recorded in lakes, although it has in streams (Bobeldyk and Lamberti 2008). However, if *O. rusticus* removes macrophytes (a preferred habitat) from a large portion of the lake, the remaining habitat (unvegetated sand) is likely to be avoided by *O. rusticus* (Hill and Lodge 1994; Kershner and Lodge 1995). Thus, crayfish may disappear from portions of the lake resulting in a range contraction. Abundance (*A_t*) may remain constant over time if habitat remains constant (cobble) and omnivory allows the species to avoid resource limitation. However, abundance may decline if macrophyte habitat (predation refuge) declines and resource limitation increases (high quality foods such as macroinvertebrates are removed). Smaller crayfish with less refuge should suffer higher predation risk (Garvey et al. 1994), which may lead to population declines. Similarly, the per capita effect (*E_t*) of crayfish is likely to decline over time: if resource limitation produces smaller crayfish that are more
susceptible to predation, *O. rusticus* should be less active and have less impact per capita (Collins et al. 1983).

1.6. Dissertation outline

This dissertation combines large-scale, long-term studies and some small laboratory experiments in order to better understand how the impacts of *O. rusticus* (a) change through time, (b) affect the transfer of energy up the food web and (c) are affected by the heterogeneity of habitats across lakes. In Chapter 2, I analyze trends in crayfish abundance from 21 lakes in northern Wisconsin covering a period of 3 decades. I look for long-term trends in the crayfish community (changes in abundance of congeneric crayfishes) through the course of invasion by *O. rusticus*. I test the hypothesis that substrate heterogeneity (availability of muck habitat) may allow for the long-term coexistence of the native *O. virilis* while the previous invader, *O. propinquus*, is generally extirpated as the invasion of a lake by *O. rusticus* proceeds. I also examine some of the mechanisms suggested by Strayer (2006) that may lead to changing impacts of *O. rusticus* through time. In particular, I look to see if changes in the invaded ecosystem (reductions in macrophyte habitat and thus increased risk of fish predation) and in the invader itself (smaller size due to resource limitation) lead to a boom-and-bust pattern in *O. rusticus* populations.

In the Chapter 3, I report on whole-lake comparisons of snail and crayfish abundance in lakes that were sampled in 1987 and again in 2002. Two lakes experienced large increases in *O. rusticus* between samplings, while two others experienced large
declines (possible example of boom-and-bust). Through natural snapshot and natural trajectory experiments, we examine the magnitude of the impact of *O. rusticus* on snails at the whole-lake scale. I also examined the rates of impact over a long time scale and analyze the influence of benthic substrate on the impact of *O. rusticus*.

In the Chapter 4 and 5, I look at how the impacts of *O. rusticus* on lake biota may alter the transfer of energy through lake food webs. In many lakes, snails are the dominant grazer (Dillon 2000). When rusty crayfish are introduced, they replace snails as the dominant herbivore (Lodge et al. 1994; Lodge et al. 1998b). Snails are more efficient grazers of periphyton than crayfish (Luttenton et al. 1998) but less is known about their ability to consume macrophytes. It has generally been assumed that snails do not consume macrophyte, but there is some evidence that grazing by snails may alter macrophyte biomass and species composition (Sheldon 1987; Elger et al. 2007; Elger et al. 2009). In Chapter 4, I investigate the ability of snails to consume macrophytes in order to understand how the change in dominant grazers (snails to crayfish) will affect top-down control of the major primary producers (macrophytes and periphyton). I analyze gut contents from field collected specimens and use laboratory feeding experiments to assess snails’ ability to consume macrophytes and to determine the role that plant toughness may have in deterring snails from grazing on macrophytes.

In Chapter 5, I use stables isotopes to compare patterns of trophic transfer of energy in lakes that have been invaded by *O. rusticus* for over a decade with lakes that are uninvaded. While past studies have clearly shown that *O. rusticus* alters some food web components (e.g. snails and macrophytes; Lodge et al. 1994; Wilson et al. 2004; McCarthy et al. 2006), it has been more difficult to determine impacts on other taxa and
trophic levels (e.g. many mobile macroinvertebrates and fish). This is in part due to the difficulty of accurately sampling populations of mobile species, but it is also possible that impacts on these species may only become evident years after initial invasion. I test the hypotheses that *O. rusticus* reduces the abundance of macroinvertebrates and small fish. I then compare the growth of fish in invaded and uninvaded lakes to see if changes in growth are likely to be an important mechanism driving changes in populations of large predatory fishes.
CHAPTER 2:

LONG-TERM TRENDS IN THE INVASION OF LAKES BY THE RUSTY CRAYFISH (*ORCONECTES RUSTICUS*): BOOM-AND-BUST?\(^1\)

2.1. Abstract

The abundance and impacts of nonindigenous species often change through the course of invasion as they alter food webs and ecosystems, but most research occurs at temporal and spatial scales that are too short and small to capture these important dynamics. For example, the invasive rusty crayfish *Orconectes rusticus* has profound impacts on north temperate lake food webs, but little is known about the long-term course of crayfish invasions at the whole-lake scale. Here, we use habitat-specific whole-lake monitoring over 3 decades to quantify the long-term fate of resident crayfish species, and to test whether nonindigenous *O. rusticus* populations exhibit boom-and-bust dynamics. We found that, while both the native *O. virilis* and the previously introduced *O. propinquus* decline after *O. rusticus* introduction, *O. virilis* coexists with *O. rusticus* to a greater degree over the long-term. Two likely explanations are a (1) previously documented hybridization between *O. rusticus* and *O. propinquus* (but not *O. virilis*) and

\(^1\) This Chapter (with co-author David M. Lodge) is in preparation for submission to Ecological Applications.
the presence of a habitat refuge (muck) that is used by *O. virilis* but not *O. propinquus*. Statistical analysis provided only weak evidence for boom-and-bust dynamics in *O. rusticus* populations, with most populations remaining high after an initial boom phase. In a few lakes, however, the initial boom phase was followed by a sustained long-term decline in *O. rusticus* populations. Mechanisms that might cause a bust phase include resource limitation (consistent with a decline in *O. rusticus* mean size through the course of invasion), an increase in predation pressure as crayfish eliminate macrophyte habitats that provide refuge, and an interaction involving greater susceptibility of smaller crayfish to predation. These mechanisms are most likely to be important in lakes with low amounts of cobble habitat (preferred habitat and probably a source of crayfish to other habitats) and large amounts of sand (non-preferred, and probably a sink habitat).

2.2. Introduction

It has long been recognized that the transportation of organisms to habitats outside of their native range can lead to a variety of ecological changes (Elton 1958; Mack 2003). As globalization has led to increased human commerce and movement, species introductions have become one of the greatest threads to global biodiversity and ecosystem function (Williamson 1996; Vitousek et al. 1996; Wilcove et al. 1998; Sala et al. 2000; Clavero and Garcia-Berthou 2005; Mooney et al. 2005). The impact of species introductions is particularly important in freshwater ecosystems (Ricciardi and Rasmussen 1999; Lodge 2001a; Rahel 2002; Dudgeon et al. 2006) where they represent
one of the primary threats to fish (Williams et al. 1989), crayfish (Lodge et al. 2000; Rahel 2002; Taylor et al. 2007) and mussels species (Williams et al. 1993).

The ecological impact of invasive species has also lead to significant economic damages to agriculture and the environment as well as increased costs for control of invasive species populations (OTA 1993; Pimentel et al. 2000; Pimentel et al. 2005). Because prevention of species introductions has consistently been found to be more cost effective than control after introduction (Mack et al. 2000; Simberloff 2003; Lodge et al. 2006), increased effort has been dedicated to developing the ability to forecast the outcome of potential introductions (Kolar and Lodge 2001). Historically, ecologists have focused primarily on attempting to determine the characteristics of species that are likely to be invasive or of habitats that are most susceptible to invasion (Williamson 1996; Mack et al. 2000; Keller et al. 2007; Keller et al. 2008). More recently, predictive efforts have explicitly recognized that the establishment of a nonindigenous species may lead to a nuisance in some cases but not in others (Kolar and Lodge 2001; Vander Zanden et al. 2004; Keller et al. 2007). These analyses attempt to distinguish between introductions that cause damage and those that are ultimately benign, allowing resource managers to focus their limited resources on species and habitats that indicate the highest risk. Species introductions in lakes are well suited to predictive analyses as the introductions of a species into multiple lakes can often be examined as independent invasions (MacIsaac et al. 2004; Vander Zanden et al. 2004; Bossenbroek et al. 2007; Keller et al. 2008). Therefore, the study of short and long-term impacts of past introductions, and how impacts are related to lake habitat characteristics, is essential to inform future management actions.
The temporal and spatial scale at which invasive species research is conducted is of particular importance in developing predictive capacity (Parker et al. 1999; Strayer et al. 2006). Small-scale short-term experiments can be very useful in elucidating the potential magnitude and mechanisms of a species’ impact. However, these experiments often do not incorporate all the relevant ecological variables (such as variation in predation or habitat quality), which leads to problems in scaling-up the results to the whole-ecosystem level (Carpenter 1996; Lodge et al. 1998b). Similarly, short-term lab experiments or large-scale correlative studies can return results quickly for implementation into policy and management, but these experiments often ignore changes in the effects of introduced species over time. Strayer et al. (2006) noted that most studies of nonindigenous species are short-term and focus on the acute effects of introductions while the long-term or chronic effects may be very different. They identified four mechanisms that may lead to changes in the effects of a species over time: (1) physical or genetic changes in the introduced species, (2) changes in the species composition of the invaded community, (3) changes in the physical or chemical characteristics of the invaded ecosystem, and (4) interaction between the introduced species and other controlling variables such as weather or disturbance. Despite the likelihood that the impact of a species changing throughout the course of an invasion, time since invasion is often ignored in studies of invasive species (Lodge et al. 1988).

Of particular interest is the possibility that a species introduction may result in a pattern of boom-and-bust, a rapid population expansion followed by collapse (Williamson 1996). If such a pattern is common for a species, then the logical management decision may be to do nothing once a species has established (Simberloff
and Gibbons 2004), although the short-term acute effects of the species may be great enough to warrant action (Strayer et al. 2006; Keller et al. 2008). While boom-and-bust patterns are relatively rare, they have been recorded for a number of different taxa, and are characteristic of introductions of a few species including reindeer, *Rangifer tarandus*; North American waterweed, *Elodea canadensis*, in Europe; the cane toad, *Bufo marinus*; and least weasels, *Mustela nivalis* in New Zealand (Williamson 1996; Simberloff and Gibbons 2004; Ricklefs 2005). For other species, such as the zebra mussel, *Dreissena polymorpha*, in Eastern Europe, cases of both boom-and-bust and long-term logistic increase occur (Parker et al. 1999). While often no definitive evidence of the cause of invasive species declines exist, the most frequently cited mechanisms relate closely with those identified by Strayer (2006), including depletion of food resources and increases in predation and disease (changes in invaded community) as well as habitat loss (changes in invaded environment).

One of the most studied freshwater invasive species in North America is the rusty crayfish, *Orconectes rusticus*, which has spread over the last 40 or 50 years from its home range in the Ohio River drainage to much of the midwestern and northeastern United States and southern Ontario (Lodge et al. 2000; Olden et al. 2006). In the northern lakes region of Wisconsin, the spread of *O. rusticus* is displacing both the native crayfish *O. virilis* and a previous invader *O. propinquus* (Olsen et al. 1991; Olden et al 2006). Introduction of *O. rusticus* can greatly alter lake food webs by reducing the abundance and diversity of macrophytes and macroinvertebrates and decreasing the abundance of some fish species (Chapter 3; Chapter 5; Lodge et al. 1994; Lodge et al.
1998a; Wilson et al. 2004; McCarthy et al. 2006; Rosenthal et al. 2006; Willis and Magnuson 2006).

While most research has focused on the magnitude of impact that *O. rusticus* can have on lake ecosystems, little attention has been paid to the variability of impact among lakes and through time. However, some surveys indicate that *O. rusticus* abundance differs markedly from lake to lake (Capelli and Magnuson 1983; Garvey et al. 2003; Roth et al. 2007; Vander Zanden and Olden 2008). This between-lake variance has generally been attributed to the availability of preferred cobble habitat (Capelli and Magnuson 1983; Garvey et al. 2003). Other habitat variables such the abundance of macrophytes (which provide predation refuge; Kershner and Lodge 1995) or of less preferred habitats (sand and muck) may also be important (Hill and Lodge 1994), but evidence supporting these is scarce. Another variable that is likely important but generally ignored is the length of time since *O. rusticus* introduction. Lakes surveyed early in the invasion process may erroneously report low crayfish abundance where it may ultimately be high. It is also possible that boom-and-bust population dynamics may lead to long-term declines after initially high abundance. Such a pattern might be expected for *Orconectes rusticus* in lakes. Extensively documented declines in macroinvertebrates and macrophytes (Lodge et al. 1994; Lodge et al. 1998b; Wilson et al. 2004; McCarthy et al. 2006; Rosenthal et al. 2006) should increase food limitation for crayfish, especially for juveniles that require high protein diets for rapid growth (Chapter 5; Momot 1995). Because smaller crayfish are more susceptible to predation (Garvey et al. 1994), and macrophytes provide predation refuge (Saiki and Tash 1979; Kershner and Lodge 1995), the result should be increased predation pressure. Aside from two intensively studied
lakes (Trout Lake and Sparkling Lake) in northern Wisconsin (Wilson et al. 2004; McCarthy et al. 2006), little is known about the long-term population dynamics of *O. rusticus* invasion.

In this study, we use habitat-specific crayfish trapping data to examine long-term population trends for crayfish in a variety of northern Wisconsin lakes that have been invaded by *Orconectes rusticus*. We expect declines in the abundance of all previously resident crayfishes, but predict that the native crayfish *O. virilis* will be more likely to persist after invasion than *O. propinquus*. Some evidence suggests that *O. rusticus* and *O. propinquus* avoid muck habitats, which may provide a long-term refuge for *O. virilis* (Hill and Lodge 1994). In addition, *O. propinquus* hybridizes with *O. rusticus* while *O. virilis* does not (Perry et al. 2001). Over time, we expect the average size of *O. rusticus* to decrease as high quality food resources (macroinvertebrates) decline and reliance on low quality foods (algae and detritus) increases (Chapter 5).

We predict that the long-term abundance of *O. rusticus* will be determined by habitat, specifically the abundance of cobble as well as its distribution within a lake. The habitat value of cobble should remain high over the long-term despite reduced crayfish size (and thus increased predation risk) as the interstices of the cobble provide effective predation refuge for even small crayfish (Garvey et al. 2003). In fact, as the primary location of crayfish reproduction, cobble will likely serve as a source of crayfish to surrounding habitats (Lodge and Hill 1994). Conversely, sand will likely decline in value as a habitat and increasingly act as a population sink as the consumption of macrophytes and macroinvertebrates by crayfish decreases the availability of food and predation refuge (macrophytes). Therefore, lakes with a high proportion of cobble should sustain
abundant *O. rusticus* populations over the long-term. Lakes with abundant sand and scarce cobble may sustain high crayfish numbers if the cobble habitat (predation refuge and source of juvenile crayfish) are spread evenly around the lake perimeter. However, if the cobble is aggregated in one part of the lake, the decreasing habitat value of sand habitats should lead to a long-term boom-and-bust pattern of *O. rusticus*. Quantifying the relationship of these lake-specific characteristics to population dynamics of *O. rusticus* would increase our understanding of lake communities, and simultaneously provide guidance for the efficient allocation of management resources to lakes most likely to suffer high long-term damage from invasion.

2.3. Methods

*Crayfish trapping*

We assembled a dataset of the results of the monitoring of crayfish populations in lakes from the Northern Highlands region of Wisconsin and the Upper Peninsula of Michigan. The dataset covers 30 years (1975-2005) and 21 lakes that have been invaded by *O. rusticus* and includes some data that have been previously published (Capelli and Magnuson 1983; Olsen et al. 1991; Garvey et al. 2003; Wilson et al. 2004). Crayfish were sampled using standard methods during the intermolt period between mid-July and mid-August (Olsen et al. 1991). Multiple (10-36) Gee Minnow traps with enlarged openings (~5 cm) were baited with beef liver (120 ± 10 g) and placed around the perimeter of lakes and left overnight. For most samples taken after 1980, the dominant benthic substrate (cobble, sand or muck) surrounding the trap was noted and recorded.
Crayfish were counted and carapace length of males was measured. For samplings from 1975-1988, a representative subsample of 200 males was measured (all males were measured if <200 were caught). Only adult male crayfish (≥20 mm carapace length) were used as an index of abundance as females and juveniles are underrepresented in traps (Olsen et al. 1991). Both males and females were used when determining the presence/absence of a species.

Data analysis

Recognizing the importance of identifying the stage of invasion in our analyses of abundance, we classified each lake sample as early invasion, when O. rusticus may be present but little impact is expected (OR comprised <10% of crayfish trapped); transitional, as they spread throughout the lake (traps where OR represented > 10% but < 90%); and invaded (OR > 90% of crayfish caught). Hereafter, we use these terms consistently throughout this paper to indicate these quantitative definitions. For all analyses (described below) where lakes serve as replicates and individual lakes were sampled multiple times during one of the invasion phases (early invasion or transitional or invaded), multiple samples taken during a phase were averaged.

We examined the long-term fate of O. virilis and O. propinquus after O. rusticus invasion by comparing the number of lakes in our database in which each species has been extirpated to the number in which the species remain extant. This analysis included only lakes that have been invaded for a minimum of 10 years. We categorized a species as extirpated if it was not collected in three consecutive samplings and did not reappear
thereafter. Frequency of extirpation for the two species was analyzed using chi-square analysis of a 2 x 2 contingency table.

In order to examine the role of benthic substrate on long-term crayfish species coexistence, we compared the abundance of *O. rusticus* and *O. virilis* in invaded lakes on cobble, sand and muck using ANOVA with Tukey’s post hoc comparisons; abundance of *O. virilis* was square-root transformed for homogeneity of variance (Levene’s test for equality of variance; p=0.021). Substrate preference for *O. propinquus* could not be analyzed because substrate was rarely recorded in the early sampling years before *O. propinquus* was completely replaced by *O. rusticus*.

We looked for changes in crayfish size through the course of invasion using within and across lake analyses. For the across lake analysis, we compared the average carapace length of *O. rusticus* from early invasion lake samples to those in invaded lake samples. Replicates were mean carapace length within each lake and, as these lake means were not normally distributed (K-S/Lilliefors; p=0.017), we used a Mann-Whitney test to compare medians instead of a t-test to compare means. When data was available for a lake during both early invasion and invaded phases, the lake was used as a replicate for both invasion categories. For within-lake analysis, we used simple linear regression to evaluate change in carapace length over time. We only included lakes in the within-lake analysis if they (a) had been sampled at least five times, (b) had been invaded for at least 10 years and (c) had at least one sample taken before the lake was invaded. Because nine regressions were run, we used a Bonferroni correction to determine significance (critical α = 0.0056).
We examined the influence of substrate on long-term *O. rusticus* population size by using simple linear regression. For all lakes that had been invaded for at least 15 years, we regressed long-term *O. rusticus* abundance (average trap catch over all years that lake had been invaded) against the percentage of the lake littoral zone that is cobble (% cobble). To estimate % cobble, we divided each lake into sectors with the crayfish traps in the middle of the sectors. The substrate of the entire sector was assumed to be the same as that which was observed at the trapping location. We calculated % cobble as the percentage of all sectors within a lake that were cobble.

To test the importance of cobble distribution around the lake perimeter, we created an index which combines the abundance of cobble with a measure of the evenness of its distribution around the lake perimeter (Cobble Proximity Index or CPI). We then regressed long-term *O. rusticus* abundance against CPI. We hypothesized that the habitat value of sand and muck will decline with time (as vegetation growing on those substrates is reduced by crayfish consumption), but that the value of cobble habitat remains unchanged. Accordingly, the CPI assigned a habitat value to all perimeter sectors. Cobble sectors were assigned a value of 1 while the values for muck and sand were inversely related to distance from the nearest cobble sector. For muck and sand sectors, one point was subtracted for every sand or muck habitat between the sector in question and the nearest cobble segment. Thus, sand adjacent to cobble would have a value of 1, whereas a sand sector separated from the nearest cobble by one sector would have a value of 0, by two sectors a value of -1, etc. We limited the lowest value to -5 to prevent bias in lakes that were more intensively sampled. The CPI value for the lake is the average of the values assigned for all sectors within a lake and could theoretically
vary from -5 (no cobble at all) to 1 (which could result from a lake that was 50% cobble evenly distributed up to 100% cobble). CPI values measured in our sampled lakes ranged from -2.8 to 0.48. Because of the arbitrariness of the CPI scoring system, we tested the sensitivity of our results to the scoring system by repeating analyses with alternative CPI point assignment schemes. Results of regressions of crayfish abundance against CPI were not strongly affected by alternative scoring systems; therefore we present results for only the scoring described above.

We looked for evidence of long-term decline (boom-and-bust) by fitting phenomenological models of population growth to our trapping data. Lakes were included in this analysis only if (a) the lake had been sampled a minimum 6 times; (b) at least one sampling was during the early invasion period; and (c) *O. rusticus* had been present in the lake for at least 15 years. The three models tested were: linear, $n = ax + b$; hyperbolic Michaelis-Menten, $n = ax/(b+x)$; and quadratic, $ax^2 + bx + c$. In all models, the variable $n$ was an index of crayfish population size as measured by whole-lake mean trap catch; the variable $x$ was time. Population growth that had not reached a maximum is most likely to be described by the linear or quadratic model, while growth to an asymptote (carrying capacity) should best fit the Michaelis-Menten function. If *O. rusticus* populations increase to a peak and decline, possibly indicating boom-and-bust, the quadratic model should best describe the data. Each model was fit to the observed data with least squares regression using the SPSS statistical package (version 16.0; SPSS Inc., 2007). When fitting the Michaelis-Menten function, the variables $a$ and $b$ were constrained to positive values. The models were compared using Akaike’s Information Criterion adjusted for small sample size (AIC$_c$) which takes into account statistical
goodness-of-fit while imposing a penalty for model complexity (Burnham and Anderson 2002; Burnham and Anderson 2004). Lower AIC$_c$ values represent a better fit. Models were compared and best fit was determined using $\Delta$AIC which is calculated as:

$$\Delta\text{AIC} = \text{AIC}_i - \text{AIC}_{\text{min}}$$

where $\text{AIC}_i$ is the AIC$_c$ value for each model being tested and $\text{AIC}_{\text{min}}$ is the lowest AIC$_c$ value (and thus for the model with best fit) of all the models. When $\Delta\text{AIC} \leq 2$ there is little support for the best-fit model over another, when $4 \leq \Delta\text{AIC} \leq 7$ there is moderate support, while $\Delta\text{AIC} > 10$ indicates strong support for the best-fit model (Burnham and Anderson 2004).

2.4. Results

As predicted, *Orconectes virilis* tended to coexist longer with *O. rusticus* than did *O. propinquus* ($p=0.016$; Figure 2.1). In the six lakes that contained both *O. virilis* and *O. propinquus* when *O. rusticus* was first recorded, both species disappeared at the same time in three, while *O. virilis* outlasted *O. propinquus* in the remaining three. In five lakes, *O. virilis* coexisted with *O. rusticus* for at least 25 years, whereas we only documented one case in which *O propinquus* and O. rusticus co-occurred for more than 15 years.

As predicted, the crayfish species differed in their habitat use in lakes that were invaded (Figure 2.2). *Orconectes rusticus* was more abundant on cobble and sand substrates than on muck ($p=0.006$), while *O. virilis* was most abundant on muck ($p<0.001$). As predicted, the average size of *O. rusticus* was smaller late in invasion
compared to the early invasion phase. In the across-lake comparison, the median carapace length was 37.2 mm in early invasion lakes and 33.9 mm in invaded lakes (p=0.016; Figure 2.3). Results from the within-lake analysis were mixed (Figure 2.4). Of the nine lakes analyzed, two (Big and Boulder Lakes) demonstrated a significant decline in size, three (Clear, Island and South Turtle) showed a similar, but nonsignificant trend, and four (Birch, Papoose, Plum and Trout) showed no trend at all. In the lakes where *O. rusticus* did not decline in size tended, they tended to start out small early in the invasion (similar to the median size of the invaded lakes from the across-lakes comparison).

**Figure 2.1.** Long-term survival of crayfish species in lakes categorized as invaded by *O. rusticus*. 

![Chi-square bar chart](image)
Figure 2.2. Abundance (mean ± 1 SE) of (a) *O. rusticus* (n=11 lakes) and (b) *O. virilis* (n=8) by benthic substrate type in lakes categorized as invaded by *O. rusticus*. 
Figure 2.3. Mean crayfish size within lakes categorized as early invasion and within lakes categorized as fully invaded. Data points represent lake-wide means for individual lakes. Dashed line represents the median lake-wide value for the invasion category.
Figure 2.4. Change in *O. rusticus* size through time. Data points are the means. After Bonferroni correction for running nine tests, critical $\alpha = 0.0056$. 
Contrary to our predictions, cobble abundance was not a good predictor of long-term crayfish abundance ($R^2=0.084$, $p=0.291$; Figure 2.5a). On the other hand, as predicted, the Cobble Proximity Index was positively related to crayfish abundance ($R^2=0.333$, $p=0.024$; Figure 2.5b), indicating that the distribution of cobble around a lake’s perimeter, in addition to the lakewide abundance of cobble, is important. Lakes with more cobble that is evenly distributed tended to have higher long-term abundance of *O. rusticus*.

Model fitting results indicated only weak support for boom-and-bust dynamics in our long-term trapping of lakes invaded by *O. rusticus* (Table 2.1; Figure 2.6). In no case did the ΔAIC indicate strong support for the quadratic model, but always provided strongest support for the linear or Michealis-Menten function as the best fit models. The estimated linear model of best fit in VanVliet lake had a negative slope and was thus the best evidence of long-term decline. There was moderate support for the quadratic model in Papoose, Trout and VanVliet lakes which can describe a peak in abundance and decline. The quadratic model that was estimated for Trout Lake does not describe a peak and decline but instead increasingly rapid growth. The model parameters for Michaelis-Menten were not estimable in Trout and VanVliet lakes. This is not surprising, because when estimating parameters for nonlinear models that capture density dependent population mechanisms, data must be observed within the region over which the dynamics occur. For example, if observations of a population's density occur when the population is not experiencing any density dependent effects, such as a carrying capacity, then there will be little evidence for density dependent effects and the value of the carrying capacity will be not estimable (Dennis and Taper 1994).
Figure 2.5. Relationship between long-term *O. rusticus* abundance and (a) % of lake littoral zone composed of cobble and (b) the Cobble Proximity Index (CPI). Low CPI values represent low cobble abundance that is aggregated while high CPI values represent high cobble abundance and/or evenly distributed cobble.
### TABLE 2.1

RESULTS OF FITTING MODELS OF POPULATION GROWTH TO *O. RUSTICUS* ABUNDANCE

<table>
<thead>
<tr>
<th>Lake</th>
<th>N^a</th>
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<th>K^b</th>
<th>AIC^c</th>
<th>Δ-AIC^d</th>
<th>SD_resid</th>
<th>K^b</th>
<th>AIC^c</th>
<th>Δ-AIC^d</th>
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^a Number of lake years sampled  
^b Number of parameters estimated, including the number of parameters from the model plus one for the estimation of variance.  
^c Akaike’s Information Criterion corrected for small sample sizes (AIC^c) estimates model-fit  
^d ΔAIC was calculated in order to judge relative support for the models.
Figure 2.6. Crayfish abundance over time in lakes that became invaded by *O. rusticus*. Lines represent phenomenological models for which the data for *O. rusticus* give strong or moderate support (as determined by Akaike’s Information Criterion for small sample sizes AICc). Models tested were linear (dashed line), hyperbolic Michaelis-Menten (solid line), and quadratic (dotted line). Data for *O. virilis* and *O. propinquus* were not included in the analyses, but are shown to further illustrate the impact of *O. rusticus* on its congeners.
2.5. Discussion

**Long-term trends in crayfish species composition**

*Orconectes rusticus* consistently displaces *O. propinquus* and *O. virilis* in northern Wisconsin lakes (Olsen et al. 1991; Olden et al. 2006). An earlier invader that has also replaced *O. virilis* in lakes (Lodge et al. 1986; Olsen et al. 1991), *O. propinquus* is more aggressive and therefore outcompetes *O. virilis* for habitat and is less susceptible to predation by fish (Garvey et al. 1994). As such, it would be logical to expect *O. virilis* to be more prone to local extirpation. However, the results reported in this paper suggest that *O. virilis* may be better able to coexist with *O. rusticus* in the long-term. In addition, Hein et al. (2006) found a similar pattern when *O. rusticus* invaded Sparkling Lake, where *O. propinquus* disappeared from annual monitoring more than 10 years before *O. virilis*. Later, during intensive trapping for the purpose of rusty crayfish removal, *O. virilis* was found to have survived in very low numbers while *O. propinquus* was absent (Hein et al. 2006).

There are two likely explanations for this pattern, differential hybridization with *O. rusticus* and the presence of a habitat refuge for *O. virilis* but not *O. propinquus*. Genetic analyses have found that *O. rusticus* hybridizes with *O. propinquus* but not *O. virilis* (Perry et al. 2001). Hybridization is a common threat to native freshwater biodiversity including crayfish, mollusks and fish (Perry et al. 2002). In the case of *O. rusticus* and *O. propinquus*, hybrids are much more likely to backcross with *O. rusticus*, contributing to the decline in *O. propinquus* (Perry et al. 2001).
When examining the importance of benthic substrate in crayfish species replacement, most work has focused on habitat as predation refuge, and therefore most research has emphasized the differences between cobble (which does not support vegetation), substrates vegetated with macrophytes, and unvegetated sand. These represent high, moderate and no predation refuge respectively (Hill and Lodge 1994; Kershner and Lodge 1995; Garvey et al. 2003). For example, in the presence of *O. propinquus* and *O. rusticus* in Trout Lake, *O. virilis* was found exclusively in macrophytes (Garvey et al. 2003). Similarly, in a survey of multiple lakes, *O. virilis* changed its habitat preference from cobble in the absence of other crayfish species to macrophytes in lakes invaded by *O. rusticus* (Hill and Lodge 1994). Limited laboratory and field evidence suggests that the substrate underlying macrophytes (which can range from relatively pure sand to very soft, organic-rich muck) may be just as important in determining crayfish distribution. In experiments in small wading pools, all three species prefer cobble substrates in the absence of congeners, but when *O. rusticus* is present, *O. virilis* and *O. propinquus* were displaced to vegetated muck and vegetated sand habitats respectively (Hill and Lodge 1994). Field measurements of crayfish density in one lake suggested that *O. rusticus* were in low density in muck (Kershner and Lodge 1995). These results are supported by our findings that *O. rusticus* was much more abundant in sand and cobble than in muck, whereas *O. virilis* was most common in muck. While *O. rusticus* trap catches in muck were five times higher than those of *O. virilis*, lower abundance of the invasive crayfish likely means reduced intensity of competition as well as fewer agonistic interactions between the congeners, and thus muck may serve as a
habitat refuge. We were not able to address substrate use by *O. propinquus* statistically because it had disappeared from most of the lakes we monitored by the time substrate was regularly recorded during sampling. In South Turtle, the one lake in which it remained in appreciable numbers in the presence of *O. rusticus*, the vast majority of individuals were trapped in sand or cobble, consistent with the small-scale pool results (Hill and Lodge 1994). Thus, it appears that only *O. virilis* may be taking advantage of muck as a refuge from competition and direct aggressive interactions with *O. rusticus*.

We cannot definitively identify the mechanism that deters *O. propinquus* and *O. rusticus* from inhabiting muck, although we hypothesize that dissolved oxygen plays a role. Mobility of crayfish on fine substrates is not likely to be important. We have observed all three crayfish species moving around with little trouble on very soft organic sediments (T. Kreps personal observation). Muck tends to have higher organic matter content than sand or cobble and therefore, decomposition should reduce dissolved oxygen levels near the sediment surface. While we do not have direct measurements of oxygen tolerances for the crayfish species in question, there is reason to believe that *O. virilis* is better able to cope with low oxygen levels than its congeners. First, both *O. propinquus* and *O. rusticus* have higher metabolic rates than *O. virilis* (Lippsion 1976), implying a greater oxygen requirement. Second, although not compared to the species in question here, *O. rusticus* has a higher oxygen demand compared to other Orconectid crayfish (*O. nais* and *O. immunis*; Eggleston and Lustick 1981). Finally, in previous field and laboratory studies it has been shown that *O. virilis* has developed physiologic adaptations to low oxygen conditions, including the ability to depress heart and metabolic rates, allowing the species to deal with extreme anoxia (Reiber 1995; Cowan and Storey 2001).
Differential habitat preferences have been shown to promote coexistence of other native freshwater and introduced species. The native amphipod North American *Gammarus fasciatus* is being replaced in the lower Laurentian Great Lakes by the introduced Ponto-Caspian amphipod *Echinogammarus ischnus*. However, in the St. Lawrence River habitat heterogeneity promotes coexistence of the two species. The introduced *E. ischnus* is more abundant in areas with high water velocity and gravel sediment, while the density of the native *G. fasciatus* is related to algal biomass and water pH (Palmer and Ricciardi 2004). Similarly, it appears that habitat heterogeneity (a mix of cobble, sand and muck) may promote the long-term coexistence of *O. virilis* and *O. rusticus*.

*Long-term O. rusticus abundance: Boom-and-bust?*

Our statistical analysis produced little evidence of a boom-and-bust pattern for rusty crayfish in the monitored lakes. There was moderate support for a quadratic model that describes a peak and decline in Papoose and VanVliet lakes (although support for both linear and Michaelis-Menten was stronger), and the linear model that best describes VanVliet had a negative slope. In fact, after peaking at a mean trap catch of 5.1 in 1980, catches for all crayfish in VanVliet were near zero in the last three trappings. It is possible that our analysis using only mean lake-wide trap catches lacks the power to identify a peak and decline in crayfish abundance that may exist in some of the lakes that were monitored (e.g. Papoose, VanVliet and Island lakes).

Data from four additional lakes that did not meet our minimum criteria for the statistical analysis of *O. rusticus* population patterns (no trapping data was available from the early invasion period) may still provide some important information about the
dynamics of the invasion (Appendix 1). First, Presque Isle Lake, which has been invaded longer than any other lake in our database (30+ years), continues to support very high *O. rusticus* abundance. Thus, while our results demonstrating a lack of long-term decline in many lakes cannot rule out a future decline, we have found that very high crayfish abundance can be sustained for long periods. Second, over the course of 15-28 years, the other three lakes (Clear, Little Star, and Spider) have shown relatively sharp negative trends. So, while boom-and-bust may not be the general pattern for lakes invaded by *O. rusticus*, our database does include a number of cases in which a sizable decline in *O. rusticus* abundance has been recorded.

In addition to the limited evidence for boom-bust from long-term crayfish monitoring, examination of the mechanisms that might limit crayfish populations supports the possibility of long-term decline in *O. rusticus*. After introduction, it can dramatically deplete its preferred food resources. Realistic densities of *O. rusticus* can eliminate macrophytes in field cages and enclosures (Lodge and Lorman 1987; Lodge et al. 1994) and observations in the field have confirmed that macrophyte declines can be extreme (Wilson et al. 2004; Rosenthal et al. 2006). Reductions of snails, prey preferred by crayfish, can be dramatic also. Declines in snail densities from 1000-10,000 snails/m\(^2\) to less than 10 snails/m\(^2\) in sand habitats have been reported in multiple lakes, while snails are virtually eliminated from cobble (Chapter 3; Wilson et al. 2004). A wide variety of other macroinvertebrates also decline due to direct consumption and loss of macrophyte habitat (Chapter 5; Wilson et al. 2004; McCarthy et al. 2006). The loss of food resources has an important direct effect on crayfish, as indicated here by the decline in mean individual size of *O. rusticus* during invasion. The loss of animal prey is
particularly important for juvenile crayfish which rely on this high protein prey to promote rapid growth, allowing them to quickly reach a size refuge from fish predation (Momot 1995). Analysis of stable isotopes has confirmed that juvenile crayfish in lakes invaded by *O. rusticus* have a lower trophic position, indicating reduced carnivory (Chapter 5).

Increased predation by fish could also contribute to a decline in *O. rusticus* populations. A variety of common fish species are able to prey on crayfish, including rockbass *Ambloplites rupestris*, yellow perch *Perca flavescens*, smallmouth bass *Micropterus dolomieu*, largemouth bass *M. salmoides*, and walleye *Stizostedion vitreum* (Garvey et al. 2003). Even-gape limited predators such as bluegill *Lepomis macrochirus* and pumpkinseed sunfish *Lepomis gibbosus* may be significant crayfish predators for short periods after crayfish hatch (Roth et al. 2007). Fish predation can remove large proportions of *O. rusticus* populations (Hein et al. 2006) and previous work has shown that high abundance of fish predators can depress crayfish densities within a lake (Kershner and Lodge 1995; Garvey et al. 2003). The dynamics of crayfish predator populations through the course of invasion are, however, not well understood. The presence of abundant crayfish prey has a positive effect on the growth of adult smallmouth bass, but no effect on bluegill (Chapter 5). Predation by crayfish on fish eggs and the loss of macrophyte habitat is likely to have a negative effect on some fish species (Chapter 5; Dorn and Mittelbach 2004; Wilson et al. 2004). Studies of changes in fish populations after the introduction of *O. rusticus* are few, but consistently find declines in bluegill and pumpkinseed and other small fish species (Chapter 5; Wilson et al. 2004; Willis and Magnuson 2006; Roth et al. 2007). Patterns are less clear for larger
crayfish predators with studies showing no change (Wilson et al. 2004) or possibly increases in smallmouth and yellow perch (Willis and Magnuson 2006). Regardless of changes in predator populations, crayfish larger than 35 mm have a size refuge from fish predation (Hein et al 2006). Thus, the reduction in crayfish size through the course of invasion should mean that a larger proportion of the population is susceptible to fish consumption.

The destruction of macrophytes by crayfish should also increase crayfish vulnerability to predation because macrophytes serve as predation refuge, and unvegetated habitats (other than cobble) are avoided by *O. rusticus* (Kershner and Lodge 1995; Hill and Lodge 1994). The effect of this loss of habitat should be greatest in lakes with littoral zones composed of high proportions of sand (where macrophytes are most likely to be cleared by crayfish) and little cobble. For this reason, it is somewhat surprising that we found no relationship between lakewide cobble abundance and long-term crayfish abundance. However, because we were attempting to examine long-term abundance (*O. rusticus* abundance in each lake was averaged over at least 15 years after lakes were fully invaded), our analysis may have partly obscured long-term declines in crayfish abundance over time. Our analysis of the Cobble Proximity Index did not correct for that potential problem, but it did more effectively address the importance of the distribution (as well as the abundance) of cobble.

Cobble is the primary location of crayfish reproduction, and the most important refuge for juvenile crayfish (Lodge and Hill 1994; Garvey et al. 2003). Non-cobble habitats may benefit crayfish populations because they can leave the protection of the rocks at night when predation risk is low to forage in surrounding areas where resources
may be more abundant (Hill and Lodge 1994; Lodge and Hill 1994). Early in the invasion process, when macrophytes are dense on sand and mean size of *O. rusticus* is large, they may forage farther from cobble and remain in the protection of macrophytes during the day. Cobble habitats are thus a source of adult crayfish to non-cobble habitats. Through the course of invasion, macrophyte habitat and macroinvertebrate food declines and crayfish size is reduced. With higher predation risk, *O. rusticus* is less likely to forage far away from cobble. For this reason, in lakes where cobble is aggregated in one portion of the lake perimeter, lake-wide crayfish abundance may be high initially, but decline as predation risk in large portions of the lake increases. When the cobble is distributed more evenly around the lake, *O. rusticus* may continue to take advantage of a larger portion of the lake littoral zone at night and lake-wide *O. rusticus* abundance remains high. Indeed, when cobble distribution was taken into account with the Cobble Proximity Index (CPI), we found a relationship between substrate and long-term *O. rusticus* abundance. While we lack the long-term substrate data to adequately determine whether this pattern is results specifically from long-term declines on sand habitats, examination of three lakes for which data is available provides some support. Presque Isle, with a high percentage of littoral cobble (33%) and a relatively high CPI score (-0.38) continually supported high abundance of *O. rusticus*. On the other hand, Little Star and Spider lakes, with lower abundance of cobble (19% and 25% respectively) that is aggregated on one side of the lake (CPI scores of -2.40 and -2.94) declined. While crayfish abundance in these lakes declined on all substrates, reductions were about two to three times greater in sand (supporting the increased importance of predation).
Conclusions

The introduction and spread of the rusty crayfish is a threat to freshwater biodiversity. Our results confirm previous reports that *O. rusticus* consistently displaces other crayfish species, and that it can cause localized extinctions of these species (Lodge et al. 1986; Olsen et al. 1991; Olden et al. 2006). At the same time, avoidance of muck habitats by *O. rusticus* appears to be providing a refuge for the native crayfish (*O. virilis*) but not for a previous invader (*O. propinquus*). The question remains as to whether this refuge may allow the native to survive over an even longer term than our 30 years observation period or whether it has simply slowed its extirpation.

Understanding the long-term dynamics of an introduced species and its interactions with the resident community can be very important in informing management actions. If boom-and-bust is characteristic of the introduction of a species then “no action” may be a reasonable management choice if: (1) declines are eventually widespread and density remains below nuisance levels after decline; (2) declines occur relatively soon after introduction, minimizing short-term environmental and economic losses and (3) ecosystems recover after decline. Our results do provide some evidence that *O. rusticus* populations may decline in some lakes (especially those with low proportions of cobble in the littoral zone). However, we have also shown that crayfish often remain abundant for long periods after introduction with little sign of decline within our 30 year observation window. Even if a bust in crayfish population does occur, recent economic analyses have shown that *O. rusticus* invasions cause significant economic losses over relatively short time periods (Keller et al. 2008). Additionally, studies of snails and macrophytes in two lakes in which *O. rusticus* has apparently declined (Little
Star and Spider) have shown that little ecosystem recovery is evident (Chapter 3; S. Rosenthal unpublished data). One explanation for this may be that even at low density, consumption rates of the crayfish population may equal or exceed the production rates of their food resources. Crayfish remain very small in these lakes, indicating continued resource limitation.

One potential management solution is to manipulate fish predator populations in these lakes in order to increase the importance of predation, thus allowing the ecosystem to recover. Such efforts have begun in the form of “catch and release only” fishing regulations for smallmouth bass in some Wisconsin lakes (Olden et al. 2006) and a successful removal effort that combined crayfish trapping and increases in fish predator populations (Hein et al. 2006). Intensive trapping is likely too costly to be a widely used management technique, and no results have been reported for lakes in which only fishing regulations have been changed. The results reported in this paper are consistent with the importance of fish predation in limiting some *O. rusticus* populations, and suggest that such efforts are most likely to be effective in lakes with limited cobble that is not evenly spread throughout the lake.

2.6. Acknowledgments

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CHAPTER 3:

THE IMPACT OF AN INVASIVE PREDATOR (*ORCONECTES RUSTICUS*) ON FRESHWATER SNAIL COMMUNITIES: INSIGHTS ON HABITAT-SPECIFIC EFFECTS FROM A MULTI-LAKE LONG-TERM STUDY

3.1. Abstract

Most studies of the impacts of invasive species are done at small spatial and short temporal scales, which limits the ability to generalize the results to natural ecosystems. This is particularly important when the abundance of a nonindigenous species differs across habitats or varies through time. We conducted a study in 11 northern Wisconsin lakes to investigate the long-term, whole-lake impacts of predation by the introduced rusty crayfish (*Orconectes rusticus*) on snail communities. In 1987 and 2002, crayfish and snails were surveyed in lakes that initially differed in *O. rusticus* abundance; in some of the lakes, crayfish abundance also changed substantially between the sampling periods. Two lakes that had been uninvaded in 1987 experienced outbreaks of *O. rusticus* by 2002, while two lakes had large declines in *O. rusticus* abundance during this 15 year period. Results from newly invaded lakes showed that *O. rusticus* caused large reductions in snail abundance over relatively short time periods, but that the rate and

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2 This Chapter (with co-author David M. Lodge) has been submitted for publication to Canadian Journal of Fisheries and Aquatic Sciences.
magnitude of impact differed among lake-bottom habitats. As predicted, snails declined much more in habitats that are preferred by *O. rusticus* (sand and cobble) than in habitats that they avoided (muck). Lakes that experienced large *O. rusticus* declines exhibited no significant increase in snail densities between sampling years, illustrating the difference in response time of snail populations to release from predation relative to increasing predation. Contrary to prediction, no consistent difference in snail species composition existed between invaded and uninvaded lakes.

3.2. Introduction

The spread of introduced invasive species is one of the leading causes of global biodiversity loss and ecosystem change (Mack et al. 2000; Sala et al. 2000; Millenium Ecosystem Assessment 2005; Clavero and Garcia-Berthou 2005). Introduced species are of particular concern in freshwater ecosystems (Richter et al. 1997; Rahel 2002; Ricciardi and Atkinson 2004; Lodge 2001b) as species loss is occurring at a faster pace than in terrestrial systems (Ricciardi and Rasmussen 1999; Dudgeon et al. 2006).

Although prevention of the spread of non-indigenous species or quick eradication after establishment are often priorities for management (Lodge et al. 2006), many invasions continue without management. Therefore, research into the long-term dynamics and effects of invasion are important in informing future policy and management of such situations (Mack 2005; Simberloff et al. 2005). Additionally, through the study of introductions that have little impact, as well as of those with large impacts, ecologists can learn much about the role of biotic interactions in structuring
communities (Lodge 1993; Sax et al. 2005). For example, predation has often been recognized as an important structuring force for ecological communities (Hairston et al. 1960; Kerfoot and Sih A. 1987; Menge and Sutherland 1987; Carpenter and Kitchell 1993). Studies of species introductions have reinforced this because introduced predators often have significant impacts on their prey (Mack et al. 2000; Bruno et al. 2005), sometimes leading to cascading trophic effects and long-term alteration of community structure (Bruno et al. 2005; White et al. 2006; Blanchet et al. 2008).

In freshwater benthic habitats, a wide variety of macroinvertebrates constitute an important part of the food web. When abiotic conditions are adequate (primarily Ca\(^{2+}\) concentrations; Lodge et al. 1987), snails are often dominant in terms of numbers and biomass, function as periphyton grazers, and as prey for many consumer species (Pip 1986; Bronmark et al. 1992; Lodge et al. 1994; Dillon 2000). While snails can be food limited, especially in low productivity habitats (Osenberg 1989; Hershey 1992), they can also be subject to strong top-down control by predators, including fish (Bronmark et al. 1992; Lodge et al. 1998b; Lodge et al. 1994; Bronmark and Weisner 1996; Bronmark 1988; Osenberg and Mittelbach 1989), insects (Kesler and Munns 1989; Turner and Chislock 2007) and crayfish (Nystrom et al. 1996; Lodge et al. 1998b; Nystrom and Perez 1998; McCarthy et al. 2006).

Previous studies examining snail predation have tended to focus on the impact on snails collectively relative to other macroinvertebrate taxa, while very little is known about the effects on snail species composition (Dillon 2000). However, there is good reason to believe that predation should favor the presence of some snails over others. Snail species demonstrate broad variation in their defenses against predators including
shell thickness and shape (Stein et al. 1984; Osenberg and Mittelbach 1989; Alexander and Covich 1991; Hoverman et al. 2005) and behavioral avoidance (Alexander and Covich 1991; Covich et al. 1994; Rundle and Bronmark 2001; Mower and Turner 2004). Laboratory experiments consistently demonstrate that shell-crushing predators such as fish and crayfish consume more thin-shelled than thick-shelled snails (Stein et al. 1984; Alexander and Covich 1991; Brown 1998; Lodge et al. 1998b) and, although species composition is rarely noted, predator studies in mesocosms (Nystrom et al. 1999), field cages (Lodge et al. 1994; Klosiewski 1991) and whole lakes (Bronmark and Weisner 1996; Chase 2003) generally indicate that predation can alter community composition. Nevertheless, how these impacts on snail abundance and species composition differ among predators and habitats at the whole ecosystem scale remains largely unknown.

In this study, we examine the effect of predation by the introduced rusty crayfish (*Orconectes rusticus*) on snails to increase understanding of snail-predator interactions. The rusty crayfish has been spread widely from its native Ohio River valley to large areas of the eastern United States (Hobbs et al. 1989; Lodge et al. 2000). When introduced into lakes in northern Wisconsin, it often occurs at high densities, replacing the native *O. virilis* and a previous invader, *O. propinquus* (Chapter 2; Capelli 1982; Olsen et al. 1991; Olden et al. 2006). As an omnivore, *O. rusticus* can have negative effects on multiple components of the food web including macrophytes, macroinvertebrates, and fish (Chapter 5; Olsen et al. 1991; Lodge et al. 1994; Wilson et al. 2004). Impacts on snail abundance can be particularly strong (Lodge et al. 1994; Lodge et al. 1998a; Wilson et al. 2004; McCarthy et al. 2006).
Most of our knowledge of predator-prey interactions, including those involving crayfish predators and snails as prey, comes from small-scale laboratory and field cage experiments, while field surveys or experiments at the whole-lake level are much more rare (Dillon 2000; McCarthy et al. 2006). Small-scale experiments often do not adequately represent ecological interactions *in situ* as they tend to be short-term, do not generally encompass the habitat heterogeneity that exists in nature, and are subject to cage effects (Carpenter 1996; Lodge et al. 1998a; Englund and Cooper 2003). Habitat heterogeneity provided by macrophytes in particular alters predator-prey relationships in lake littoral zones (Crowder and Cooper 1982; Gilinsky 1984; Lodge et al. 1988; Diehl 1992). Heterogeneity of benthic sediments (e.g., sand, cobble, soft organic substrates or muck) is also likely to affect these relationships, but this has rarely been tested.

The temporal scale of experiments is particularly crucial in the study of introduced species as the population dynamics of the species may change through time, with consequently varying effects on the invaded community (Strayer et al. 2006). In addition, the effects of invasive species are generally studied using either comparative or experimental approaches, but rarely both (Parker et al. 1999). Here, we combine the strengths of these two approaches by conducting two multi-lake field surveys (separated by 15 years) in which we examine the impacts of *O. rusticus* on snails at the whole-lake scale in natural snapshot experiments (comparing invaded and uninvaded lakes in each year) and in natural trajectory experiments in two lakes that were invaded between samplings. We examine (1) the long-term dynamics of the introduced predator and prey, including potential recovery in two lakes in which *O. rusticus* populations have declined;
(2) the effect of habitat heterogeneity on crayfish snail predation; and (3) the effect of predation on snail species composition.

In our study area, *Orconectes* crayfishes prefer firm substrates (cobble and sand) over soft (muck) and habitats that provide cover from predation (interstices provided by cobble and cover provided by vegetation) over open substrates (Capelli and Magnuson 1983; Hill and Lodge 1994; Kershner and Lodge 1995). Therefore, we predict that crayfish impact on snails will be strongest and occur most quickly on firm substrates. Snail reductions in mucky habitats may occur, but are likely to become apparent over a longer time as availability of prey for crayfish in habitats preferred by crayfish declines. In lakes where crayfish abundance declines, we expect that if snails recover, increases in snail abundance would occur first in open sand where refuge for crayfish from predation (macrophytes; Kershner and Lodge 1995) has been reduced by crayfish herbivory (Lodge and Lorman 1987; Lodge et al. 1994).

We predict also that crayfish invasion should shift snail species composition towards large thick-shelled snails while thin-shelled snails should be most reduced (Lodge et al. 1998b). Specifically, laboratory preference experiments have shown that crayfish select for thin-shelled snails such as *Gyraulus parvus* and *Physella* sp. and against thick-shelled species such as *Helisoma aniceps* and *Campeloma decisum* (Brown 1998; Lodge et al. 1998b). *Physella* species appear to be among the most susceptible to predation. Laboratory and field tests with shell-crushing predators (crayfish, fish and dragonflies) almost universally find *Physella* species declining relative to thicker-shelled snails (Alexander and Covich 1991; Klosiewski 1991; Stein et al. 1984; Lodge et al. 1994; Turner and Chislock 2007; for exception see Mower and Turner 2004). Osenberg
and Mittelbach (1989) even found that all snails tested (*Amnicola, Valvata, Gyraulus*) except for *Physella* reached a size-refuge from crushing by pumpkinseed sunfish. Therefore, the introduction of a crayfish predator such has *O. rusticus* should have an especially strong impact on *Physella*.

3.3. Methods

*Snail and crayfish sampling*

During the summers of 1987 and 2002, snails and crayfish were sampled in 11 moderately productive northern Wisconsin lakes (Lodge et al. 1998b; Table 3.1). All lakes had calcium levels adequate to support abundant populations of snails and crayfish (*O. virilis, O. propinquus* and/or *O. rusticus*). Before sampling, littoral substrate was mapped and the lake perimeter was divided into sectors of equal perimeter length. Twelve sectors were allotted for each habitat type (cobble, open sand, and macrophyte) that was common within a lake (see Lodge et al. 1998b for details). Because all lakes had at least two common habitats, each lake had 24 or 36 sectors. As substrate firmness is a strong determinant of crayfish abundance, macrophyte sectors were reclassified in 2002 based on underlying substrate (sand or muck). In 1987, snails and crayfish were sampled within each sector at a randomly selected location, at a randomly selected depth (0.75 m, ½ of Secchi depth or ¾ of Secchi depth). In 2002, sampling locations were the same location as in 1987, based on maps and notes.

Snails were sampled by divers in July of each year. In sand and muck, a cylindrical PVC sampler (0.018 m²) was pushed about 5 cm into the sediments and a core
<table>
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<th>Lake</th>
<th>County</th>
<th>Latitude (N) (dec deg)</th>
<th>Longitude (W) (dec deg)</th>
<th>Area (ha)</th>
<th>Max Depth (m)</th>
<th>% Cobble</th>
<th>% Sand</th>
<th>% Muck</th>
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<td>89</td>
<td>4</td>
<td>25</td>
<td>58</td>
<td>17</td>
</tr>
<tr>
<td>Wild Rice</td>
<td>Vilas</td>
<td>46.066</td>
<td>89.797</td>
<td>153</td>
<td>8</td>
<td>25</td>
<td>63</td>
<td>13</td>
</tr>
</tbody>
</table>

*Substrate composition was calculated as the % of all lake sectors designated as cobble, sand or muck.
sample was removed. When macrophytes were present, the same area was sampled with a modified sampler, which consisted of two hinged PVC halves which could be closed around macrophytes at the sediment surface. A net cylinder (1-mm mesh) that was attached to the top of the sampler was then zipped closed in order to enclose the the macrophytes rising above the sediments. In cobble habitats, different sized rings (0.1-0.5 m$^2$, depending on snail density) was placed on the bottom; all rocks within the ring were gently placed into plastic bags under water, and transferred to the surface where snails were removed by hand. At the surface, samples from sediment cores were sieved (1-mm mesh) to remove fine sediments and large debris and preserved in 70% ethanol. In the lab, snails were picked from the remaining sediments and identified to species (with the exception of Physella sp., which was identified to genus).

In late July and early August, crayfishes were trapped in each sector using standard methods (Capelli 1982; Olsen et al. 1991): Gee minnow traps with enlarged openings were baited with 120 ± 10 g of beef liver and set at approximately the same location as the snail samples. Traps were retrieved the following morning and crayfish were identified. The number of adult male crayfish (≥20 mm carapace length) per trap was used as an index of crayfish abundance. Females and juveniles were excluded from analyses because they are generally underrepresented in traps, and catch per effort is more variable for them than for adult males (Capelli 1975; Olsen et al. 1991)

_data analysis_

We conducted within-year snapshot comparisons of lakes that fell into different categories of invasion status (Table 3.2). Lakes were defined as invaded if they had an average trap catch of ≥ 10 _O. rusticus_ males/trap. Previous studies suggest that this
threshold is ecologically relevant. For example, in Trout Lake, WI, Wilson et al. (2004) analyzed long-term changes and found that this catch per unit effort of crayfish corresponded to discernable changes in the benthic community and fishes. Our results are also robust to the exact value of this threshold because lakes in the uninvaded category had trap catches far below this threshold (with the exception of High Lake, addressed in results). Using this threshold, five (1987) and seven (2002) lakes were invaded. We used ANOVA to test for differences in snail abundance and species richness across invasion categories within years for 1987 and 2002.

Two lakes that were invaded in 1987 became uninvaded in 2002 as the catch per effort of *O. rusticus* declined; in 2002, we categorized these lakes in a separate “bust” category. In contrast, two lakes invaded between sampling periods are referred to as “boom” lakes. These changes in invasion status for four lakes provided natural trajectory experiments (Diamond 1986). For the natural trajectory experiments, we tested for differences across years within lakes using independent sample t-tests. We excluded Van Vliet Lake from all comparisons involving 2002 because catch per effort of crayfish declined from low (uninvaded) in 1987 to zero in 2002, a pattern unlike any other lake.

In order to examine the effect of habitat on crayfish predation, we compared mean snail density between invaded and uninvaded lakes in each habitat using one-tailed independent sample t-tests. Snail abundance in cobble was not examined statistically because, in all but one invaded lake, no snails were found in the cobble habitat, and data were therefore not distributed normally. As four t-tests were required for this comparison, we took a conservative approach to controlling experiment-wise error rates by applying a Bonferroni correction when testing for significance (critical $\alpha = 0.0125$).
We examined the strength of habitat association by calculating Chesson’s $\alpha$ (Chesson 1983) for cobble, sand and muck within each lake:

$$\alpha = \frac{(r_i/p_i)/\sum (r_i/p_i)}{\sum (r_i/p_i)}$$

where $r_i$ is the abundance of snails in habitat $i$ (the sum of snail density from all sectors designated as habitat $i$) and $p_i$ is the total snail abundance (the sum of snail density from all sectors). We hypothesized that crayfish preference for firm habitats (sand and cobble) would lead to an increase in the association of snails with muck (including the macrophytes rooted in the muck). This may be a result of (1) higher rate of snail consumption by crayfish in firm habitat, (2) snails moving to avoid predation and/or (3) reduction in snail habitat in firm habitats as macrophytes are consumed. We tested this prediction with an independent samples t-test comparing Chesson’s $\alpha$ for muck (arc-sine square root transformed for normality) in invaded and uninvaded lakes in the 1987 sampling.

We examined patterns in snail species composition using Nonmetric Multidimensional Scaling (NMS) ordination (McCune and Grace 2002). In 2002, only three lakes could be classified as uninvaded. As we are dealing with relatively small numbers of lakes to begin with, we only analyzed 1987 data for which results would be more meaningful. The ordination was performed on relative abundances of species using Sørenson distance measures (PC-ORD version 4.25; MjM Software). In order to eliminate rare species from the analysis, only those that occurred in at least half of the uninvaded lakes were included (excluding 5 of the 21 species found). A preliminary ordination was performed from a random starting position and using 100 runs with real data and 100 runs of randomized data to select a dimensionality. We selected a 2-
dimensional solution because additional dimensions lead to a minimal reduction in stress (a measure of the optimality of the ordination solution; McCune and Grace 2002). We then ran 1500 iterations with the selected dimensionality to find a stable solution with minimum stress. We used multi-response permutation procedures (MRPP; McCune and Grace 2002) to test for differences in species composition between invaded and uninvaded lakes.

3.4. Results

At the whole-lake scale, both natural snapshot (Figure 3.1; 1987, p=0.040; 2002, p=0.009) and trajectory (Figure 3.2; L. John, p=0.003 and Plum, p=0.007) experiments indicate that *O. rusticus* greatly reduced snail density. Lakes demonstrating a bust in crayfish populations between 1987 and 2002 did not demonstrate a strong recovery in snail abundance; rather snail densities in bust lakes were similar to those in invaded lakes (Figure 3.1).

The effect of crayfish predation differed by habitat as we predicted. In uninvaded lakes, snail abundance was low in cobble, but similar in sand and muck in both 1987 and 2002 (Figure 3.3). In invaded lakes, snails disappeared almost completely from cobble (only 3 snails found in 82 cobble sectors sampled in invaded lakes), and snail density was significantly lower in sand in both sampling years (1987, p=0.012; 2002, p=0.008) but not in muck (1987, p=0.65; 2002, p=0.111) (Figure 3.3). Chesson’s α showed that, as predicted, snails were associated more closely with muck in invaded than in uninvaded lakes (p=0.037) (Figure 3.4). Results were similar within the lakes invaded during this
study. After introduction of *O. rusticus*, Chesson’s α declined to near zero in cobble and sand while increasing markedly in muck (0.47 to 0.91 and 0.37 to 0.98 in L. John and Plum respectively).

**Figure 3.1.** Mean (+ 1 SE) snail density from natural snapshot comparisons of lakes that are invaded, uninvaded or exhibited a large decline in crayfish (bust).
Figure 3.2. Mean (+ 1 SE) snail density from natural trajectory experiments—before (1987) and after (2002) within each of two lakes that became invaded.
Figure 3.3. Mean (+ 1 SE) snail density by habitat in (a) 1987 and (b) 2002. After Bonferroni correction, critical alpha = 0.0125.
Figure 3.4. Snail habitat association in invaded and uninvaded lakes. Values are the mean (+ 1 SE) Chesson’s α calculated for cobble, sand and muck from individual lakes. P-value is for independent t-test comparing mean Chesson’s α for muck in invaded and uninvaded lakes. The dashed line represents an α value of 0.33, indicating no association. Values above or below this line represent higher or lower habitat use (respectively) than would be expected based on habitat availability.
Summing over all lakes, we collected 21 species of snails. Uninvaded lakes contained 12 to 15 species. Snail species richness was much lower in invaded lakes; the difference was statistically significant in 1987 and not 2002 (p=0.012 and p=0.071 respectively; Figure 3.5). After crayfish invasion, Plum Lake lost 12 of its 17 snail species, while Little John lost only one (Table 3.2). Plum Lake has been invaded for longer than Little John as *O. rusticus* was already present (but only occupying about 1/3 of the lake perimeter) in 1987, while it was first detected (at low abundance) in Little John in 1995 (W.L. Perry, unpublished data). Contrary to our prediction, the presence of *O. rusticus* had no consistent effect on snail species composition. The 2-dimensional NMS ordination on the 1987 data explained 75% of the variation in the snail species composition data (final stress = 14.56; Figure 3.6), and both axes accounted for significantly more variance than would be expected by chance (Monte Carlo tests on both axes had p<0.01). However, the MRPP test indicated no significant difference in species composition between invaded and uninvaded lakes (p=0.523). Visual examination of the data supports this conclusion. Small snails from the family Hydrobiidae (*Amnicola walker, A. limosa* and *Pyrgulopsis lustrica*) dominated snail numbers in uninvaded lakes (75-83% of all snails found), with the exception of Little John Lake (43%). Hydrobiids remained the dominant group (>50%) in most of the invaded lakes, with the exceptions of Presque Isle and Spider lakes in which the most numerous snails were a combination of *Ferrisia obrussa, Physella* sp. and *Campeloma decisum*. 
Figure 3.5. Mean (± 1 SE) snail species richness from natural snapshot comparisons of lakes that are invaded, uninvaded or exhibited a large decline in crayfish (bust).
### TABLE 3.2

**CRAYFISH AND SNAIL RESULTS**

**IN 10 WISCONSIN LAKES**

| Lake      | 1987 Invasion status | 2002 Invasion status | Change  | Crayfish abundance (mean # of males/trap)
<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Allequash</td>
<td>Uninvaded</td>
<td>Uninvaded</td>
<td>Unchanged</td>
<td>0</td>
</tr>
<tr>
<td>High</td>
<td>Uninvaded</td>
<td>Uninvaded</td>
<td>Unchanged</td>
<td>5.7</td>
</tr>
<tr>
<td>Wild Rice</td>
<td>Uninvaded</td>
<td>Uninvaded</td>
<td>Unchanged</td>
<td>0.1</td>
</tr>
<tr>
<td>VanVliet</td>
<td>Uninvaded</td>
<td>Invaded</td>
<td>Boom</td>
<td>1.1</td>
</tr>
<tr>
<td>Little John</td>
<td>Uninvaded</td>
<td>Invaded</td>
<td>Invaded</td>
<td>0.5</td>
</tr>
<tr>
<td>Plum</td>
<td>Uninvaded</td>
<td>Invaded</td>
<td>Boom</td>
<td>1.4</td>
</tr>
<tr>
<td>Papoose</td>
<td>Invaded</td>
<td>Invaded</td>
<td>Unchanged</td>
<td>0</td>
</tr>
<tr>
<td>Presque Isle</td>
<td>Invaded</td>
<td>Invaded</td>
<td>Unchanged</td>
<td>0</td>
</tr>
<tr>
<td>Squirrel</td>
<td>Invaded</td>
<td>Invaded</td>
<td>Unchanged</td>
<td>0.2</td>
</tr>
<tr>
<td>Little Star</td>
<td>Invaded</td>
<td>?</td>
<td>Bust</td>
<td>0</td>
</tr>
<tr>
<td>Spider</td>
<td>Invaded</td>
<td>?</td>
<td>Bust</td>
<td>0</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th>Snail density (mean #/m²)</th>
<th>Snail species (#)</th>
</tr>
</thead>
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<tr>
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<td>1673</td>
<td>685</td>
<td>14</td>
<td>12</td>
<td></td>
</tr>
<tr>
<td>High</td>
<td>1511</td>
<td>1839</td>
<td>17</td>
<td>15</td>
<td></td>
</tr>
<tr>
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<td>1627</td>
<td>1399</td>
<td>15</td>
<td>10</td>
<td></td>
</tr>
<tr>
<td>VanVliet</td>
<td>1263</td>
<td>-</td>
<td>12</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>Little John</td>
<td>1564</td>
<td>454</td>
<td>12</td>
<td>11</td>
<td></td>
</tr>
<tr>
<td>Plum</td>
<td>859</td>
<td>22</td>
<td>17</td>
<td>5</td>
<td></td>
</tr>
<tr>
<td>Papoose</td>
<td>837</td>
<td>34</td>
<td>12</td>
<td>8</td>
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</tr>
<tr>
<td>Presque Isle</td>
<td>48</td>
<td>2.3</td>
<td>4</td>
<td>1</td>
<td></td>
</tr>
<tr>
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<td>1785</td>
<td>294</td>
<td>12</td>
<td>8</td>
<td></td>
</tr>
<tr>
<td>Little Star</td>
<td>0</td>
<td>70</td>
<td>0</td>
<td>4</td>
<td></td>
</tr>
<tr>
<td>Spider</td>
<td>5</td>
<td>18</td>
<td>2</td>
<td>6</td>
<td></td>
</tr>
</tbody>
</table>

---

*a* Crayfish species collected included the native *Orconectes virilis* (OV) and the introduced *Orconectes propinquus* (OP) and *Orconectes rusticus* (OR).

*b* Lakes were determined to be invaded if trap catches were greater than 10 male OR/trap.

*c* Lakes which demonstrate large declines in OR are not classified (?) in 2002 but are examined separately for their response to the decline (Bust) or were not resampled for snails because of unique changes in crayfish abundance (VanVliet).
Figure 3.6. Nonmetric Multidimensional Scaling (NMS) ordination of snail species composition in invaded and uninvaded lakes. Symbols represent individual lakes.
In general, we did not see the predicted pattern of increases in thick-shelled relative to thin-shelled snails. As would be expected, the strong-shelled *Helisoma aniceps* was common in invaded (present in 6 out of 12 lake years sampled; 3 of 5 in 1987 and 2 of 7 in 2002) as well as uninvaded lakes (found in all lake years sampled). However, relative abundance changed little after *O. rusticus* introduction (1% of all snails in uninvaded lakes compared to 2% in invaded). The very strong-shelled *Campeloma decisum* was only collected in one invaded lake (Spider) and that was after crayfish declined in 2002. The thin-shelled *Physella* sp. and *Gyraulus parvus* were commonly found in uninvaded lakes (collected in almost all uninvaded lake years sampled; *Physella* was absent only from the 1987 sampling of Wild Rice). While both were consistently reduced in absolute density in invaded lakes, neither appeared to decline more than other snails. *Physella* was surprisingly common in the presence of *O. rusticus*. In fact, it was one of the most common species in invaded lakes. It was found in 9 of the 12 invaded lake years sampled (4 of 5 lakes in 1987 and 5 of 7 lakes in 2002), more than any other snail taxa. Proportionally, *Physella* actually increased in abundance averaging about 5% of all snails in uninvaded lakes and 9% in invaded.

3.5. Discussion

*Magnitude and rate of impact*

The magnitude and rate of snail reductions by crayfish predation can be dramatic. Lodge et al. (1994) found that *Orconectes rusticus* reduced snails in enclosures to about 1% of their abundance in exclosures over a three month period. However, in addition to
controlling the density of crayfish, enclosure cages also excluded predators. The presence of predatory fish is known to reduce crayfish activity (Stein and Magnuson 1976; Collins et al. 1983; Hill and Lodge 1995), and therefore this experiment might have overestimated the intensity of the impacts of crayfish predation. Nevertheless, field results, including those reported here, indicate that even in the presence of natural abundance of crayfish predators, the impacts of crayfish predation on macroinvertebrates is very large. Wilson et al. (2004) reported that the introduction of *O. rusticus* led to a decline over 5 years from 10,000+ snails/m$^2$ to less than 10 snails/m$^2$ in a sandy bay of Trout Lake, WI. In our survey, we found snail densities at the whole lake scale of 685-1839 snails/m$^2$ in uninvaded lakes, and below 100/m$^2$ in invaded lakes. In three cases, lake-wide snail densities were less than 10 snails/m$^2$ in invaded lakes.

Our results confirm the rapid rate of impact seen in earlier studies in Trout Lake (Wilson et al. 2004). Rusty crayfish were first detected in Little John Lake (at very low abundance) in 1995 (W.L. Perry unpublished data). Our results show that only seven years later, snail abundance was reduced by over 70%. Changes were even more rapid in some habitats. Over the same time period, snail density declined by 97% in cobble and 94% in sand (see below for discussion of the effect of habitats). While snails are not abundant in cobble even in uninvaded lakes, the reductions in sand represent a very large magnitude change in snail density. In addition to these large initial impacts, the effects of predation may continue to increase for many years. All three of the lakes that maintained high densities of *O. rusticus* through both sampling years showed further decline in snails between 1987 and 2002. This includes Presque Isle, which has had abundant *O. rusticus* for at least 27 years before our second sampling in 2002 (Capelli and Magnuson 1983).
Effect of habitat

As predicted, our results showed that lake benthic substrate composition was important in determining the dynamics of crayfish impact. In invaded lakes, snails virtually disappeared from cobble where *O. rusticus* was most abundant. At the same time, the proportion of snails in muck increased, consistent with the avoidance of muck habitat by *O. rusticus* (Chapter 2; Kershner and Lodge 1995). For the most part, the longer a lake has been invaded, the higher the association of snails with muck. The impacts of *O. rusticus* predation on snails is greatest and most rapid in sand and cobble while muck provides a refuge for snails from predation by crayfish. This refuge may be short-lived though, as lower abundance of crayfish in muck may slow the impact but not necessarily prevent it. There was no statistical difference in snail abundance in muck between invaded and unininvaded lakes during either sampling period (Figure 3.3). However, snail numbers in muck declined between 1987 and 2002 in all lakes that had maintained high *O. rusticus* density during both sampling periods.

While these changes in snail habitat association result largely from the greater reduction of snails in habitats preferred by crayfish, they may also result partly from the migration of snails to areas of low predation risk. In his study in Big Lake, WI, Lewis (2001) found that snails avoid *O. rusticus* during warm water periods by inhabiting macrophytes. In the winter, when crayfish are not active, many snails then move into open sand where periphyton is more abundant. Considering the large declines in total snail abundance found here, however, it seems unlikely that migration alone accounts for the change, but that greater mortality rates in sand and cobble play a larger role.
Our data indicate that the magnitude of impact within a lake is habitat dependent. It is therefore logical that the effect of crayfish invasion at the whole-lake scale may also depend on lakewide habitat availability. Lakes with a high percentage of sand and cobble are likely to have a high risk of impact, while lakes dominated by muck should be lower risk. Among our lakes, the lowest whole-lake snail densities (Table 3.2; <10 snails/m²) occurred in invaded lakes with very low muck (Table 3.1), consistent with our hypothesis, but we lack a large enough dataset to test this hypothesis rigorously. In addition, we only sampled lakes that we expected to have good crayfish habitat (cobble) and thus our sample of 11 lakes did not include a very wide range of percentage of littoral habitat consisting of muck (Table 3.1). Thus, while we were able to show that the effect of *O. rusticus* predation was lower in muck, we cannot speculate as to exactly how different the impact of invasion is in lakes with large areas of muck in the littoral zone.

**Crayfish bust lakes**

While not extremely common, some species invasions have exhibited a rapid decline (bust) after the initial phase of population increase. A bust phase may be attributed to multiple causes including the appearance of disease, increases in predators or the depletion of resources (Williamson 1996; Simberloff and Gibbons 2004). While it would not be surprising if *O. rusticus* exhibited population declines in light of the considerable impact that it can have on its food resources (Lodge et al. 1994; Wilson et al. 2004; results reported in this paper), long-term monitoring has found that most invaded lakes maintain high crayfish abundance (Chapter 2). However, two of the lakes in this study (Little Star and Spider) have shown relatively large declines to levels well
below our invaded threshold of 10 crayfish/trap (Table 3.2). It is unlikely that these reductions in crayfish abundance are simply a result of random yearly variation. When trap catches were high in 1987, snail densities were among the lowest of all lakes sampled, indicating strong impact. The low crayfish abundance in 2002 was confirmed in both lakes with three further samplings during the summers of 2003-05 (mean trap catches of adult males of 9.2 and 6.5 in Little Star and Spider respectively).

Despite the decline in crayfish abundance, snail abundance and species richness showed only small, positive responses to the decline in crayfish in both Little Star and Spider lakes (Table 3.2). Snail abundance and species richness after crayfish bust were all still within the low end of the range seen in invaded lakes. This result is not surprising for two reasons. First, *O. rusticus* declined but were not extirpated from the lakes. Although we do not expect a new invasion to have much impact at abundances of less than 10 males/trap (as discussed previously), after the invasion has progressed and prey populations have been reduced to low levels, even a small crayfish population may be able to keep the resource suppressed if predation rate equals or exceeds the prey production rate. Second, snail populations are likely to be less resilient than other macroinvertebrates. In a 24-year study of Sparkling Lake, WI, McCarthy et al (2006) found that as *O. rusticus* abundance varied annually, the abundance of many insect taxa recovered somewhat when crayfish populations temporarily declined, but snail populations did not. Unlike many aquatic insects, snails lack a terrestrial adult stage that facilitates dispersal within and between lakes (McCarthy et al 2006). Thus, the long-term impact on snails is likely to be as great if not greater than on many other prey taxa.

In the bust lakes, snails were found only on open sand habitat. One might expect
snails to recover in muck habitats or in macrophytes where crayfish abundance is lowest and/or snails can escape by crawling up macrophytes (Lewis 2001). However, neither Little Star nor Spider lakes contained muck habitat. Open sand is also generally avoided by crayfish due to risk of predation by fish (Hill and Lodge 1994; Kershner and Lodge 1995). Risk of snail predation by fish in open sand is also likely low because the most common molluscivorous fish in the region, pumpkinseed sunfish (*Lepomis gibbosus*), is probably reduced by *O. rusticus* also through competition for food and egg predation (Wilson et al. 2004). Thus, in the absence of muck, open sand probably represented the lowest risk habitat in lakes where crayfish abundance declined.

The importance of open sand as a refuge from crayfish in bust lakes is supported when we examine the location of the collected snails in relation to cobble. At night, when the visual predators of crayfish are less active, crayfish often leave the safety of cobble to forage (Hill and Lodge 1994). Hence, habitats that are farther away from cobble should have lower predation risk for snails. In fact, none of the snails collected in the Little Star or Spider were in sectors adjacent to cobble sectors, and the highest abundance of snails found in either lake (>1000/m² in one sample from Little Star) was found far removed from any cobble.

**Species composition**

The effect of predation on snail species composition has rarely been studied (Dillon 2000), but when examined at the whole-lake scale, significant effects have been found. In a survey of ponds of different productivity, Chase (2003) found that higher predator biomass (a combination of insects, salamanders and fish) led to an increase in
large thick-shelled *Helisoma trivolvis*. Bronmark and Weisner (1996) found that thin-shelled *Lymnaea stagnalis* were associated with ponds lacking molluscivorous fish while thick-shelled *Bythinia tentaculata* and *Gyraulus albus* were favored in lakes with high densities of molluscivores. Similar patterns resulted from experiments with crayfish and pumpkinseed sunfish in pools (Nystrom et al. 1999) and *in situ* cages (Klosiewski 1991; Lodge et al. 1994). Therefore, it is surprising that we found no pattern in this study. In fact, we found that the snail that is among the most susceptible to shell-crushing predators (*Physella* sp.) was one of the most common snails in invaded lakes.

There are a number of possible explanations for the lack of pattern in snail species composition. First, small hydrobiid snails (*Amnicola limosa*, *A. walkeri* and *Pyrgulopsis lustrica*) were numerically dominant in almost all lakes regardless of invasion status. These snails have relatively strong shells for their size (Stein et al. 1984; Osenberg and Mittelbach 1989) and might be expected to be somewhat resistant to crayfish predation (Brown 1998; Lodge et al. 1998a). It is possible that these abundant species drive snail community patterns in the ordination, obscuring patterns in other species. To test this, we ran a *post hoc* ordination removing the three Hydrobiid species. The results were similar, with the same lack of pattern as when they were included.

Another possibility is that, while thick-shelled snails are generally more resistant to predation, they are susceptible when they are small (Stein et al. 1984; Osenberg and Mittelbach 1989; Alexander and Covich 1991; Nystrom and Perez 1998). Short-term experiments may only test certain size classes of snail, but in reality, snails likely have to deal with the threat of predation from the time that eggs are laid. Osenberg and Mittelbach (1989) found this to be the case when they examined the preference of
pumpkinseed sunfish in Michigan lakes. While pumpkinseeds more easily consumed thin-shelled snails in the laboratory, they found that they could not create a single hierarchy of snail preference using gut contents from the field. They linked this result to changing snail size distributions throughout the summer (i.e. different snails were small and vulnerable at different times).

Other life history traits other than shell-thickness may also be important in reducing mortality due to predation. Behavioral avoidance strategies are effective in deterring snail predation. For example, some snails avoid crayfish by crawling up macrophytes (Lewis 2001) or out of the water entirely (Alexander and Covich 1991; Covich et al. 1994). In a survey of lakes and ponds in western Pennsylvania, Mower and Turner (2004) found that Physella acuta or Stagnicola elodes can both exist in fishless ponds, but that only P. acuta was found in the presence of fish. Laboratory and mesocosm experiments established that this was consistent with behavioral avoidance, as P. acuta would actively seek out structural cover in the presence of fish predators while S. elodes did not.

Other responses to predators include the ability to alter shell thickness and morphology (Vermeij and Covich 1978; Hoverman et al. 2005) and to put off reproduction in favor of growth (Crowl 1990; Hoverman et al. 2005). This variety of behavioral and life history strategies may explain why Physella populations can survive in the presence of high predation pressure despite the susceptibility to predation that has been previously demonstrated. While Physella’s shell provides very little protection from predators, it has exhibited greater behavioral flexibility in response to predators when compared to prosobranchs as well as other pulmonate snails (Covich et al. 1994;
Mower and Turner 2004). In addition, some *Physella* species (such as *Physella acuta*) exhibit a high reproductive rate (Dillon 2000). This may allow these species to be opportunistic in habitats where crayfish are scarce or during years when crayfish abundance is depressed.

**Conclusions**

One of the primary goals of invasion biology has long been to identify the characteristics of communities that are related to susceptibility to invasion by nonindigenous species. However, previous studies of the invasive crayfish *Orconectes rusticus* have assumed that all lakes with sufficient calcium are susceptible to invasion and impact. Smaller-scale experiments of crayfish predation on snails (Olsen et al. 1991; Lodge et al. 1994) and destruction of macrophytes (Lodge and Lorman 1987; Lodge et al. 1994) have supported this, uniformly showing large impacts of by *O. rusticus*. Studies on other invasive crayfish have been similarly consistent (McCarthy et al. 2006). The large-scale study that we are reporting here also found that rusty crayfish caused very dramatic reductions in snails in a relatively short period of time in a variety of lakes. In addition, no snail species appeared to be especially resistant to to predation.

Some recent studies have concluded that the outcome of *O. rusticus* invasion may be more variable than previously thought (Chapter 2; Garvey et al. 2003; Olden et al. 2006; Roth et al. 2007). Some of this variability has been attributed to possible invasion resistance by the native fish community. Abundant crayfish predators (fish) may be able to suppress crayfish abundance (Garvey et al. 2003; Roth et al 2007). As we discovered here, lake benthic substrate is also likely to explain some of this variability.
Cobble abundance has been found to be a strong predictor of *O. rusticus* abundance (Capelli and Magnusson 1983; Garvey et al. 2003), and our results extend the consideration to multiple substrate types as we examined the impact of crayfish predation on snails. We found that after invasion, *O. rusticus* essentially eliminated snails from cobble, but that the largest impact in terms of the magnitude of reduction occurred on sand. Snails in muck were not reduced significantly in the short term (although results hinted at a slow long-term impact). While our results demonstrate that muck habitats are less susceptible to impact within a lake, the lakes for this study were chosen specifically because they were deemed to have suitable crayfish habitat (mostly firm substrates), and therefore do not represent a good test of the impact of lake-wide habitat on susceptibility of invasion. Further study of lakes with a wide range of habitats and a variety of fish community composition is necessary to determine the relative importance of habitat and fish predation on the impact of crayfish invasion.

3.6. Acknowledgments

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CHAPTER 4:  

SNAIL HERBIVORY ON FRESHWATER MACROPHYTES: THE EFFECTS OF ALTERNATIVE FOODS AND PLANT STRUCTURE

4.1. Abstract

Snails are abundant freshwater herbivores that often live in close association with macrophytes. It is often assumed that snails avoid consuming the macrophyte in favor of its periphytic algal covering due primarily to the tough structure of the macrophyte. Using field and lab techniques, we tested these assumptions.

We found that when periphyton was available, snails consumed little macrophyte. Gut contents from four snail taxa (*Lymnaea stagnalis*, *Physella* sp, a Hydrobiid and a Planorbid) collected directly from macrophytes in lakes showed that live macrophyte comprised <5% of snail diets. These results were supported in laboratory feeding experiments where *Lymnaea stagnalis* were able consumers of macrophyte when offered alone (feeding rate: 352 mg FW / g DW snail / day) but consumed much less (39 mg FW / g DW snail / day) when periphyton was provided simultaneously. A smaller snail, *Physella* sp., consumed no macrophyte when periphyton was available and ate nothing when macrophyte was offered alone.

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3This Chapter (with co-author David M. Lodge) has been submitted for publication to Freshwater Biology.
Macrophyte texture was a strong deterrent to snail herbivory. When snails were offered live macrophyte and macrophyte that was ground up and reconstituted as a gel both *Lymnaea* and *Physella* consumed the ground macrophyte almost exclusively. While the snails tested in this experiment generally avoided live macrophyte when offered an alternative, feeding rates from the no-choice feeding trials were comparable to those of other generalist herbivores that are known to have an impact on macrophyte biomass and species composition. Therefore, it is possible that when alternative foods such as periphytic algae are scarce, snails might alter the biomass and species composition of their host macrophyte.

4.2. Introduction

Herbivores can strongly influence plant standing crop and species composition in both terrestrial (e.g. Augustine and McNaughton 1998; Lodge et al. 1998c) and aquatic (Lodge 1991; Newman 1991; Lodge et al. 1998c) ecosystems. While terrestrial herbivores primarily graze on vascular plants, aquatic grazers choose between vascular (macrophytes) and nonvascular plants (algae). For decades, it was generally accepted that freshwater herbivores rarely consumed aquatic macrophytes (e.g. Hutchinson 1975), with the result that macrophytes entered the food web primarily through detrital pathways (Porter 1977; Cummins and Klug 1979; Thomas 1987). These assertions were supported by the argument that, compared to macrophytes, algae are a higher quality food source in an easier to bite package. Both the assertions and the argument were however poorly supported by observational or experimental data (Lodge 1991; Newman 1991).
In fact, more recent literature reviews indicate that, while freshwater herbivores
do have stronger impacts on nonvascular than vascular plants, their impact on vascular
plant standing crop is similar to the effect of terrestrial herbivores on terrestrial plant
standing crop (Cyr and Pace 1993, Lodge et al. 1998c). Thus, better quantification of the
impact of invertebrate grazers on aquatic plants and the determinants of herbivore food
choices between vascular and nonvascular species are important challenges to better
understand community and ecosystem function in lakes and streams.

As some of the most abundant freshwater grazers, snails often alter algal biomass,
species composition and productivity (Hunter 1980; Kesler 1981; Brown 1991; Steinman
1996), but the impact of snail herbivory on macrophytes is less clear. From an
evolutionary perspective, Thomas (1987) argued that because invasion of freshwaters by
terrestrial snails pre-dated the invasion of freshwaters by terrestrial angiosperms, the
primary foods initially available to freshwater snails were periphytic algae and bacteria,
detritus and dissolved organic matter. When aquatic angiosperms appeared, the snail
feeding apparatus (the radula) was adapted for efficient scraping of small particles, not
for tearing the surface of vascular plants. Most ecologists continue to believe that snails
are deterred by the tough structure of live macrophytes and prefer algae or decaying
macrophyte tissue (Hunter 1980; Brönmark 1989; Dillon 2000; Pinowska 2002) but
direct evidence of this is lacking.

Qualitative field observations by some researchers suggest that high abundances
of some snail species can reduce macrophyte biomass (Boycott 1936; Pip and Stewart
1976) but few field tests of snail impact on macrophytes have been conducted (Lodge et
al. 1998c). The best available example, an extensive study that combined field and lab
experiments, found a negative correlation between snail density and relative abundance of the most palatable macrophytes, suggesting a grazing effect by snails on macrophyte abundance and community structure (Sheldon 1987). The results were, however, not as conclusive as they first seemed because the density of non-snail herbivores was not considered and other potential macrophyte herbivores were present (Brönmark 1990). A more controlled mesocosm experiment has recently suggested that the presence of snails during the regeneration phase may alter macrophyte species composition. The lack of field experiments has led to a reliance on studies of gut contents and lab feeding experiments to evaluate snail-macrophyte interactions.

Studies of snail gut contents, although few in number (Brönmark 1989; Dillon 2000), generally show consumption of large amounts of detritus and algae and very little vascular plant tissue (Bovberg 1968; Calow 1970; Clampitt 1970; Calow 1973; Soszka 1975; Reavell 1980; Kesler et al. 1986; Dillon 2000) while a few have found macrophyte to be prominent (Bovberg 1968; Thomas and Tait 1984). However, only a small number of these studies even mention the presence or absence of vascular plants at snail sampling locations (Bovberg 1968; Soszka 1975; Reavell 1980), and very rarely have snails taken directly from macrophytes been examined (but see Calow 1970).

Snails are routinely cultured in aquaria on diets of vascular plant tissue (Dillon 2002), and snails have shown the ability to consume macrophytes in lab feeding experiments (Sheldon 1987; Thomas 1987; Thomas and Tait 1984; Kornijow et al. 1995; Elger and Barrat-Segretain 2002; Lombardo and Cooke 2002; Pinowska 2002; Pieczyńska 2003). However, many of these studies likely overestimate the importance of
macrophytes in snail diets because snails were offered no alternative to macrophytes (Sheldon 1987; Thomas 1987; Thomas and Tait, 1984; Grantham et al. 1993, Elger and Barat-Segretain, 2002; Pieczynska 2003). Only infrequently has snail food preference been tested in the presence of alternative foods (Brown 1982; Lombardo and Cooke 2002; Pinowska 2002; Elger et al. 2007). Additionally, feeding experiments frequently use macrophytes *Ceratophyllum demersum* and *Elodea canadensis* (Calow 1970; Clampitt 1970; Brönmark 1985; Lombardo and Cooke 2002; Pinowska 2002; Pieczynska 2003) that are among the least palatable species (Soszka 1975; Reavell 1980; Sheldon 1987; Newman 1991; Estebenet 1995). These factors make it difficult to interpret how the experimental results relate to the situation in the field.

In this study, we clarify the role that snail herbivory on macrophytes may play in freshwater communities by using a combination of techniques. To overcome a common shortcoming of previous observational studies, we examined gut contents of four snail species collected from northern Wisconsin lake habitats containing multiple potential foods (macrophyte, periphyton, detritus). In laboratory experiments with two of these snail species, we compared the consumption of *Potamogeton richardsonii* (Bennett) Rybd.when offered alone and in the presence of periphyton, thus finding the high and low ends of the range of possible consumption rates.

We used *Potamogeton richardsonii* because it was the macrophyte species found by Sheldon (1987) to be most preferred as a food by snails when snails were offered choices among macrophyte species. Finally, we provide a direct test of the effect of macrophyte structure on snail herbivory by offering snails a choice between live
macrophyte tissue and macrophyte where structure was altered as they were ground up and reconstituted as a gel.

4.3.Methods

Lab experiments and gut content analysis were carried out at the University of Notre Dame’s Environmental Research Center (UNDERC) in the western Upper Peninsula of Michigan (89°32' W, 46°13' N). Snails and macrophytes were collected in summer from lakes on the UNDERC property and from nearby lakes in Vilas County, WI.

*Snail gut contents*

We collected snails from live macrophytes in Morris (46.257°N, 89.521°W), Brown (46.217°N, 89.474°W) and Tenderfoot (46.219°N, 89.527°W) lakes on UNDERC property. In all three lakes, macrophytes had periphyton growing on them (as is typically the case), and substrates under the macrophytes included sediments and rocks covered with a film of periphyton and detritus. Thus field-collected snails had ready access to multiple food sources. We collected snails directly from macrophytes, ensuring that macrophyte was available for consumption, and placed ten individuals of four common snail taxa on ice: *Lymnaea stagnalis; Physella sp.; Planorbidae [either Planorbellla campanulata or Helisoma anceps]; and Hydrobiidae [either Amnicola walkeri, A. limosus or Pyrgulopsis lustrica].* In the lab, the crop was dissected from each *Lymnaea, Physella,* and planorbid, and the contents were placed on a microscope slide.
and examined under a dissecting scope. Using a grid (1 mm$^2$ or 0.83 mm$^2$) we quantified the proportion of fresh (green) macrophyte in the snail diets relative to all other items (algae, detritus, decaying macrophyte, etc.). Anicola fecal pellets were examined, as a crop could not be identified. Fecal pellets were examined under a compound microscope at 200x using a smaller grid (0.059 mm$^2$). Gut contents from snails used in the first feeding experiment (Experiment A below) were also examined to verify that changes in macrophyte biomass were due to snail consumption.

Potamogeton richardsonii, the macrophyte most preferred by snails in Sheldon’s (1987) feeding experiments, was used in all feeding choice experiments. Plants were collected from Tenderfoot Lake and periphyton was removed prior to use in experiments by gently rubbing the leaves under a gentle stream of water.

Experiment A - Consumption of live macrophyte in the presence and absence of alternative food.

We compared the consumption by Physella and Lymnaea of macrophytes when no alternative food was present to consumption when periphyton was also present. Treatments consisted of six Lymnaea offered either (1) macrophyte alone or (2) macrophyte and periphyton; 20 Physella offered either (3) macrophyte alone or (4) macrophyte and periphyton; and (5) controls consisting of macrophyte and no snails. Periphyton was provided as periphyton covered rocks (diameter of 7-15 cm, collected from Tenderfoot Lake). Controls were necessary to correct macrophyte consumption for autogenic change (Peterson and Renaud 1989). Nine replicates were run for each treatment.
Experimental arenas were arranged in a 9 x 5 arrangement on a bench top with treatments assigned randomly within rows. In treatments requiring periphyton, enough periphyton covered rocks were added to cover the bottom of the container. Rocks were replaced daily to assure an adequate supply of periphyton. Excess water was removed from *P. richardsonii* shoots using a salad spinner (approximately 100 revolutions), and 3.4-4.5 g of macrophyte were added to each arena. Finally, snail shell lengths were measured and snails were added to treatments 1-4. Arenas were cleaned three times during the experimental period (9 days) and new lake water added. At the conclusion of the experiment, macrophyte shoots were removed, excess water removed (salad spinner), and weighed. One snail from each replicate was frozen for gut content analysis.

We constructed a regression of log (shell length) to log (body mass) in order to estimate the shell-free mass of snails used in the experiment and thus calculate mass specific feeding rate [mg fresh weight (FW) macrophyte consumed/g shell-free dry weight (DW) snail/day]. Eleven *Physella* (6.0-20.0 mm shell length) and 10 *Lymnaea* (25.0-38.0 mm shell length) were collected and frozen so that their bodies could be easily removed from their shells. The bodies were dried for three days in a drying oven at 60°C and weighed. The resulting regression equations for predicting body mass from shell length were:

\[
Lymnaea \quad \log (\text{body mass}) = 3.4782 \log (\text{shell length}) - 6.3494 \quad (R^2 = 0.9535, \ p<0.001)
\]

\[
Physella \quad \log (\text{body mass}) = 2.3877 \log (\text{shell length}) - 4.5698 \quad (R^2 = 0.9066, \ p<0.001)
\]

Each replicate of the snail treatments was paired with the nearest control (macrophyte with no snails) and macrophyte consumption was calculated using the
following equation \[ (H_0 \times C_f/C_0) - H_f \]; where \( H_0 \) and \( H_f \) are the masses of macrophyte subject to herbivory before and after the trial, and \( C_f \) and \( C_0 \) are the masses of macrophyte in the paired control before and after the trial.

**Experiment B – Preference: live macrophyte vs. macrophyte gel**

We tested the role of macrophyte structure in deterring herbivory by offering snails *P. richardsonii* as fresh plant and as an alginate gel (after Cronin 2002). Macrophyte tissue was freeze-dried and ground into a fine powder. The powder was then mixed with a 2% solution of sodium alginate, and this mixture was poured into a thin mold (0.25 mm thick) on top of fiberglass window screening, which provided support for the gel. The amount of solution added was calculated to restore the original water content of the macrophytes (90%). Finally, 0.25 M CaCl\(_2\) solution was added to harden the gel. The resulting strip of macrophyte gel and window screening was cut to produce pieces of gel (2.5 x 2.5 cm), each containing 400 square cells (1 mm X 1 mm).

For each experimental arena, one piece of gel and live macrophyte leaves of equivalent area were blotted with paper towel to remove excess water and weighed to the nearest 0.01 g. The fresh and reconstituted macrophytes were then anchored in the center of each arena using small rubber suction cups. In half of the arenas, we placed two *Physella* (5.1-19.5 mm; n = 9) or two *Lymnaea* (31.7-51.5 mm; n = 15). To control for autogenic change, each arena with snails was paired with a control with no snails.

Because *Physella* were considerably smaller than *Lymnaea*, *Physella* treatments were run for a longer period (4 days as opposed to 36 hours for *Lymnaea*) in order for there to be measurable consumption of plant material. At the conclusion of the experiment, the gel squares and macrophyte leaves were removed, blotted dry and weighed.
**Experiment C - Preference: macrophyte gel vs. periphyton gel**

In Experiment C, we tested snail feeding preference for macrophyte and periphyton when offered in a similar form (alginate gel). Alginate gel was created as in Experiment B. Enough 2% sodium alginate solution was added to dried periphyton or macrophyte that had been dried and ground into a powder in order to restore original water content (periphyton = 66% water; macrophytes = 90%). The solutions were then spread onto pieces of window screening that were previously glued (Krazy Glue® gel) onto clay tiles (5 cm x 3.5 cm). The gel solution was scraped level with the screen using a razorblade, creating a thin layer of gel similar to a natural periphyton mat. Each tile was dipped in 0.25 M CaCl₂ solution to solidify the gel.

One periphyton tile and one macrophyte tile were placed in the middle of each arena along with either two *Physella* (9.0-20.0 mm; n = 11) or two *Lymnaea* (33.0-50.0 mm; n = 11). Trials ended when 1/3 of one food type had been consumed or after 24 hours. At the completion of the experiment, empty window screen cells were counted.

**Experiment D - Preference: macrophyte gel vs. live periphyton**

To control for any effects of sodium alginate on snail feeding preference, we repeated Experiment C offering *Lymnaea* (32.0-51.0 mm; n = 10) live periphyton instead of periphyton gel. If snail preference between macrophyte gel and live periphyton is the same as between macrophyte gel and periphyton gel, then we can conclude that the sodium alginate itself does not play a significant role in snail food choice.

Window screen covered tiles were placed in a shallow tray and submerged in the littoral zone of Tenderfoot Lake (water depth = 0.25-.5m) for two weeks for colonization by periphyton. The tray was covered with a screen to exclude macroinvertebrates; any
organisms observed on the tray were removed. Periphyton colonization was somewhat patchy, and the number of empty squares on each tile was recorded before presentation to the snails. The number of squares consumed equaled the number of empty squares after the experiment minus the initial number of empty squares.

*Data analysis*

The proportion of macrophyte in the gut contents of field collected snails (*Lymnaea stagnalis*, *Physella*, Planorbids an Hydrobiids) were compared using ANOVA after arcsine square root transformation followed by Tukey’s *post-hoc* multiple comparisons. We used a 2-way ANOVA to examine the effect of snail species (*Lymnaea* vs. *Physella*) and the presence of alternative food (periphyton) on snail feeding rates on macrophyte. In experiments B-D, two food types were offered simultaneously, which means that food choice may not have been independent. Therefore, we modified the method proposed by Lockwood (1998) for 3 or more food types offered simultaneously. Food preference in each arena was tested by calculating the consumption of one of the food items as a proportion of the total consumption within that arena. In other words, we calculated $x_i = a_i/(a_i + b_i)$; where $x_i$ is the consumption of one food type ($a$) in replicate $i$ relative to the total consumption of both food types ($a$ and $b$). A one-sample T-test was then used to test the null hypothesis of no preference or equal consumption of both food types ($H_0: \bar{X} = 0.5$).
To test whether the alginate gel affected snail feeding preference, *Lymnaea* food preferences from experiments C and D were compared. We used a two-sample t-test to test for a difference between $\bar{X}$ for macrophyte gel from experiment C to $\bar{X}$ for macrophyte gel from experiment D. If alginate gel does not affect snail feeding preference, then macrophyte consumption relative to total consumptions should not differ regardless of whether the snail’s second food choice was periphyton gel (experiment C) or live periphyton (experiment D).

4.4. Results

Macrophyte accounted for only a small percentage of the gut contents from field-collected snails (Figure 4.1). Macrophyte was more common ($p<0.001$) in *Lymnaea stagnalis* diets (4.8%) than in the diets of the three smaller snail taxa collected from the field (0.33-0.41%). Similarly, in the lab, *L. stagnalis* feeding rates on macrophyte were significantly higher than those of *Physella* (experiment A; $p=0.043$; Figure 4.2). The presence of an abundant alternative food source (periphyton) had a significant effect on snail feeding rates on macrophyte (experiment A; $p<0.001$; Figure 2). Snails consumed very little macrophyte when periphyton was available and increased macrophyte consumption when there was no alternative, indicating that the snails were capable of consuming macrophyte but prefer periphyton when both foods are readily available. *Lymnaea* was more able than *Physella* to increase consumption on macrophyte in the absence of an alternative. Gut contents from experiment A showed that all *Lymnaea*
from the macrophyte-only treatment that were examined had consumed macrophyte, while the guts of seven of the nine Physella were empty.

Macrophyte structure was important in determining snail food preference (Figure 4.3). Macrophyte gel was strongly preferred over live macrophyte by both Physella (p<0.001) and Lymnaea (p<0.001). However, experiment C indicated that structure is not likely to be the only explanation for the preference that snails demonstrated for periphyton in the field (Figure 4.1) and the laboratory (Figure 4.2). When both periphyton and macrophyte were offered in gel form (Figure 4.4), Physella still selected periphyton gel over macrophyte gel at a ratio of greater than 10:1 (p<0.001). Lymnaea exhibited a similar but weaker trend (p=0.076). Alginate gel did not affect snail food preference (Figure 4.5). Lymnaea preferred periphyton to macrophyte gel at an approximate ratio of 2:1 regardless of whether periphyton was offered live or as a gel (p=0.847).
Figure 4.1. Macrophyte in gut contents (percent of total gut contents) of field-collected snails sampled directly from macrophytes (mean ± 95% CI). Snail taxa were *Lymnaea stagnalis*, *Physella* sp., Hydrobiidae and Planorbidae.

ANOVA: p < 0.001
Figure 4.2. Results of Experiment A: Mean snail mass-specific feeding rate on live macrophyte (*Potamogeton richardsonii*) in the presence (MP) and absence (M) of periphyton. Negative values indicate that plant growth was greater than consumption by snails.
Figure 4.3. Results of Experiment B: Mean snail mass specific feeding rate on live macrophyte and macrophyte gel when offered simultaneously.
Figure 4.4. Results of Experiment C: Snail food preference when both foods were offered in the same form.
Figure 4.5. Testing the effect of the gel on snail feeding preference. Consumption of macrophyte (as proportion of all food consumed proportion of cells consumed) by *L. stagnalis* was compared between experiments C and D. The result of no difference between the experiments indicates that gel does not affect snail feeding preference.
4.5. Discussion

*Snail diet preference: macrophyte vs. periphyton*

Our results show that both *Lymnaea* and *Physella* have a strong preference for periphyton over macrophyte. The preference for periphyton is strong, especially considering that the macrophyte offered to snails, *Potamogeton richardsonii*, is the macrophyte species most preferred by *Physa gyrina* (Sheldon 1987). We can then reasonably conclude that snails generally prefer epiphytic algae to their macrophyte hosts (Lombardo and Cooke 2002; Kornijow et al. 1994), consistent with what many previous authors have suggested without strong evidence. This finding is also consistent with many previous field studies showing the strong negative impact that snails often have on periphyton biomass even when macrophytes are abundant (Lodge et al. 1994).

High consumption of macrophyte gel relative to fresh macrophyte also provides strong support for Thomas' (1987) hypothesis that the structure of macrophytes is a significant deterrent to snail herbivory, as it is for other invertebrates (Cronin et al. 2002; Bolser et al. 1998). However, the preference by both snails for periphyton even when both periphyton and macrophyte were offered as gel suggests that factors in addition to structure are important in determining food preference by snails. This is supported by previous studies on snail preference between macrophyte species, where chemical defenses (Li et al. 2004; Elger and Lemoine 2005), dry matter content (possibly a surrogate for structure) and protein content (Elger and Lemoine 2005) all influenced food choice.
Can snails impact macrophytes?

While previous evidence and the current results consistently suggest that snails will more strongly reduce periphyton abundance, potential impact on macrophytes remains possible because some species of snail, e.g., *Lymnaea* and *Physella*, will eat substantial quantities of macrophyte when other foods are in short supply. The one field experiment designed to test this possibility is subject to multiple interpretations (Sheldon 1987, Bronmark 1990), pointing out the need for further field studies on this topic.

Our results, combined with earlier laboratory measurements of feeding rates of snails on macrophytes provide a basis for estimating the potential impact by snails on macrophyte standing crop. Such estimates will be useful to guide predictions about results of future field experiments. Studies that provided snails with only macrophytes represent maximum possible consumption (Sheldon 1987; Thomas 1987; Thomas and Tait 1984; Kornijow et al. 1995; Elger and Barrat-Segretain 2002; Lombardo and Cooke 2002; Pinowska 2002; Pieczyńska 2003). To provide a fair estimate of the range of consumption rates of which an herbivore is capable, feeding rates must be measured in no-choice (providing the high end of the range) and choice (low end) feeding trials. Based on this logic, our results estimate the range of snail feeding rates on the macrophyte *P. richardsonii* to be between 50 and 350 mg/g/day for *Lymnaea* and 0-160 mg/g/day for *Physella* (all feeding rates in this paper are given as mg fresh weight of macrophyte consumed/g snail shell free dry weight/day). Other no-choice experiments have found snail herbivory rates as high as 368 mg/g/day (*Radix swinhoei*, Li et al. 2004) and 3000 mg/g/day (*Lymnaea*, Elger & Wilby 2004). The highest estimates (Elger &
Wilby 2004) were found in snails that were raised in the lab on a lettuce diet (vascular plant), which might bias their feeding preference. These rates are well within the range of those measured for other generalist herbivores that are known to reduce macrophyte biomass. For example, no-choice feeding trials found feeding rates by crayfish of 38 mg/g/day (*Procambarus clarkii*; Lodge et al. 2005) to 95 mg/g/day (*Orconectes rusticus*; Olsen et al. 1991) and by caddisfly larvae of 1161-1617 mg/g/day; (*Anabolia nervosa*; Jacobsen and Sand-Jensen 1994).

There are obvious limitations to this type of comparison. For example, crayfish herbivory can result in large amounts of non-consumptive losses (i.e. severed plants floating away, which would not be included in laboratory feeding rates above), magnifying their impact beyond their actual feeding rate (Lodge et al. 1994). Nevertheless, given the measured feeding rates by snails and given conditions of high snail abundance and low periphyton abundance, it remains conceivable that macrophyte communities could be affected by snail herbivory. Herbivory by snails at levels too low to alter total macrophyte standing crop could also result in a change in community composition similar to that recorded by Sheldon (1987). We hypothesize that appropriate conditions might be found early in the season as new plants are beginning to grow and are yet to be colonized by epiphytic algae (Sheldon 1990) or in nutrient poor lakes, situations in which alternative food availability would be low. Additionally, young macrophytes are more palatable, presumably because older plants have tougher structure (Elger et al. 2006). Laboratory and mesocosm experiments support this hypothesis as high abundance of *Lymnaea stagnalis* during the early regenerative phase for
macrophytes was shown to reduce the biomass of more palatable macrophytes, altering species composition (Elger et al. 2007; Elger et al. 2009).

Prosobranch snails in general have larger radular teeth than pulmonate snails (Brown et al. 1998), and might therefore generally consume even more macrophyte than the pulmonates tested here (L. stagnalis and Physella); plant structure would presumably be less of a deterrent to larger radular teeth. For example, large prosobranchs from the largely tropical family Ampullariidae readily consume macrophytes (Dillon 2000). Therefore, potential impact on macrophytes is also a reasonable concern as several large prosobranch snails, including Viviparus georgianus, Cipangopaludina chinensis, and Pomacea canaliculata continue to invade North America (Clench 1962; Clench and Fuller 1965). Little is known about their diet, but these species can occur at very high densities and therefore represent a large potential impact on macrophytes as well as periphyton.

Conclusions

In this study, we have provided the first strong direct tests of the common assertion that snails generally prefer to consume periphyton and detritus over live macrophyte tissue when these foods are available. We also provided the first direct evidence that the structure of macrophytes is a strong deterrent to snail herbivory. A comparison of snail feeding rates to those of other known herbivores demonstrates, nevertheless, that when periphyton is scarce, snails could alter macrophytes biomass or species composition. Determining when and where such conditions occur in nature will require additional field experiments.
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CHAPTER 5:

THE DECOUPLING OF BENTHIC AND PELAGIC ENERGY FLOW IN LENTIC FOOD WEBS BY THE INVASIVE RUSTY CRAYFISH (ORCONECTES RUSTICUS)\textsuperscript{4}

5.1. Abstract

Linkages between ecosystems and habitats can strongly affect ecosystem function through exchange of energy and materials. In lake food webs, large piscivorous fishes integrate littoral and pelagic energy sources through the consumption of smaller fishes and macroinvertebrates. We tested the hypothesis that the introduction of the invasive rusty crayfish (Orconectes rusticus) decouples benthic and pelagic food webs by reducing the abundance of small fish and non-crayfish benthic macroinvertebrates. Using stable isotope ratios of carbon ($\delta^{13}$C) and nitrogen ($\delta^{15}$N), we examined differences in patterns of energy flow between lakes with high abundance of rusty crayfish ("invaded") and lakes with native crayfish only or with low abundance of non-native crayfish ("uninvaded"). The trophic position of juvenile crayfish was lower in invaded relative to uninvaded lakes, likely indicating decreased reliance on macroinvertebrate prey and greater dependence on lower quality detritus and algae. In invaded lakes, diets of piscivorous fishes relied more strongly on littoral energy sources, and walleye, an

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obligate piscivore, had a lower trophic position than in uninvaded lakes. These results suggest that invasion by rusty crayfish causes a reduction in the abundance of benthic macroinvertebrates and small fishes, and the decoupling of the littoral and benthic food webs. This decoupling of habitats is likely to lead to an overall reduction in energy flow to the top of the lake food web.

5.2. Introduction

Ecosystems do not occur in isolation but instead are connected by the movement of materials and organisms across their boundaries (Polis et al. 1997, 2004). Sometimes these transfers are very important to ecosystem functioning. For example, energy and nutrients are transferred between terrestrial habitats (Rand et al 2006; Pringle and Fox-Dobbs 2008), from terrestrial to freshwater ecosystems (Fisher and Likens 1973; Vannote et al. 1980) and from freshwater to terrestrial (Nakano and Mrakami 2001; Sabo and Power 2002). Translocation of nutrients by migrating salmon and seabirds can fertilize terrestrial ecosystems increasing biomass and altering food webs (Gende et al. 2002; Maron et al.2006). When human activities reduce these linkages, the decoupling of the ecosystems can have important impacts. The introduction of nonindigenous mammals (rats and foxes) to islands can lead to seabird population declines and thus reduced subsidies of marine nutrients to terrestrial habitats. This in turn can alter the biomass and composition of plant and invertebrate communities (Maron et al.2006; Towns et al. 2009). Human development of lake riparian zones reduces inputs of large woody debris into lake littoral zones which leads to changes in the diets of top predators (largemouth bass) and changes in fish community composition (Sass et al. 2006).
The same perspective applies within ecosystems. In the past, many limnologists have treated the pelagic and littoral zones as separate, independently functioning ecosystems (Vadeboncoeur et al. 2002). From this viewpoint, lakes are often described as being comprised of a linear pelagic food chain (phytoplankton → zooplankton → plantivorous fish → piscivorous fish) and a separate more complex littoral food web (comprised of benthic algae, macroinvertebrates or zoobenthos, and fish with a variety of feeding habits). There is growing recognition however that a number of important interactions link these habitats (Lodge et al. 1988; Schindler and Scheuerell 2002; Vadeboncoeur et al. 2002). Studies of cultural eutrophication have demonstrated strong linkages between planktonic and benthic primary producers (Sand-Jensen and Borum 1991; Vadeboncoeur et al. 2001; Chandra et al. 2005). The littoral zone provides nesting sites and refugia (in the form of macrophytes or large woody debris) for phytoplankton (Rengefors et al. 1998), zooplankton (Burks et al. 2002), and zooplanktivorous fish (Werner et al. 1983). Through consumption of smaller fish and macroinvertebrates, large fish are important integrators of pelagic and littoral derived energy (Figure 5.1A; Schindler and Scheuerell 2002; Vadeboncoeur et al. 2002; Vander Zanden and Vadeboncoeur 2002; Vander Zanden et al. 2006).

Any abiotic or biotic change that disrupts these linkages may fundamentally alter energy flows between littoral and pelagic habitats. In many ecosystems, including freshwaters, invasive species are one of the leading drivers of biodiversity loss (Richter et al. 1997; Sala et al. 2000; Dudgeon et al. 2006) and changes in ecosystem function, including the decoupling of linked ecosystems (Maron et al. 2006; Towns et al. 2009). The invasive rusty crayfish (*Orconectes rusticus*) has been introduced to many lakes of the upper Midwest from the Ohio River drainage (Olden et al. 2006) replacing resident
As an omnivore, crayfish affect multiple trophic levels, reducing the diversity and abundance of macrophytes (Lodge and Lorman 1987; Lodge et al. 1994), macroinvertebrates (Lodge et al. 1994; Lodge et al. 1998c; Wilson et al. 2004; McCarthy et al. 2006), and some fishes (Wilson et al. 2004; Willis and Magnusson 2006; Roth et al. 2007).

Evidence of invasive species impacts, especially on linkages among ecosystems and habitats can be elusive because of the difficulty of carrying out experiments at an ecologically relevant temporal or spatial scale (Lodge et al. 1998a). Thus, the full scope of the impact of *O. rusticus* invasion is still not clear. For example, experiments at multiple scales consistently show a negative impact on macrophytes (Lodge and Lorman 1987; Lodge et al. 1994; Wilson et al. 2004) and slow moving macroinvertebrates such as snails and dipteran larvae (Lodge et al. 1994; Lodge et al. 1998c; McCarthy et al. 2006). However, results for many other macroinvertebrate taxa have been inconsistent (Lodge et al. 1994; Wilson et al. 2004; McCarthy et al. 2006). Possible explanations for this are that (a) crayfish consume the slower, more accessible food items preferentially and only as they are depleted do crayfish move on to more mobile prey or (b) reductions of some macroinvertebrate taxa occur as an indirect effect as crayfish consume their macrophyte habitat. In either case, the effect may not be evident in short-term, small-scale experiments. Similarly, there is a strong argument (but less direct evidence) that *O. rusticus* negatively affects many fish species through competition for food, destruction of macrophyte habitat and direct egg predation (Dorn and Mittelbach 1999; Dorn and Mittelbach 2004; Wilson et al. 2004; Willis and Magnusson 2006; Roth et al. 2007). Small fishes that are unable to protect their eggs from crayfish predation and any small
fishes reliant on macrophytes as a refuge from predation or a food rich habitat are likely to be reduced.

We hypothesize that the cumulative effect of rusty crayfish alteration of lake food webs is to decouple lake littoral and pelagic food webs. Large fish predators link the pelagic and littoral food webs by feeding on small fish (which derive their energy from a variety of littoral and pelagic sources) and benthic-feeding littoral macroinvertebrates (Figure 5.1A; Vander Zanden and Vadeboncoeur 2002). If macroinvertebrates and small fish undergo large declines as predicted, these reductions in food web linkages will lead to decreased exchange of energy between the two habitats (Figure 5.1B). However, in part because of the large experimental scale necessary to observe these effects, little evidence exists to test this prediction. We tested five predictions drawn from this hypothesized food web model (Figure 5.1) with comparisons between invaded lakes (high abundance of *O. rusticus*) and uninvaded lakes (native crayfish with no or very low *O. rusticus* abundance). In the predictions described below, we primarily consider five common fish species; one that is likely a crayfish competitors [bluegill (*Lepomis machrochirus*)] and four that are likely crayfish predators [rock bass (*Ambloplites rupestris*), smallmouth bass (*Micropterus dolomieui*), yellow perch (*Perca flavescens*), and walleye (*Stizostedion vitreum*)].

1. **Juvenile crayfish in invaded lakes will have a lower trophic position than in uninvaded lakes.** While omnivorous, gut content and stable isotope analysis demonstrate that crayfish are functionally predators in most aquatic systems, especially juveniles that require animal protein for quick growth to reach a size
Figure 5.1. Conceptual model of lake food webs where (A) large piscivorous fish integrate littoral and pelagic energy sources, a pattern supported by abundance empirical evidence (see text), and (B) rusty crayfish are hypothesized to have decoupled the littoral and pelagic food webs through negative direct and indirect effects on small fish and benthic invertebrates. The hypothesized effects of rusty crayfish are exaggerated (complete elimination of benthic macroinvertebrates and small fish) to illustrate the predicted effects.
refuge from predation (Momot 1995, Whitlege and Rabeni 1997; Roth et al. 2006).  The loss of macroinvertebrate prey should result in a lower trophic position for juvenile crayfish in invaded relative to uninvaded lakes.  Adult crayfish may not differ because cannibalism is likely to be more common in large crayfish, providing a protein subsidy in replacement of other macroinvertebrate prey.

1. *Piscivorous fish will rely more on littoral energy sources in invaded lakes.* If *O. rusticus* reduces the abundance of small fish and macroinvertebrates, the fish that remain must increase consumption of zooplankton, crayfish or both or see a reduction in growth.  Diet shifts cannot be predicted for species that readily consume both (yellow perch) However, a clear prediction emerges for piscivores/benthivores (rock bass, smallmouth bass and walleye) that rarely consume zooplankton in large quantities: these species should depend more on crayfish (and therefore on littoral energy sources) in invaded relative to uninvaded lakes.

2. *Piscivorous fish diets will vary less within invaded lakes.* In invaded lakes, fishes that normally consume a variety of food items will be forced to rely more consistently on crayfish.  Thus, the within-lake variation of the diets of fishes that include crayfish in their diet (rock bass, smallmouth bass, walleye and yellow perch) will be reduced as the availability of other dietary items declines.

3. *Walleye trophic position will be lower in invaded lakes.* Walleye are more exclusively piscivorous than rock bass and smallmouth bass, and thus an increase in crayfish consumption should reduce their trophic position.  While we predict that rockbass and smallmouth bass consume more crayfish in invaded lakes, no specific prediction of trophic position change is possible for these species because small
crayfish (most likely to be consumed by fish predators) are predicted to have a lower trophic position (<3) in invaded lakes. Therefore, the trophic position of a fish preying solely on crayfish might be similar to one consuming a mix of small fish (trophic position 3+) and benthic macroinvertebrates (trophic position 2-3). In contrast, if walleye replace fish in their diet with small crayfish, their trophic position should decrease with invasion.

4. **Effective crayfish predators will have higher growth in invaded lakes while crayfish competitors will have lower growth rates.** If the large foodweb changes predicted do occur, there is likely to be an effect on fish as consumers. For bluegill (crayfish competitor), we predict that the younger age classes will exhibit reduced growth in invaded lakes while the older fish would be unaffected because they exhibit an ontogenetic diet shift from macroinvertebrates to zooplankton at about 75 mm (Mittelbach 1984). Smallmouth bass (crayfish predator) shift from benthivory to piscivory late in their first year as gape size increases (Mittelbach and Persson 1998), and are thus likely to show lower growth in year one while they compete with crayfish and then higher growth thereafter as they readily consume the abundant crayfish as they are able to consume larger prey.
5.3. Methods

Study lakes

Between 2000 and 2002, we sampled 13 lakes in Vilas County in (northern Wisconsin) and Iron and Gogebic Counties (Upper Peninsula of Michigan; Table 5.1). Seven lakes had high densities of *O. rusticus* (‘invaded lakes’) and the other six lakes (‘uninvaded’) had only native crayfish or had very low abundance of rusty crayfish because they had very recently been colonized by *O. rusticus*. At the time of sampling, all invaded lakes had contained high abundance of *O. rusticus* for at least 10 years (Lodge unpublished data).

Food web analysis

We used stable isotope analysis to test for changes in food web structure between invaded and uninvaded lakes (predictions #1-4). Carbon and nitrogen stable isotope ratios ($\delta^{13}$C and $\delta^{15}$N) are commonly used to infer energy flow through aquatic food webs (Peterson and Frey 1987; Vander Zanden et al. 1999; Vadeboncoeur et al. 2002). Stable isotopes of carbon are useful for tracing assimilated food sources because benthic algae are generally more $\delta^{13}$C enriched than are phytoplankton, but there is little enrichment in $\delta^{13}$C from one trophic level to the next (France 1995; Hecky and Hesslein 1995). In contrast, $\delta^{15}$N is useful for calculation of trophic positions because there is consistent enrichment of about 3.4/o with each trophic transfer (Minagawa and Wada 1984; Post 2002).

Benthic macroinvertebrates and crayfish for stable isotope analysis were collected by hand (depth 1-3 m) from all major littoral habitats including macrophytes, rock and soft sediments (sand and muck). For crayfish and unionid mussels only
abdominal and foot muscle were analyzed. All other macroinvertebrates were held live for 24 hours in order to clear their guts prior to processing (Mulholland et al. 2000). Zooplankton were collected from throughout the epilimnion and metalimnion at the middle of each lake with a plankton net (150 μm mesh). Fish were caught using fyke nets (5/8 in mesh) at multiple locations around the lake periphery. To minimize fish mortality, fish dorsal muscle was removed for analysis using a biopsy punch. The site of removal was then treated with antibiotics, sealed with tissue glue and fish were released.

Within 24 hours of collection, all stable isotope samples were dried for 24 hours at 60°C and ground to a fine powder with mortar and pestle. Samples were loaded into 8 mm x 5mm tin capsules and δ¹³C and δ¹⁵N were measured using a Finnegan Model 252 mass spectrometer at the University of Notre Dame’s Center for Environmental Science and Technology. Stable isotope ratios are expressed in standard δ notation:

\[ \delta = \frac{(R_{\text{sample}} - R_{\text{standard}})}{R_{\text{standard}}} \times 1000^\circ/oo \]

where \( R = ^{15}N/^{14}N \) or \(^{13}C/^{12}C\) and atmospheric N and PeeDee Belemnite are the standards respectively. About 20% of samples were run in duplicate, producing a mean analytical error of 0.15\(^\circ/oo\) for \( \delta^{13}C \) and 0.11\(^\circ/oo\) for \( \delta^{15}N \).

In order to calculate the relative importance of littoral and pelagic energy sources, we used a two-source mixing model with pelagic and littoral endpoints. Instead of directly measuring stable isotope ratios of primary producers, which can vary seasonally, we used values from primary consumers which integrate isotopic values of their food
### TABLE 5.1

CHARACTERISTICS OF STUDY LAKES
SAMPLED FOR FOOD WEB ANALYSIS

<table>
<thead>
<tr>
<th>Lake</th>
<th>Crayfish&lt;sup&gt;1&lt;/sup&gt;</th>
<th>Invasion Status&lt;sup&gt;2&lt;/sup&gt;</th>
<th>Area (ha)</th>
<th>Mean depth (m)</th>
<th>Secchi (m)</th>
<th>Fish&lt;sup&gt;3&lt;/sup&gt;</th>
</tr>
</thead>
<tbody>
<tr>
<td>Big Lake (WI)</td>
<td>0.0</td>
<td>Invaded</td>
<td>338</td>
<td>6.3</td>
<td>3.8</td>
<td>X X X X X X</td>
</tr>
<tr>
<td>Boulder Lake (WI)</td>
<td>0.0</td>
<td>Invaded</td>
<td>212</td>
<td>3.7</td>
<td>2.0</td>
<td>X X X X X X</td>
</tr>
<tr>
<td>Crab Lake (WI)</td>
<td>11.5</td>
<td>Uninvaded</td>
<td>384</td>
<td>6.7</td>
<td>1.0</td>
<td>X X X X X X</td>
</tr>
<tr>
<td>Forest Lake (WI)</td>
<td>5.2</td>
<td>Uninvaded</td>
<td>189</td>
<td>8.8</td>
<td>5.5</td>
<td>X X X X X X</td>
</tr>
<tr>
<td>Lake Ottawa (MI)</td>
<td>0.0</td>
<td>Invaded</td>
<td>223</td>
<td>12.3</td>
<td>5.4</td>
<td>X X X X X X</td>
</tr>
<tr>
<td>Papoose Lake (WI)</td>
<td>0.0</td>
<td>Invaded</td>
<td>173</td>
<td>12.9</td>
<td>3.9</td>
<td>X X X X X X</td>
</tr>
<tr>
<td>Plum Lake (WI)</td>
<td>0.0</td>
<td>Invaded</td>
<td>448</td>
<td>6.2</td>
<td>4.6</td>
<td>X X X X X X</td>
</tr>
<tr>
<td>Plum Lake (MI)</td>
<td>2.1</td>
<td>Uninvaded</td>
<td>92</td>
<td>3.0</td>
<td>1.7</td>
<td>X X X X X X</td>
</tr>
<tr>
<td>Pomeroy Lake (MI)</td>
<td>1.7</td>
<td>Uninvaded</td>
<td>123</td>
<td>3.2</td>
<td>1.3</td>
<td>X X X X X X</td>
</tr>
<tr>
<td>Presque Isle Lake (WI)</td>
<td>0.0</td>
<td>Invaded</td>
<td>518</td>
<td>6.5</td>
<td>4.9</td>
<td>X X X X X X</td>
</tr>
<tr>
<td>Taylor Lake (MI)</td>
<td>1.1</td>
<td>Uninvaded</td>
<td>66</td>
<td>4.6</td>
<td>2.3</td>
<td>X X X X X X</td>
</tr>
<tr>
<td>Tenderfoot Lake (MI/WI)</td>
<td>2.1</td>
<td>Uninvaded</td>
<td>177</td>
<td>4.8</td>
<td>1.5</td>
<td>X X X X X X</td>
</tr>
<tr>
<td>Wildcat Lake (WI)</td>
<td>4.5</td>
<td>Uninvaded</td>
<td>123</td>
<td>3.6</td>
<td>3.1</td>
<td>X X X X X X</td>
</tr>
</tbody>
</table>

<sup>1</sup> Crayfish trap catch (mean # of adult crayfish/trap). Crayfish species are abbreviated as OV (*Orconectes virilis*), OP (*O. propinquus*) and OR (*O. rusticus*).

<sup>2</sup> Invasion status is invaded (high OR trap catch) or uninvaded (no OR). Pomeroy Lake is classified as uninvaded despite OR presence because *O. rusticus* is in low abundance and had not spread through much of the lake.

<sup>3</sup> Lakes used for food web and fish growth analysis indicated with (X). Fish species are abbreviated as follows: BG = bluegill (*Lepomis macrochirus*); PS = pumpkinseed (*Lepomis gibbosus*); RB = rock bass (*Ambloplites rupestris*); SM = smallmouth bass (*Micropterus dolomieui*); WE = walleye (*Stizostedion vitreum*); YP = yellow perch (*Perca flavescens*).
over a longer period (Vander Zanden et al. 1999; Post 2002). We used unionid mussels to define the pelagic endpoint. In the one case where no live mussels were found (Lake Ottawa), we used the mean of zooplankton samples collected in June, July and August in 2001 and 2002. For the littoral endpoint, we averaged the values of snails, mayflies and amphipods collected from all littoral habitats. Following Vander Zanden et al. (1999) and Vadeboncoeur et al. (2002), we calculated the relative importance of consumers on littoral and pelagic energy sources (percent littoral diet or LD_{consumer}) as:

Equation 1: \[ \text{LD}_{\text{consumer}} = \left( \delta^{13}\text{C}_{\text{consumer}} - \delta^{13}\text{C}_{\text{pelagic}} \right) / \left( \delta^{13}\text{C}_{\text{littoral}} - \delta^{13}\text{C}_{\text{pelagic}} \right) \times 100 \]

where \( \delta^{13}\text{C}_{\text{consumer}} \), \( \delta^{13}\text{C}_{\text{pelagic}} \), and \( \delta^{13}\text{C}_{\text{littoral}} \) are the \( \delta^{13}\text{C} \) of the consumer of interest and the pelagic and littoral endpoints.

Likewise, consumer trophic positions (TP_{consumer}) were estimated based on lake-specific baselines calculated from the \( \delta^{13}\text{C} \) and \( \delta^{15}\text{N} \) of primary consumers. This baseline compensates for inter- and intra-lake variations in primary producer \( \delta^{15}\text{N} \) (Vander Zanden and Rasmussen 1999; Post 2002). We estimated trophic position with a linear baseline approximation using the \( \delta^{15}\text{N} \) of the secondary consumers used at the littoral and pelagic endpoints (Post 2002):

Equation 2: \[ \text{TP}_{\text{consumer}} = 2 + \left[ \delta^{15}\text{N}_{\text{consumer}} - \left( \delta^{15}\text{N}_{\text{littoral}} \times \text{LD}_{\text{consumer}} + \delta^{15}\text{N}_{\text{pelagic}} \times \left[ 1 - \text{LD}_{\text{consumer}} \right] \right) \right] / \Delta \delta^{15}\text{N} \]
where \( \text{LD}_{\text{consumer}} \) is the littoral contribution to the diet of the consumer (from equation 1), \( \delta^{15}\text{N}_{\text{consumer}} \) is the \( \delta^{15}\text{N} \) of the consumer, \( \delta^{15}\text{N}_{\text{littoral}} \) and \( \delta^{15}\text{N}_{\text{pelagic}} \) are the \( \delta^{15}\text{N} \) of the secondary consumers used for as the littoral and pelagic endpoints, and \( \Delta \delta^{15}\text{N} \) is the estimated increase in \( \delta^{15}\text{N} \) with each trophic level (3.4/oo).

For the analysis of food web structure for a given taxon, data from a lake were only used as replicates in food web comparisons if a minimum of 10 individuals of that taxon (fish or crayfish) were collected from that lake. Analysis of fish \( \text{LD}_{\text{consumer}} \) and \( \text{TP}_{\text{consumer}} \) was performed only on fish greater than 100 mm to assure that they were large enough to have made any transition from benthivory to piscivory (Mittelbach and Persson 1998). In order to minimize procedure-wise error in the food web analysis, statistical comparisons were only done for crayfish and fish species for which specific predictions were made. For predictions 1, 2 and 4, we compared \( \text{LD}_{\text{consumer}} \) for rockbass, smallmouth bass, and walleye, and \( \text{TP}_{\text{consumer}} \) of walleye and adult and juvenile crayfish in invaded and uninvaded lakes using independent sample t-tests with lake means as replicates. Data for \( \text{LD}_{\text{consumer}} \) were arcsine transformed so that they would conform to the assumptions of normality. We tested for diet narrowing of piscivore diets (prediction 3) by calculating the variance of \( \text{LD}_{\text{consumer}} \) for each crayfish predator (rock bass, smallmouth bass, walleye and yellow perch) within each lake. Mean variance was then compared between invaded and uninvaded lakes using independent sample t-tests.

**Fish growth**

Fish were collected by fyke net and boat electroshocker, weighed (nearest gram), and measured (maximum total length to nearest mm). From each fish, several scales
were sampled from behind the pectoral fin. Two measurements to examine fish growth were used: (a) the Fulton Condition Factor, a measure of “plumpness” or weight relative to length (Anderson and Neumann 1996), and (b) back-calculations of lengths from the most recent scale annulus and subtracting the back-calculated length from the previous year using the Fraser-Lee method (Carlander 1982). Only fish age 1-4 were analyzed for growth because there can be bias in back-calculated lengths of fish age 5+ (Casselman 1987). Data were included in analyses only if at least 10 individual fish per age class per species were sampled from a lake. Growth and condition factors of smallmouth bass and bluegill were compared in invaded and uninvaded lakes for each age class (1-4) using single factor ANOVA with Tukey’s post hoc comparisons (prediction 5).

5.4. Results

As expected (predictions 1 and 4), trophic position was lower in invaded lakes for both walleye (p=0.01) and juvenile crayfish (p=0.02), while adult crayfish showed no difference between invaded and uninvaded lakes (p=0.78; Figure 5.2). Supporting prediction 2, smallmouth bass (p=0.04) and walleye (p=0.02) relied more heavily on littoral energy sources in invaded lakes (Figure 5.3). Contrary to prediction 2, rock bass showed no difference (p=0.65). Consistent with prediction 3, rock bass (p=0.03) and smallmouth bass (p=0.02) in invaded lakes showed significantly less within lake diet variance than those in uninvaded lakes, while contrary to prediction, walleye did not differ (p=0.43) and yellow perch diets showed greater variation in invaded lakes (p=0.04; Figure 5.4).
Contrary to prediction 5, crayfish invasion appeared to have no effect on bluegill growth for any age class, and no effect on the growth of young smallmouth bass (ages 1 and 2) (Figure 5.5). However, as predicted, growth for smallmouth of ages 3 (p=0.04) and 4 (p=0.02) was significantly higher in invaded relative to uninvaded lakes (Figure 5.5). Results were similar for fish condition factor (not shown).

**Figure 5.2.** Trophic position of walleye and crayfish in lakes invaded by *O. rusticus* compared to uninvaded lakes as determined by analysis of stable isotopes of nitrogen (mean ± 1 SE). * p< 0.05
Figure 5.3. Reliance of fish on littoral energy sources in lakes invaded by *O. rusticus* compared to uninvaded lakes (mean ± 1 SE). * p< 0.05
**Figure 5.4.** Within lake variance of $LD_{\text{consumer}}$ of four crayfish predators (mean ± 1 SE). Lower values indicate more homogenous diets of fish within lakes. * $p< 0.05$
Figure 5.5. Growth of presumed (A) crayfish competitors (bluegill) and (B) crayfish predators (smallmouth bass) ages 1-4 in lakes invaded and uninvaded by *Orconectes rusticus* (mean ± 1 SE). * p< 0.05
5.5. Discussion

Overall, our results were largely consistent with the hypothesized decoupling of the littoral and pelagic food webs by rusty crayfish invasion. The primary trophic link between these two habitats is fish, particularly large piscivores that consume a combination of fish and macroinvertebrate prey which derive their energy from both littoral and pelagic sources (Hecky and Hesslein 1995; Schindler and Scheuerell 2002; Vadeboncoeur et al. 2002; Vander Zanden and Vadeboncoeur 2002). Reduction of these prey fish and benthic macroinvertebrate consumers means that the littoral energy pathways (through crayfish) is more important to fish at the top of the food web in invaded relative to uninvaded lakes.

Our results are consistent with earlier observational and experimental work showing that benthic macroinvertebrates are significantly reduced by rusty crayfish introductions. The trophic position of juvenile crayfish in invaded lakes was reduced to below that of secondary consumer; a pattern consistent with the replacement of much needed high protein macroinvertebrates by lower quality primary producers or detritus. This result could also be explained by reduced consumption of an animal food from a higher trophic level (fish or fish eggs). However, there is little evidence that fish ever make up a large portion of crayfish diets, especially that of juveniles. Fish eggs may be a seasonally important food for some adult crayfish, which are less vulnerable than small crayfish to parent fish guarding their nests.

The greater reliance of piscivorous fish on littoral energy sources in invaded than in uninvaded lakes and the narrowing of fish diets in invaded lakes provides strong evidence that piscivores are replacing fish in their diets with crayfish. Because littoral
macroinvertebrates are reduced by *O. rusticus*, greater crayfish consumption is the most plausible explanation for the shift to littoral energy sources. The narrowing of fish diets within a lake is consistent with a shift from a food web with a wide variety of food sources to one where most of the energy consumed by top predators in invaded lakes is derived from a single food source (crayfish).

There are alternative explanations for these patterns that are not as plausible. First, it is possible that fish are preying more intensely on crayfish simply because more crayfish are available and not necessarily because there are fewer alternative prey (small fish). This argument is problematic because there is evidence that *O. rusticus* is not necessarily more abundant than the crayfish that they replace but rather that they more active, as indicated by comparisons of SCUBA surveys and trap catches (Olsen et al. 1991). This difference is partly due to the fact that they are less susceptible to predation by fish as they have bigger claws and are more aggressive (Garvey et al. 1994) and thus should be a more energetically expensive prey than the native crayfish. Also, unlike smallmouth bass, whose diets frequently include crayfish, walleye are obligate piscivores, rarely consuming crayfish (Vander Zanden et al. 1997, Garvey et al. 2003). Therefore, the shift in walleye diets is strong support for a reduction in small prey fish.

Another alternative explanation for the increased reliance on littoral prey is that the piscivores’ fish prey are shifting to a diet that is more strongly tied to littoral energy sources. The reduction in mean walleye TP from 4.13 to 3.90, though not great in magnitude suggests that, while this could in part be true, it is unlikely to be the only explanation. Most fish, unless strongly herbivororous or detritivorous have a TP of 3 or higher (with trophic position generally increasing with size). For the trophic position to
drop below 4, as observed for walleye in this study, a piscivore must increase consumption of prey with a trophic position below 3 (such as juvenile crayfish or other macroinvertebrates). Thus, the combination of food web changes that we have documented provide strong support for the hypothesis that *O. rusticus* invasion reduces the abundance of small fish.

Our results indicating a reduction in small fish are generally supported by the few intensive studies of fish communities in lakes with invasive crayfish. Benthivorous fishes such as bluegill and pumpkinseed sunfish that are abundant in many northern Wisconsin lakes have declined as a result of crayfish invasions in Trout Lake (*Orconectes rusticus*) and Big Muskellunge Lake (*Orconectes propinquus*) in Wisconsin (Wilson et al. 2004; Willis and Magnusson 2006; Roth et al. 2007). Other fishes such as white sucker (*Catostomus commersonii*), mottled sculpin (*Cottus bairdii*) and logperch (*Percina caprodes*) were also reduced (Willis and Magnusson 2006). The fact that we found it difficult to sample enough bluegill or pumpkinseed in invaded (but not uninvaded) lakes to allow food web or growth analysis is consistent with these earlier studies of fish abundance and with our stable isotope analysis.

Additionally, a few studies suggest that some fish species may benefit from the introduction of invasive crayfish, although results are not clear and are partly contradictory. For example, smallmouth bass abundance has shown a positive relationship with crayfish abundance in some cases (Garvey et al. 2003; Willis and Magnusson 2006) and no relationship in others (Wilson et al. 2004; Roth et al. 2007), rockbass and largemouth bass abundance have been found to have both positive and negative associations with crayfish abundance (Garvey et al. 2003; Willis and Magnusson
and mimic shiners, *Notropus volucellis*) increased significantly in Trout and Big Muskellunge lakes as invasive crayfish abundances increase (Willis and Magnusson 2006). Some of the conflicting results may be explained by study design. Snapshot experiments that compare fish and crayfish abundance (e.g. Garvey et al. 2003 and Roth et al. 2007) do not take into account invasion history. If crayfish density alters fish abundance, results will differ if a lake is sampled soon after introduction or years later after food web changes have occurred. In addition, comparative studies can suffer from covariance of possible independent variables. For example, a positive relationship between *O. rusticus* and smallmouth bass may not be due to interaction between the species but a result of similar preference for cobble habitat (Garvey and others 2003; Olson et al. 2003).

One potential cause of the decline in small fish is competition with crayfish for macroinvertebrate prey. The results from our analysis of fish growth do not support this as an important mechanism. No difference in bluegill growth was found between invaded and uninvaded lakes. Similarly, smallmouth bass growth was unaffected during its first year when it would be most dependent on macroinvertebrate prey. While crayfish may reduce macroinvertebrate abundance, declines in benthivorous fish populations may alleviate competition for remaining prey. In addition, even species that are not generally considered crayfish predators, such as bluegill, may consume juvenile crayfish for short periods after crayfish hatch and before they reach a size refuge (Roth et al. 2007). Fish species that lack the ability to consume even juvenile crayfish may be more affected but
More likely explanations for fish declines are an increase in crayfish predation on fish eggs and the reduction of macrophyte habitat. Experiments in small ponds have shown that the presence of crayfish can delay or even prevent reproduction of pumpkinseed and bluegill (Dorn and Mittelbach 2004) and crayfish exclosures in Trout Lake appeared to increase nesting by these same species (Wilson 2002). Egg predation is likely to be most important for smaller fish species that are unable to consume large crayfish, and are therefore less able to intimidate crayfish that are attacking their nests (Wilson et al. 2004). When fish are able to successfully reproduce, macrophytes provide habitat for many small fish as well as their macroinvertebrate prey, and the presence of macrophytes can increase fish abundance and species richness (Randall et al. 1996; Jeppesen et al. 1998). Macrophyte species differ in their habitat value; thus macrophyte diversity can also affect fish abundance and species composition. *Orconectes rusticus* can greatly reduce macrophyte abundance and diversity in lakes, often eliminating large areas of macrophyte and thus reducing fish habitat (Lodge et al. 1994; Wilson et al. 2004; Rosenthal et al. 2006).

The increased growth of larger smallmouth bass (ages 3+ and 4+) in invaded lakes could support a positive relationship between smallmouth bass abundance and invasive crayfish populations. Increased growth rates can benefit smallmouth by increasing fecundity (Hair 1979) and reproductive success. Nest-guarding requires large energy reserves and smaller fish are more likely to abandon their nests (Ridgway and Shuter 1994; Mackereth et al. 1999). However, the presence of an abundant nest predator
(O. rusticus) could offset these benefits. Steinhart et al. (2005) found that the presence of
an abundant nest predator, the invasive round goby (Neogobius melanostomus), caused
smallmouth bass to increase nest-guarding behavior and decrease feeding, a significant
overall energetic cost. In addition, no significant increase in growth was found for young
smallmouth (ages 1+ and 2+) when they are most susceptible to predation from
piscivorous fishes. Increased threats of nest predation and the loss of macrophyte refuge
(likely resulting in higher predation rates on juveniles) may offset possible fecundity
increases altering recruitment of adult smallmouth. This may explain why Willis and
Magnusson (2006) found significant increases in smallmouth bass in Trout Lake when
they included young-of-year (YOY) fish in their analyses, while Wilson and others
(2004) found no change when they excluded YOY fish from their dataset.

The increase in fathead minnows and mimic shiners in Trout and Big
Muskellunge Lakes contradicts our inference that small fishes decline in the presence of
O. rusticus. We acknowledge that fish species may differ in their response to O. rusticus
invasion. Mimic shiners and fathead minnows may avoid competition with crayfish as
they have very flexible diets, readily consuming algae, detritus, and zooplankton as well
as benthic macroinvertebrates (Becker 1983). Also, unlike ground nesting fishes, these
species can suspend their eggs from vegetation and woody debris (Black 1945; Jenkins
and Burkhead 1993). Lakes with large amounts of woody debris or sufficient vegetation
in muck habitats, which are avoided by O. rusticus (Chapter 2) may provide adequate
nesting sites where eggs remain out of the reach of crayfish. We cannot say with
certainty that the lakes in our study do not contain similar fish species that may avoid the
negative impacts of invasive crayfish. However, we rarely caught small fishes in our
invaded lakes while we often collected large numbers of common shiners, golden shiners, and YOY perch in uninvaded lakes. More importantly, our stable isotope results indicated decreased importance of small fish as a trophic link to top predators in invaded lakes.

Conclusions

Links between habitats or ecosystems can have important consequences for ecosystem productivity and reducing those linkages can lead to reductions in productivity (Nakano and Murakami 2001; Sass et al. 2006; Maron et al. 2006; Towns et al. 2009). We have provided evidence at the whole-lake scale that the introduction of an invasive crayfish into lentic ecosystems alters food web structure and decouples energy flow between the littoral and pelagic habitats. We now assess in greater detail what inferences about energy flow to the top of the food web can be drawn from our results (Table 5.2). Some of the effects of *O. rusticus* on lake food webs likely lead to reduced flow of energy to top predators. In field experiments, the introduction of *O. rusticus* causes an increase in algal biomass, presumably because crayfish are less efficient grazers than the macroinvertebrates that they replace (Lodge et al. 1994; Luttenton et al. 1998). In addition, if littoral and pelagic habitats are decoupled, much pelagic energy may not be available to littoral predators. The strength of this effect will depend on at least two factors. First, we expect that linkages between littoral and pelagic habitats are most important in mesotrophic lakes because littoral and benthic production dominates in oligotrophic lakes and pelagic production dominates in eutrophic lakes (Vadeboncoeur et al. 2001). Top predators in mesotrophic lakes are thus most likely to consume a combination of littoral and benthic energy sources. Second, the presence of
zooplanktivores that may be unaffected by crayfish (perhaps including mimic shiners and
bluntnose minnows) could continue to provide a link to pelagic energy resources. We
were unable to assess the role of such zooplanktivores, but the consistent shift of
piscivores toward littoral energy sources in our invaded lakes indicates that they were
either uncommon or did not provide an important trophic link.

It is also possible that the amount of energy reaching the top of the food web will
increase due to these food web changes. Crayfish are very efficient processors of
terrestrial detritus. Also, the reduction in trophic position of some top fish predators
(such as walleye) would result in less energy lost with trophic transfer. These impacts,
however, are likely to be minor as the shift in trophic position documented here for
walleye is small and terrestrial detritus is generally going to be a significant energy
source only in small, low nutrient lakes (France 1995).

To be certain of the effect of *O. rusticus* invasion on food web energy flow, the
production of top predators would have to be compared between invaded and uninvaded
lakes or in a whole-lake experimental manipulation of crayfish. No such data currently
exist. Based on our results, however, we suggest that in large mesotrophic lakes,
invasion by *O. rusticus* not only decouples littoral and pelagic food webs, but decreases
the net energy transferred to top trophic levels. This would represent the majority of
lakes invaded by *O. rusticus* in our study area (the northern lakes region of Wisconsin
and the Upper Peninsula of Michigan), and thus the impacts we document are likely to be
important in many lakes throughout the invaded range of *O. rusticus*. 
### Table 5.2.

**EFFECTS OF INVASIONS BY *ORCONECTES RUSTICUS* ON LAKE FOOD WEBS AND LIKELY RESULTANT CHANGE IN ENERGY TRANSFER TO TOP TROPHIC LEVELS**

<table>
<thead>
<tr>
<th>Food web change</th>
<th>Mechanisms</th>
<th>Likely change in energy transfer to top trophic levels</th>
<th>Evaluation</th>
</tr>
</thead>
<tbody>
<tr>
<td>Crayfish replace snails and other benthic invertebrates</td>
<td>Grazing efficiency on periphyton reduced</td>
<td>Reduction</td>
<td>Crayfish are generally less efficient grazers on algae than the macroinvertebrates that they replace (Lodge et al 1994)</td>
</tr>
<tr>
<td></td>
<td>Terrestrial detritus efficiently processed</td>
<td>Increase</td>
<td>Most important in small, low productivity lakes (France 1995). Such small, oligotrophic/dystrophic lakes are not susceptible to crayfish invasion because calcium concentrations are limiting.</td>
</tr>
<tr>
<td>Pelagic and littoral habitats decoupled</td>
<td>Top predators lose access to pelagic energy sources.</td>
<td>Reduction</td>
<td>Reduction of macroinvertebrate and small fish abundance reduces links through which littoral piscivores access pelagic energy. Most important in mesotrophic lakes. Less important if zooplankton specialists (cisco, smelt, some cyprinids) unaffected.</td>
</tr>
<tr>
<td>Trophic position of top predators reduced</td>
<td>Less energy lost with trophic transfer</td>
<td>Increase</td>
<td>Magnitude of the effect is small. In addition, fishes that are more obligately piscivorous (those that would exhibit the most reduced trophic position) are not likely to be as efficient at capturing crayfish relative to fish, minimizing the overall gain.</td>
</tr>
</tbody>
</table>
5.6. Acknowledgments

We are thankful to T. Davidson, S. Rosenthal, J. Frentress, and S. Stevens for assistance with field and lab work. We would like the following for financial support: the Arthur J. Schmitt Foundation and the University of Notre Dame for fellowship support (TAK), a grant from EPA STAR (DML), and a grant from NSF IRCEB in support of the Integrated Systems for Invasive Species (ISIS) project (DML, P.I.). We also thank UNDERC for use of facilities.
CHAPTER 6:
CONCLUSIONS

6.1. The importance of scaling-up invasive species research

In this dissertation, I examined the invasion of the rusty crayfish at a larger scale than has often been done in the past. I have investigated how the impacts that have been studied in smaller-scale analyses scale up (a) through longer time periods (a decade or more after lakes are fully colonized); (b) to the whole-lake scale, taking into account habitat heterogeneity; and (c) throughout the food web as trophic links are altered.

The importance of studying the impacts of nonindigenous species at larger scales can be clearly illustrated in the example of another well studied invasive species, the zebra mussel *Dreissena polymorpha*. The zebra mussel was introduced from Eurasia to Europe and North America, where it now occupies large areas of both continents (Strayer 2009). As it colonizes most available hard substrates, often at high densities, it has caused massive declines in unionid mussel diversity (Strayer and Malcom 2007) and great economic costs through the fouling of industrial water intake pipes (Leung et al. 2002). It is also a prolific filter feeder which, combined with high densities, can significantly reduce phytoplankton abundance. The zebra mussel has now been in the
U.S. for around 20 years, and as research into the effects of the species has been scaled-up, an understanding of the complexity of the species’ impacts has emerged that was not possible to achieve with only small-scale experiments.

Zebra mussels have displaced unionid mussels in a large number of habitats and, early on, it appeared that extinction was eminent for large numbers of native mussel species. While many native mussels have declined greatly, it has been found that habitat heterogeneity may provide refuges for some native unionids and permit long-term coexistence (Jokela and Ricciardi 2008; McGoldrick et al. 2009). In lake St. Claire, variation in lake currents appear to create areas where zebra mussel colonization is low and unionid survival high (McGoldrick et al. 2009). Examination of sites in the St. Lawrence and Richelieu rivers with a broad range of habitat variation demonstrated that low water calcium concentration and large substrate size promote coexistence of the native and introduced mussels (Jokela and Ricciardi 2008).

Long-term study of the zebra mussel invasion has also provided important insights not available from short-term studies. For example, some impacts require long periods before they are evident. Mud and sand habitats with low zebra mussel abundance can slowly build up layers of dead mussel shells which can improve settling habitat for zebra mussel veligers. As a result, the abundance of adults can increase markedly after a period of many years (Strayer 2009). Also, population dynamics may change through time. Unionids in the Hudson River initially demonstrated steep declines after colonization by zebra mussels. After about a decade, however, populations of many species have been recovering, with no clear explanation (Strayer and Malcom 2007). Zebra mussel populations, when followed over time, exhibit a variety of population
trends. In some ecosystems they exhibit logistic growth and high long-term densities while in others they exhibit patterns of boom-and-bust or periodic oscillations (Ramcharan et al. 1992; Strayer and Malcom 2006).

Other impacts are not evident until the effects that cascade through the food web are considered. For example, at the site level, the complexity created by zebra mussel shells increases macroinvertebrate abundance. However, at the whole-ecosystem level, macroinvertebrate densities decline (Strayer 2009), because filtering of phytoplankton by zebra mussels reduces ecosystem productivity. Reduced phytoplankton biomass can also alter zooplankton diets (Maguire and Grey 2006) and fish abundance (which may both increase and decrease; Strayer et al. 2004).

6.2. Synthesis of results

6.2.1. Changing impact through time

My results indicate that the long-term outcomes of the introduction of rusty crayfish are variable over time and differ among lakes. Previous studies have demonstrated only increases (with some interannual variation) in *O. rusticus* populations through time unless humans intervene (Olsen et al. 1991; Wilson et al. 2004; Hein et al. 2006). Similarly, in most lakes that I examined in Chapter 2, *O. rusticus* increased in abundance and showed no sign of decline. However, a few lakes appear to have experienced a boom-and-bust of *O. rusticus* populations. The lack of a boom-and-bust in lakes that currently have high abundance does not preclude future declines, but results
from one lake (Presque Isle) do indicate that very high abundance can be sustained for decades.

It is likely that resource limitation and variation in benthic habitat play a role in determining the long-term abundance and size structure of *O. rusticus*. Previous analyses have indicated that cobble abundance is important in determining lake-wide *O. rusticus* abundance but that above a certain threshold (about 15% cobble) abundance can vary widely (Capelli and Magnuson 1983; Garvey et al. 2003). My results indicating that both the amount and distribution of cobble is important in determining long-term *O. rusticus* abundance may help explain the variance in past results. Lakes with high cobble (long-term predation refuge and crayfish nursery habitat) should maintain high abundance over the long-term. Sand habitat, however, can change from a preferred habitat (when it is vegetated) to one that is avoided when macrophytes are eliminated (due to high risk of fish predation; Kershner and Lodge 1995). Therefore, lakes with intermediate amounts of cobble may reach and maintain high *O. rusticus* abundance if the cobble (source of crayfish) is distributed evenly throughout the lake. If the cobble is aggregated in one part of the lake, *O. rusticus* may never reach high abundance or may decline in the long-term when macrophyte refuge is eliminated and large areas of habitat become uninhabitable. Resource depletion may magnify this effect as declines in *O. rusticus* size further increase their predation risk in habitats that provide little shelter (Garvey et al. 1994).

In Chapter 3, I showed that the impacts of *O. rusticus* predation on snails can be rapid and snail declines can be very large in magnitude at the whole-lake scale. It is also evident that the full impact of invasion may not be evident until years after initial
colonization. Lakes that had been fully colonized for 15+ years at the time of our first sampling continued to experience declines in snail abundance during the 15 year interval between samplings. The impact of *O. rusticus* varied by habitat. Snail reductions are largest and most rapid on firm habitats (cobble and sand) that are preferred by *O. rusticus*. Declines were much slower in muck (which is generally avoided by *O. rusticus*) which likely explains continued lake-wide declines over long periods. Examination of snails in two lakes that experienced boom-and-bust indicated little recovery. This may mean that low densities of crayfish may continue to depress snail abundance or that ecosystem recovery is not rapid.

### 6.2.2 Long-term fate of *O. virilis* and *O. propinquus*

Over the long-term, I found that *O. rusticus* often extirpated entirely the previous invader *O. propinquus* while the native *O. virilis* is was likely to remain extant (Chapter 1). Hybridization with *O. rusticus* has previously been identified as a mechanism of replacement for *O. propinquus* but not *O. virilis* (Perry et al. 2001). In addition, I have identified a likely habitat refuge that exists for *O. virilis* and not *O. propinquus*. Muck habitats are avoided by *O. rusticus* (and likely *O. propinquus*) possibly due to low tolerance for anoxia. Because *O. virilis* is better adapted to low oxygen, the presence of muck may promote coexistence, although it is still unknown whether this refuge simply slows extirpation or promotes long-term coexistence.
6.2.3. Alteration of energy flow through lake food webs

In Chapter 4, I demonstrated that freshwater snails common to the lakes invaded by *O. rusticus* do not generally consume live macrophyte tissue in the presence of alternative foods. I found that the tough structure of macrophytes is likely an important deterrent to snail grazing. Snail grazing on macrophytes may still be important early in the growing season when alternative foods are rare or when macrophytes are less tough (Sheldon 1987; Elger et al. 2007; Elger et al. 2009). Regardless, replacement of snails (efficient algal grazers) with crayfish (effective macrophyte consumers and inefficient periphyton grazers) is likely to result in less total area colonizable by periphyton (fewer macrophytes) but increased periphyton biomass on remaining surfaces. This confirms previous findings of a trophic cascade in an enclosure-exclosure experiment (Lodge et al. 1994).

In Chapter 5, my comparison of food webs in invaded and uninvaded lakes supported the hypothesis that *O. rusticus* decreases the overall abundance of macroinvertebrates (not just snails) and small fish. I also demonstrated that these reductions can have an important functional effect. The reduced trophic position of juvenile *O. rusticus* late in invasion is likely due to a decrease in consumption of animal prey (macroinvertebrates). In conjunction with the findings in Chapter 2 that crayfish are smaller late in invasion, this probably indicates that *O. rusticus* growth rates are reduced as they deplete their resources.

My results also support a decline in small fish abundance. Results from the monitoring of the introductions of *O. rusticus* and *O. propinquus* in Trout and Big Muskellunge lakes have also found direct evidence for reductions in some fish species.
that are likely to compete with crayfish for prey (Wilson et al. 2004; Willis and Magnuson 2006). However, the results of my analysis of fish growth does not support competition as an important mechanism in these declines as there was no difference in the growth of bluegill in invaded and uninvaded lakes. It is likely that crayfish egg predation (Dorn and Mittelbach 2004) and loss of macrophyte habitat (Roth et al. 2007) are more important. This also indicates that changes in the populations of crayfish predators (e.g. smallmouth bass) in \textit{O. rusticus} lakes may depend on the relative importance of the benefits of increased growth and the costs of increased threat of nest predation and reduction in macrophyte habitat.

The cumulative effect of reductions in macroinvertebrates and fish (which integrate littoral and pelagic energy sources) is the decoupling of the lake’s littoral and pelagic food webs. As a result, top predators (piscivorous fish) have reduced access to pelagic energy sources and increase their reliance on littoral sources. The combination of this decoupling of food webs and the reduced periphyton grazing efficiency (due to the loss of snails and other more efficient periphyton grazers) is probably a decline in total transfer of energy to large piscivores at the top of the food web.

6.3.Management implications

The rusty crayfish has spread throughout large areas of the eastern United States and southeastern Canada. In order to prevent secondary spread in these regions, it is important to know the factors that make lakes susceptible to establishment. A predictive model for northern Wisconsin lakes created by Keller et al. (2008) indicates that the
presence of sportfish (walleye and largemouth bass), the number of cabins on the lake, calcium concentration and lake size combine to best predict the presence of *O. rusticus*. The next level of analysis that is needed is to identify what characteristics make a lake vulnerable to impact if *O. rusticus* establishes a population (Vander Zanden and Olden 2008). My analyses confirm previous results that indicate that the composition of habitat in the lake littoral zone is likely to be an important factor. Lakes with greater abundance of cobble, and a greater dispersion of cobble around the littoral zone, are more likely to be negatively impacted by *O. rusticus* introduction (Capelli and Magnuson 1983; Garvey et al. 2003). In addition, I found that *O. rusticus* occurs in much lower abundance in muck than sand or cobble and therefore lakes with a high proportion of muck in the littoral zone should be less vulnerable.

As efforts increase to control *O. rusticus* populations in lakes where they have established, my results provide some support for attempts to manage crayfish predator populations. The importance of cobble distribution in determining long-term abundance of *O. rusticus* supports the role of fish predation in limiting *O. rusticus* populations over the long-term. In addition, the decline in the mean size of *O. rusticus* through the course of invasion means that an increasing proportion of the population is susceptible to fish predation. It is important to identify lakes that are strong candidates for management. Based on my results, increases in fish predator populations should have the greatest effect in lakes with high proportion of sand habitat (especially where the existing cobble is aggregated). Cobble remains effective predation refuge over the long-term, and therefore may set a limit to the effect that fish predation can have on crayfish populations.
APPENDIX

SUPPLEMENTARY ANALYSIS OF LONG-TERM O. RUSTICUS POPULATION TRENDS

We present here data and analysis from four lakes (Clear, Little Star, Spider and Presque Isle) that did not meet our minimum criteria for inclusion in model fitting of long-term O. rusticus abundance in Chapter 1. Lakes were only included in this analysis if (a) the lake had been sampled a minimum 6 times; (b) at least one sampling was during the early invasion period; and (c) O. rusticus had been present in the lake for at least 15 years. Three of these lakes violated the criteria for sample size (see table below) and all of them lacked a sample from the early invasion period. Because there is no data from the early invasion period (the expansion phase of the invasion), it is impossible to fit a model of hyperbolic growth (Michaelis-Menten). It is, however, possible and logical to fit linear or quadratic models to the data in an attempt to detect a peak or decline in the population using the same methods described in Chapter 1. The results are presented in the table and figure below.
TABLE A.1

RESULTS OF FITTING MODELS OF POPULATION GROWTH TO

*O. RUSTICUS* ABUNDANCE\(^a\)

<table>
<thead>
<tr>
<th>Lake</th>
<th>Linear</th>
<th>Quadratic</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Linear</td>
<td>Quadratic</td>
</tr>
<tr>
<td></td>
<td>$n^b$</td>
<td>$SD_{\text{resid}}$</td>
</tr>
<tr>
<td>Clear</td>
<td>6</td>
<td>3.33</td>
</tr>
<tr>
<td>Little Star</td>
<td>5</td>
<td>3.18</td>
</tr>
<tr>
<td>Presque Isle</td>
<td>5</td>
<td>7.29</td>
</tr>
<tr>
<td>Spider</td>
<td>5</td>
<td>1.46</td>
</tr>
</tbody>
</table>

\(^a\) The models tested were: linear, $n = ax + b$ and quadratic, $ax^2 + bx + c$

\(^b\) Number of lake years sampled

\(^c\) Number of parameters estimated, including the number of parameters from the model plus one for the estimation of variance.

\(^d\) Akaike’s Information Criterion corrected for small sample sizes ($\text{AIC}_c$) estimates model-fit

\(^e\) $\Delta\text{AIC}$ was calculated in order to judge relative support for the models.
Figure A.1. Crayfish abundance over time in lakes invaded by *O. rusticus*. Lines represent phenomenological models of patterns of population growth for which the data gives strong or moderate support (as determined by Akaike’s Information Criterion for small sample sizes $\text{AIC}_c$). Models tested were linear (dashed line) and quadratic (dotted line).


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