EVALUATING STRATEGIES FOR CONTROLLING INVASIVE CRAYFISH USING HUMAN AND FISH PREDATION

A Thesis

Submitted to the Graduate School of the University of Notre Dame in Partial Fulfillment of the Requirements for the Degree of

Master of Science

by

Brett W. Peters

David M. Lodge, Director

Graduate Program in Biological Sciences

Notre Dame, Indiana

April 2010
Invasive species cause significant ecological and economic impacts in a variety of ecosystem types around the world. Preventing the introduction of new invasive species is usually the economically optimal management. However, since prevention is rare, typical management practices rely on reducing the abundance of invasive species populations or maintaining populations at low abundance to mitigate the ecological and economic impacts of the invasion. However, the costs of controlling invasive species are often prohibitively high. Populations of invasive crayfish have been successfully reduced using a combination of mechanical harvest (baited traps) and biocontrol (enhancement of predatory fish populations by using conservative fishing regulations). The large scale application of these management strategies is currently unlikely due to the high costs associated with conducting long term trapping which require a substantial investment in personnel. Furthermore, the optimal fish species for controlling crayfish populations has never been rigorously identified. This thesis investigates ways to improve both crayfish trapping techniques and the manipulation of predatory fish communities to control crayfish populations.
Our analyses show that small changes in trapping techniques (protecting the bait and increasing the size of the trap) can greatly increase the effectiveness of trapping and significantly lower the amount of effort necessary to reduce crayfish populations. In addition to manually removing crayfish, the manipulation of fish communities to consume more crayfish is an essential part of any program designed to reduce populations of invasive crayfish. Bioenergetics modeling, informed by a literature review of diet composition, shows smallmouth bass (*Micropterus dolomieu*) consume the most crayfish when younger (ages 2-9), while rock bass become the best crayfish predators when older (ages 10+). When analyzed at the community scale, our analysis suggests that community wide crayfish consumption decreases with increasing piscivore abundances, indicating that enhancement of piscivore populations, a common practice of fisheries managers, may harm crayfish control efforts. Furthermore, analysis of inter-water body diet composition suggests that certain predatory fishes may be ideal for controlling abundant (smallmouth bass, rock bass and yellow perch) while others (*Lepomis* spp. and rock bass) may be more effective in controlling sparse crayfish populations.

The integration of empirical experiments, theoretical ecology and economics in this thesis yielded results which could directly inform cost effective management of invasive species. A similar multi-disciplinary approach could be used to inform the management of other invasive species where current technology is prohibitively costly to implement on a large scale.
CONTENTS

Figures................................................................................................................................ iv

Tables....................................................................................................................................... v

Acknowledgments.................................................................................................................. vi

Chapter 1: Introduction ....................................................................................................... 1

Chapter 2: Human Harvest of Invasive Crayfish: Cost Effectiveness of Alternative Long-
Term Management Regimes................................................................................................. 4
  2.1 Abstract ...................................................................................................................... 4
  2.2 Introduction ............................................................................................................... 5
  2.3 Methods .................................................................................................................... 9
    2.3.1 Study sites ......................................................................................................... 9
    2.3.2 Bottom trawling ............................................................................................... 10
    2.3.3 Baited traps ..................................................................................................... 10
    2.3.4 Standardizing results across lakes .................................................................. 12
    2.3.5 Lake Ottawa crayfish population estimate .................................................. 12
    2.3.6 Matrix elasticity analysis .............................................................................. 13
    2.3.7 Age-structure matrix harvest model ............................................................... 13
  2.4 Results .................................................................................................................... 18
    2.4.1 Bottom trawling ............................................................................................... 18
    2.4.2 Calibrating Trout Lake trap catches to Lake Ottawa trap catches .......... 19
    2.4.3 Baited traps ...................................................................................................... 19
    2.4.4 Lake Ottawa crayfish population estimate .................................................. 22
    2.4.5 Elasticity analysis ............................................................................................ 22
    2.4.6 Simulated management regimes using harvest model ................................ 23
  2.5 Discussion ............................................................................................................... 27
  2.6 Acknowledgments ................................................................................................... 32

Chapter 3: Potential to Manage Invasive Crayfishes With Fisheries Management ....... 33
  3.1 Abstract ..................................................................................................................... 33
3.2 Introduction ........................................................................................................ 34
3.3 Methods .............................................................................................................. 37
  3.3.1 Determining importance of crayfish to diet of different fishes ......... 37
  3.3.2 Bioenergetics ............................................................................................ 39
  3.3.3 Estimating community-wide crayfish consumption ................... 41
3.4 Results ............................................................................................................... 42
  3.4.1 Patterns of consumption by different fishes across lakes .......... 44
  3.4.2 Bioenergetics analysis ............................................................................ 46
  3.4.3 Consumption of crayfish by the fish community ............................. 46
3.5 Discussion ......................................................................................................... 49
3.6 Acknowledgments ............................................................................................ 56

Chapter 4: Conclusion ............................................................................................. 57

Literature Cited ........................................................................................................ 61
FIGURES

Figure 2.1: Results from the Trout Lake experiment testing alternative trapping methods. Mean ±SE male crayfish trap catch. a. A significant interaction existed between bait protection and days of trap soaking (repeated measures 3-way ANOVA df=1,36 F=6.73, P=0.01). b. There was a significant interaction between bait protection and trap type (repeated measures 3-way ANOVA df=3,36 F=2.91, P<0.05). .................................................................................................................. 20

Figure 2.2: Growth rates (λ) as a function of person hours and harvest method. .......... 24

Figure 2.3: Population growth rates (λ) as a function of the proportion of population removed and removal method in order to illustrate the impact of age selectivity. All trapping methods produced a very similar response and are therefore condensed into one line. .................................................................................................................. 25

Figure 3.1: Composition of fish diets. BC= black crappie, LEP= Lepomis spp., LMB= largemouth bass, NP=a northern pike, RB= rock bass, SMB = smallmouth bass, WAL= walleye, YP= yellow perch ........................................................................ 44

Figure 3.2: Intra-water body comparisons of dependence (proportion of diet) on crayfish by several fishes (y-axis) compared to smallmouth bass dependence on crayfish (x-axis). Linear regression was used to test the null hypothesis of β=0. .......... 45

Figure 3.3: Per-capita annual crayfish consumption estimates (mean±SD) from bioenergetics analysis. Error bars represent variability in diet proportions of each species. .................................................................................................................. 48
TABLES

Table 2.1 Leslie matrix for estimating the effect of harvest on population growth rate... 13

Table 2.2 Stable age distribution (SAD) of rusty crayfish population not subjected to any harvest ................................................................................................................... 15

Table 2.3 Method-specific estimates of CPUE (female crayfish per person-hour) used in population simulations .......................................................................................................................... 19

Table 2.4 Elasticities of transition parameters between age classes within the Leslie matrix for rusty crayfish ........................................................................................................................ 22

Table 2.5 Stable age distributions (SAD) of rusty crayfish populations as a function of removal method and proportion of total population removed annually ............... 26

Table 3.1 Search terms used in literature search .............................................................................................................................................................................. 38

Table 3.2 Studies and water bodies that were included in literature review .......... 43

Table 3.3 Effect of piscivore removal or addition on population and community-wide crayfish consumption .......................................................................................................................... 47
ACKNOWLEDGMENTS

I would like to thank my advisor, David Lodge, for his guidance and support throughout my graduate studies. Not only has he significantly contributed to and improved my research, but my interaction with him has fostered my maturation both professionally and personally. I’d also like to thank my committee members, Gary Belovsky and Gary Lamberti. Their mentoring and insightful feedback has greatly improved my research.

I am very thankful for the great group of people (The Lodge Lab) that I have had the opportunity to work with at Notre Dame. A special thanks to Joanna McNulty for all her help as I have progressed through all the stages of graduate school. My research has benefited greatly from feedback and conservations with post-doctoral researchers and graduate students in the Lodge Lab--- Ashley Baldridge, Matt Barnes, Andy Deines, Kevin Drury, Chris Jerde, Reuben Keller, Tim Kreps, Konrad Kulacki, James Larson, Andy Mahon, Jody Peters, John Rothlisberger and Darren Yeo. Many research technicians --- Jamin Dryer, John Rodstrom, Rebecca Hale, Sarah Sutton, Erick Elgin and Michelle Budny--- and undergraduate researchers--- Tyler Cullender and Katie Baltzer, have also contributed to my research. I’d also like to thank Sadie Rosenthal who first introduced me to the Lodge Lab and research in aquatic ecology.
Last but not least, I thank my wonderful wife Jody for her moral support and also her intellectual contribution to my research. I could not have done it without her.
CHAPTER 1:
INTRODUCTION

On broad time scales, species’ ranges change in response to global climatic patterns, geological processes and rare long distance dispersal events. The rate of these long distance dispersal events has increased markedly due to human activities. The intentional and unintentional transport of live organisms around the world has led to the introduction and establishment of thousands of species outside their previous ranges. Most introduced species do not result in large scale disturbances to their recipient ecosystem; however some have very drastic ecological and sometimes economic consequences and are then considered to be “invasive”. Preventing the introduction of new invasive species is often the optimal management approach because eradication of established populations is difficult and costly (Leung et al. 2002). However, since prevention is rare, typical management practices rely on reducing the abundance of invasive species populations or maintaining populations at low abundance to mitigate the ecological and economic impacts of the invasion (Mack et al. 2000).

Freshwater ecosystems are some of the most imperiled ecosystems in the world with higher past and predicted future extinction rates than terrestrial and marine systems
Ricciardi and Rasmussen 1999, Jenkins 2003). Crayfish in North America are an excellent example of a highly diverse, yet highly endangered group of organisms (Taylor et al. 1996, Lodge et al. 2000). Limited natural connectivity between freshwater systems has led to a heterogeneous distribution of crayfish species over rather small spatial areas, with small populations susceptible to extirpation (Taylor 1996). The introduction of non-native crayfish often leads to the extirpation of native species (Olsen et al. 1991) and is considered the largest threat to crayfish biodiversity in North American (Lodge et al. 2000).

In addition to their impacts on biodiversity, invasive crayfish have other ecological impacts in aquatic ecosystems. Crayfish are generally omnivores and therefore have wide ranging impacts in the ecosystems they invade (Dorn and Wojdak 2004). Invasive crayfish reduce the abundance of organisms in lower trophic levels such as primary producers (Lodge et al. 1994, Rosenthal et al. 2006, Peters et al. 2008) and macroinvertebrates (Lodge et al. 1994, Charlebois and Lamberti 1996, Lodge et al. 1998) through direct consumption. Crayfish also disrupt spawning of some fishes (Savino and Miller 1991, Wilson 2002, Dorn and Mittelbach 2004) and abundances are negatively correlated to fish densities (Garvey et al. 2003, Wilson et al. 2004, Roth et al. 2007).

Interest in reducing invasive crayfish populations has grown recently as stakeholders and managers have come to recognize the impacts that invasive crayfish can inflict. In many cases invasive crayfish threaten anthropogenic values related to biodiversity and recreational fishing (Taylor et al. 1996, Keller et al. 2008). Previous research has investigated the use of chemicals (Bills and Marking 1988, Ray and Steven 1970), and a combination of trapping and biocontrol (Hein et al. 2007, Rach and Bills
1989) to reduce crayfish populations. Research has also tested the efficacy of benthic crayfish barriers to exclude crayfish in lakes (Peters et al. 2008) and streams (M. Ellis unpublished data). This previous research has had limited success in effectively reducing crayfish populations. In addition, all studies required intense effort in a specific water body and have never been implemented on a large spatial scale (multiple water bodies) due to high costs. My thesis research is focused on using ecological theory to develop better strategies for reducing invasive crayfish populations. I focused my research on what I believe to be the two most promising crayfish control techniques: trapping and biological control.

Previous studies have used only a standard trapping configuration to remove crayfish (Rach and Bills 1989, Hein et al. 2006). In Chapter 2, I test the effectiveness of several new trap designs and bottom trawling (a novel technique for crayfish removal) and use the results to parameterize crayfish population models which include various intensities of harvest. Harvest intensity is modeled using person-hours as units; therefore, my results directly inform managers regarding the cost effectiveness of different removal techniques.

Many fish species prey on crayfish (Dorn and Mittlebach 1999) and at least two species have been used in attempts to control crayfish: smallmouth bass (*Micropterus dolomieu*) (Hein et al. 2006) and largemouth bass (*Micropterus salmoides*) (Rach and Bills 1999). In order to implement the most effective biocontrol program, we must know which species of fish consume the most crayfish. Previous literature comparing consumption of crayfish by fishes has used very limited data sets and only considered the proportion of the fish diet contributed by crayfish (Dorn and Mittlebach 1999). These
proportions have little utility when designing a biocontrol program because the actual magnitude of consumption of crayfish is the important metric. In Chapter 3, to better inform the selection of the ideal fishes for biocontrol, I conduct a quantitative literature review of the diets of multiple sportfish species that prey on crayfish. I use the results of my literature review to parameterize a bioenergetics model from which I estimate the annual consumption of crayfish by each fish species during each year of its life cycle. I then use the per-capita consumption estimates from the bioenergetics analysis to model the community-wide predatory demand for crayfish before and after common fisheries management efforts are applied. I also explore mechanisms that create feedbacks between crayfish and fish populations and their implications for managing invasive crayfish populations. This thesis is the first rigorous combination of empirical work, modeling, and cost considerations designed to put the population biology of crayfish into a form useful for natural resource managers.
2.1 Abstract

The reactive nature of invasive species management often leaves maintenance control as the most viable management option. Interest in the management of rusty crayfish (*Orconectes rusticus*) is increasing, but successful population reduction has been achieved in only one water body. Uncertainty about the effectiveness and costs of control are current impediments to more widespread control efforts. Therefore, it is imperative that improved removal methods, which improve catch per effort (CPUE) and cost effectiveness, are implemented. We evaluated the effectiveness of alternative crayfish removal methods in reducing crayfish population growth rate ($\lambda$), including bottom trawling and four different trap designs. For each trap design we also tested the effectiveness of bait enclosures and duration of trap soaking (the time traps are left in the water to trap crayfish). CPUE and age selectivity of each removal method were
estimated from experimental trials and then incorporated into an age-structured population model to evaluate the effects of long term management with alternative methods and different degrees of overall effort. When modeled as a function of person-hours invested, the double bucket trap with protected bait, soaked for two days, was the most effective method in reducing crayfish population growth rate. The responses of population growth rate to increasing harvest were nonlinear, with distinct thresholds which triggered large declines in population growth rate. Our analysis does not explicitly integrate any population feedback mechanisms. However, we expect that depensatory feedback will be stronger than compensatory feedbacks and will enhance the effectiveness of trapping efforts. This research demonstrates that small changes to trap design and strategy can greatly improve the overall ability of management to reduce crayfish population growth rates.

2.2 Introduction

Invasive species, species that have established populations outside their native range and which have negative ecological and economic impacts, threaten aquatic biodiversity, ecosystem function, and economic systems throughout the world (Kolar and Lodge 2000, Pimentel et al. 2000, Sala et al. 2001, Dextrase and Mandrak 2006). Preventing the introduction of such species is often the most cost effective long term management strategy (Leung et al. 2002, Keller et al. 2007), but in situations where a species has already been introduced and established, eradication and maintenance control are the two remaining management options. Although increasing spread and growing
harm of such invasions are often accepted as inevitable, many examples exist of successful eradication and maintenance control efforts, both of which are often cheaper in the long term than the damages from unmanaged invasions (Wittenberg and Cock 2005, Simberloff 2009).

In many situations, however, eradication is impossible or unfeasible due to the biology of the invading organism, characteristics of the invaded ecosystem, potential non-target effects, or the high probability of subsequent introductions. In such cases, maintenance control is the only remaining management option, and the goal of management becomes to reduce the invasive population to a level at which some or all of the undesirable impacts are mitigated or eliminated (Mack et al. 2000). Despite the growing need for management options, development and testing of control methods is in its infancy for many taxonomic groups of invaders.

Here we experimentally test alternative harvest methods, and use a matrix population model to simulate the long term impact of harvest on populations of the invasive rusty crayfish (*Orconectes rusticus*). Rusty crayfish are native to the Ohio River basin, and have invaded the upper Great Lakes region, likely spread by anglers who discarded unused live crayfish bait into uninvaded lakes (Capelli and Magnuson 1983). Rusty crayfish reduce the abundance of native crayfish (Olsen et al. 1991), macrophytes and macroinvertebrates (Lodge et al. 1994, Rosenthal 2004), and recreationally important fishes (Garvey et al. 2003, Wilson et al. 2004, Roth et al. 2007, Keller et al. 2008). In an effort to slow the spread of rusty crayfish to additional waterways, several Great Lakes states regulate the sale, transport and use of crayfish (Peters and Lodge 2009). In
addition, fishermen, lake-front property owners and other stakeholders have increasingly called for management of existing populations of rusty crayfish.

Eradication of rusty crayfish is not however feasible in most situations. Their cryptic behavior in the benthos of lakes, streams and rivers makes early detection difficult with current technology. Eradication is unfeasible because traps and other removal methods are insufficiently effective at low crayfish population densities, and toxins are insufficiently selective. There are many chemicals that effectively kill crayfish (e.g., Baytex, Baythroid, temephos), but these chemicals were developed as insecticides and kill all arthropods and sometimes fish (e.g., Baythroid) (Bills and Marking 1988). Furthermore, even if eradication were possible, subsequent immigration of crayfish is sometimes likely, especially when streams connect invaded waterways (Puth and Allen 2005) or additional anthropogenic translocation is insufficiently discouraged through voluntary or regulatory efforts.

Therefore many invasive populations of rusty crayfish are ideal candidates for maintenance control programs if removal methods can be employed to lower crayfish populations enough to restore lost ecosystem goods and services sufficiently to produce a net benefit (Keller et al. 2008). Many of the impacts of rusty crayfish can be mitigated by reducing the population of rusty crayfish (Rosenthal et al. 2006). The possibility that enhancement of predatory fishes can contribute to control of crayfish, and lower the costs of sustainable control, increases the motivation for the development of additional crayfish control strategies (Hein et al. 2006, Hein et al. 2007).

In this paper we estimate the effects of alternative harvest methods on crayfish population growth rate, using a model parameterized with new experimental results.
Unlike earlier work (e.g., Hein et al. 2006), we compare a broader range of alternative management regimes, and compare their costs, in order to maximize the usefulness of our work to management agencies and private groups interested in crayfish control. Specifically, in field experiments we tested five harvest methods (four baited trap designs and trawling), two baiting strategies, and two durations of trap soaking the time traps are left in the water to trap crayfish). We hypothesized that two day trap sets would increase traps catches per effort, especially in traps with bait that was protected from consumption. Because earlier studies with lobsters (Idhe et al. 2006) and crayfish (Ogle and Kret 2008) show that trap occupants can inhibit other individuals from entering traps, we hypothesized that larger traps would catch more crayfish per effort by decreasing aggressive interactions. We hypothesized that trawling would have the benefit of being less sex and size selective than traps. We estimated the catch per unit effort (CPUE) and size selectivity of each method in experimental trials.

We then used an age-structured harvest model, parameterized with experimental results, to simulate the rusty crayfish population response to alternative “management regimes”. We define a management regime as a long term management program in which a given amount of effort (person-hours) is invested in crayfish harvest using a particular removal technique each year. Our analysis is similar to matrix elasticity analyses (de Kroon et al. 1986, Caswell 1989), which have been used to inform management of both imperiled (Crowder et al. 1994, Heppel et al. 2000) and invasive (Buhle et al. 2005, Davis et al. 2006) species. In matrix elasticity analyses, the effects on population growth rate of proportionally equal perturbations to different demographic parameters (fecundities and transition probabilities) are assessed to determine the optimal
life history component to alter through management. The usefulness of matrix elasticity analysis to management is, however, limited because these analyses do not take into account the feasibility of altering different life history components. Instead we conducted our simulations as a function of effort so the real world feasibility of altering population growth rates can be assessed. We use person-hours as an index of total cost because personnel costs are often the most expensive component of a large scale removal effort and capital investments will be similar for all removal methods.

2.3 Methods

2.3.1 Study sites

We conducted the trawling experiment in Lake Ottawa (46° 5'2" N, 88°45'47" W, Iron County, Michigan) on July 26, 2005. Two large unvegetated sandy areas of the lake were trawled to avoid obstructions (rocks, woody debris) and habitat destruction. The trapping experiment was conducted in Trout Lake (46° 1’15”N, 89° 39’42” W, Vilas County, Wisconsin) on August 4-8, 2007 around the rocky reef point in the southeastern corner of the southern basin. This area was selected because it provided a large area of relatively homogenous substrate. Both lakes have high densities of rusty crayfish, and very low abundance of other species of crayfish, similar to other lakes which would be candidates for maintenance control programs for crayfish.
2.3.2 Bottom trawling

Bottom trawling was conducted using a 4.9 m Marinovich semi-balloon trawl with a 6.4 m trawl entrance, 19 mm (bar) body mesh and a 16 mm cod end mesh. Multiple trawl hauls were conducted in both day and night in both Lake Ottawa locations for a total of 10 hours. For each trawl, the time of active bottom trawling was recorded, all crayfish captured were counted, and a random sub-sample (n=1166) was sexed and measured. The age of each crayfish was determined using the age classes defined by Hein (2004) which were based on the size-frequency analyses by Lorman (1980). CPUE was calculated by dividing the total female crayfish catch per trawl by time of trawling for each trawl. Only female crayfish were included in CPUE calculations for trawling because the female population is the only portion of the population modeled in the Leslie matrix population model. CPUE was exponentially distributed (one sample Kolmogorov-Smirnov-Exponential test), and we tested the effects of time of day and location on log transformed CPUE using a 2-way ANOVA.

2.3.3 Baited traps

We tested four different trap designs and also the use of a bait enclosure device. The four trap designs were: 1) Gee minnow trap (41.9 cm long, 22.7 cm diameter, with funnel openings expanded to 2.5cm diameter on each end); 2) extended Gee minnow trap (same as number 1 above with an added cylindrical 38.1 cm long mesh spacer in the middle); 3) single bucket design constructed of a perforated five gallon plastic bucket (35.6 cm length X 30.5 cm diameter) with a mesh (6.4 mm X 6.4mm) funnel in one end and the other end covered with a perforated lid; 4) double bucket design constructed by
connecting two perforated five-gallon buckets (71.2 cm length X 30.5 cm diameter), each with their bottom cut out and replaced with a mesh (6.4 mm X 6.4 mm) funnel. The first two trap designs were commercially available while we constructed the latter two based on designs used by private crayfish trappers in the study region.

We also compared the effectiveness of bait that could be consumed with bait protected from consumption with a bait enclosure. The bait enclosure was a perforated plastic container containing the bait wrapped in cheesecloth. These two factors (four trap types and two bait types) were fully crossed and replicated three times, except for extended Gee minnow trap treatments, which only had two replicates (for a total of 22 experimental units). This experiment was conducted twice (4-6 August and 6-8 August 2007), increasing the replication for each treatment combination to six (four for extended minnow traps).

At the beginning of each experiment, all traps were baited with about 120 g of beef liver, set in about 1.5 m of water, and retrieved 24 hours later. Every crayfish was measured (carapace length) and sexed and returned to the trap, which was re-submerged with the remaining bait. The age of each crayfish was determined as for trawl catches. Traps were pulled again after a total of 48 hr, and all crayfish measured and sexed. For each 2-day trial we randomized the location of the different treatment combinations to minimize bias and ensure independence of replicates. CPUE for each trapping method was normally distributed (one sample Kolmogorov-Smirnov-Lillifores test). The effects on catch of trap type, bait protection, and duration of trap soaking were evaluated using a 3-way repeated measures ANOVA.
2.3.4 Standardizing results across lakes

For comparison of trapping to trawling, we converted the CPUEs from the Trout Lake trapping experiment to estimates of Lake Ottawa trap CPUE by calibrating Gee minnow trap catches (first trap type described above with exposed bait) from Trout Lake (N=6) against results from the same trapping technique (N=20 traps) conducted in the trawled locations in Lake Ottawa one day prior to the trawling experiment. Dividing the Lake Ottawa CPUE by the Trout Lake CPUE yielded a conversion factor by which Trout Lake trap catches from all trapping treatments were multiplied to estimate the analogous Lake Ottawa CPUE. This conversion is consistent with the linear relationship between trap catch and rusty crayfish density documented in previous studies (Capelli and Magnuson 1983, Olsen et al. 1991).

2.3.5 Lake Ottawa crayfish population estimate

The population size of rusty crayfish in Lake Ottawa, which served as the initial population in harvest simulations, was estimated using a stratified sampling approach. Divers using SCUBA and snorkeling counted crayfish (Age 1+) in one-meter$^2$ PVC quadrats. Crayfish were counted at each of four depths: 1m, 3m, 6m and 9m, at twelve sites around the lake. The area of each depth stratum was estimated using a bathymetric map (USFS 1929) and digital image analysis software (Uthscsa Image Tool 3.0). The population of age 1+ crayfish was estimated by multiplying the depth-specific densities by the area of each depth strata. The population of age 0 crayfish was estimated by assuming the crayfish population in Lake Ottawa was at the stable age distribution associated with the Leslie matrix (Table 2.1) used for the simulation model with zero
harvest mortality ($K_{0.3}=1$). This is a reasonable assumption given that rusty crayfish invaded Lake Ottawa at least 19 years prior to our study (Rosenthal et al 2006).

### TABLE 2.1

**LESLIE MATRIX FOR ESTIMATING THE EFFECT OF HARVEST ON POPULATION GROWTH RATE**

<table>
<thead>
<tr>
<th></th>
<th>Age 0</th>
<th>Age 1</th>
<th>Age 2</th>
<th>Age 3</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fecundity</td>
<td>0</td>
<td>$F_1*S_0$</td>
<td>$F_2*S_0$</td>
<td>$F_3*S_0$</td>
</tr>
<tr>
<td>Age 1</td>
<td>$S_2*K_1$</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Age 2</td>
<td>0</td>
<td>$S_2*K_2$</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Age 3</td>
<td>0</td>
<td>0</td>
<td>$S_3*K_3$</td>
<td>0</td>
</tr>
</tbody>
</table>

*NOTE: $F_i$, $S_i$, $K_i$ represent the age-specific fecundities, survival probabilities and harvest survivor probabilities, respectively*

2.3.6 Matrix elasticity analysis

The elasticity ($E_{ij}$) of each life table parameter ($a_{ij}$) was calculated using Eq. (1)

$$E_{ij} = \frac{a_{ij}v_jw_i}{\lambda(v,w)}$$

2.3.7 Age-structure matrix harvest model

The Leslie matrix harvest model (Table 2.1) was parameterized with CPUE and age selectivity data from the trapping and trawling experiments to explore the effects of different management regimes (removal method X effort) on crayfish population growth
rate. The age-specific survival rates and fecundities for the Leslie matrix come from Hein et al. (2006). Harvest is included in the population matrix (Table 2.1) as \( K_i \), calculated using Eq. (2).

\[
K_i = e^{-mP_i}
\]  

(2.2)

Where \( P_i \) is the age selectivity of a particular removal method, and \( m \) is a scaling variable, which is adjusted so that a specified proportion (based on removal regime) of the total crayfish population is removed at a given timestep while also ensuring that the age composition of the crayfish removed reflects a given method’s selectivity. To calculate the age selectivity \( (P_i) \) of each removal method, the proportion of the total catch which is age(\( i \)) is divided by the proportion of the actual crayfish population which is age(\( i \)). Because we did not estimate the crayfish age structure in Trout Lake or Lake Ottawa where the experimental trials took place, we assumed that all removal methods were targeting crayfish populations which were at the stable age distribution (SAD) associated with the Leslie matrix with no harvest mortality \( (K_{0,3}=1, \text{Table 2.2}) \).

Because we used a matrix population model, we only included the female portion of the crayfish population in the simulations, and all CPUEs used in the harvest model were in units of female crayfish removed per person-hour. However, because trap catches are biased toward males and female CPUE is therefore much more highly variable than that of males (Capelli and Magnuson 1983, Olsen et al. 1991), we used male trap catches to calculate CPUE for trapping methods. Female trap CPUE increases as males in a population are depleted by continual harvest (Hein et al. 2007). We therefore converted our short-term experimental male trap CPUE to female trap CPUE.
TABLE 2.2

STABLE AGE DISTRIBUTION (SAD) OF RUSTY CRAYFISH POPULATION NOT SUBJECTED TO ANY HARVEST

<table>
<thead>
<tr>
<th>Age Class</th>
<th>Proportion of Population</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>0.57</td>
</tr>
<tr>
<td>1</td>
<td>0.32</td>
</tr>
<tr>
<td>2</td>
<td>0.10</td>
</tr>
<tr>
<td>3</td>
<td>0.01</td>
</tr>
</tbody>
</table>

for use in the harvest model. We parameterized the lag in female CPUE using sex composition data in trap catches over time from a long term harvest experiment (Hein et al. 2007). Specifically, we modeled female CPUE as 48 percent of male CPUE until 4 percent of the female population was removed, at which point the female trap catches increased to the initial male trap catch level (from Table 1 in Hein et al. 2007). For bottom trawling we directly computed female CPUE because the sex ratio for trawling was approximately equal and there is no reason to expect that the sex ratio would change as a crayfish population decreased from trawl harvesting.

For use in the Leslie matrix, we converted CPUE from female crayfish per person-hour to proportion of the female population removed per person-hour by dividing each method-specific numerical CPUE by the estimate of the female crayfish population size from Lake Ottawa. To consider CPUE variability, the CPUE for a particular regime was selected randomly from a normal (parameterized by mean and SD of CPUE from the experimental trials) or exponential (parameterized by the mean CPUE from the trawling
trials) distribution for each unit of effort being simulated. These randomly selected catches were then “summed” to calculate the total proportion removed using Eq. (3).

\[
\text{Proportion Removed}_{\text{effort (e), method (m)}} = \sum_{x=1}^{c} \text{Catch}_x \quad (3.3.1)
\]

\[
\text{Catch}_x = (1 - \sum_{x=1}^{c-1} \text{Catch}_x) \times \text{CPUE} \quad (3.3.2)
\]

for trapping methods \( CPUE \sim N(\overline{CPUE}_m, \sigma^2_m) \) \quad (3.3.3)

for trawling \( CPUE \sim \text{EXP} \left( \frac{1}{\overline{CPUE}} \right) \) \quad (3.3.4)

Equation 3 takes into account the assumption of a Type I functional response (Holling 1959) that the CPUE decreases due to diminishing crayfish abundance. For each unit of effort being simulated, the selectivity of a particular management regime was determined by randomly drawing from a multinomial distribution which was parameterized by the maximum likelihood estimate (MLE) of the age specific capture probabilities from the experimental trials. After selectivities were determined for each unit of effort, the MLE for the age specific probabilities was calculated for the randomly drawn set and used for the selectivity calculations for that management regime. At each simulation time step (one year) a proportion of the total population was removed via harvest mortality, which was dependent on the CPUE of the harvest method and the effort level being simulated (Eq. 3).

To assess the influence of age selectivity of alternative harvest methods (controlling for CPUE differences) we conducted additional simulations, in which an equal proportion of the crayfish population was harvested using each method (rather than
equal effort levels), but the age classes harvested were determined by the empirically
derived method specific age selectivities. This isolated the method specific age
selectivities as the only parameters differing between simulations. We also used these
simulations to explore the effects of differing age selectivities on the SAD of populations
subjected to different harvest methods.

For each simulation time step, the value of scaling variable $m$ (Eq. 2) was
determined that removed the proportion dictated by the experimentally-derived CPUE of
the method and the effort level being simulated (Eq. 3). Estimating the value of $m$ was
accomplished using an iterative procedure in which values of $m$ between 0 and
10,000,000 were evaluated at decreasing intervals (increasing precision) bounded by a
decreasing range dictated by the best estimate of $m$ from the previous iteration ± the
range of the previous interval. The interval size started at 1,000,000 and after 14
iterations ended with an interval of 1.0 e^−7. After each simulation time step, the
population age distribution changed and therefore $m$ had to be re-estimated for the next
time step. This procedure was continued until $m$ stabilized across time steps, indicating
the population had reached its stable age distribution (SAD) for a particular removal
regime. After the $m$ value had stabilized, the population growth rate ($\lambda$) was determined
by calculating the dominant eigenvalue of the Leslie matrix with final harvest mortality
rates ($K_{0.3}$) included (Table 2.1). Each removal regime was simulated independently 100
times with effort levels from 0 to 8,000 person-hours in intervals of 80 person-hours.
Populations subjected to intense removal regimes failed to converge on a SAD because
all fecund age groups were removed from the population. If populations did not
converge on a SAD after 100 time steps, the population was assumed to crash ($\lambda$ =0).
2.4 Results

2.4.1 Bottom trawling

During the 199 minutes of active bottom trawling time, a total of 10,809 crayfish were caught, of which 1166 were sexed and measured. A slightly higher proportion of the trawl catch was male (54%) than female (46%). The CPUE (female crayfish hr$^{-1}$ of active trawling) did not differ between trawl locations (2-way ANOVA, df=1, F=0.66, P = 0.43) or time of day (df=1, F=1.41, P=0.25); mean ± 1SD CPUE was 2004±1775 female crayfish·hr$^{-1}$. The distribution of the CPUE fit an exponential distribution (Kolmogorov-Smirnov-Exponential p>0.9, max. diff. = 0.115, n=22). From our experience and other information (Gary Czypinski, USFWS, personal communication), we estimated that a management application of trawling would require two crew members, with only 20% of total time spent actively trawling. The remainder of the time is spent processing catch and deploying and retrieving the trawl. Thus, in the population simulations (below), we used an estimate for the mean of 200.4±177.5 female crayfish per person-hour. Because of the trawl mesh size, no age 0 crayfish were captured. Age 1 crayfish were captured most readily, followed by age 2; almost none (<1%) of the trawl catch was age 3 (Table 2.3).

Our field experience demonstrated that a major logistical limitation of trawling is its susceptibility to snagging and net damage in the habitats with structure (e.g., cobble, coarse woody debris, macrophytes) that generally support the highest populations of crayfish. Although we chose predominantly sandy-bottom habitats for our trawling experiment, we nevertheless experienced snagging.
TABLE 2.3

METHOD-SPECIFIC ESTIMATES OF CPUE (FEMALE CRAYFISH PER PERSON-HOUR) USED IN POPULATION SIMULATIONS

<table>
<thead>
<tr>
<th>Removal Method</th>
<th>Age 0</th>
<th>Age 1</th>
<th>Age 2</th>
<th>Age 3</th>
<th>CPUE</th>
<th>SD (CPUE)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Minnow Trap, exposed bait</td>
<td>0.0</td>
<td>0.03</td>
<td>0.78</td>
<td>0.19</td>
<td>469</td>
<td>199.1</td>
</tr>
<tr>
<td>Minnow Trap, protected bait</td>
<td>0.0</td>
<td>0.03</td>
<td>0.64</td>
<td>0.33</td>
<td>1037.4</td>
<td>262.8</td>
</tr>
<tr>
<td>Double Bucket Trap, protected bait</td>
<td>0.0</td>
<td>0.02</td>
<td>0.78</td>
<td>0.20</td>
<td>1648.4</td>
<td>469.4</td>
</tr>
<tr>
<td>Trawling</td>
<td>0.0</td>
<td>0.72</td>
<td>0.28</td>
<td>&lt;0.01</td>
<td>200.4</td>
<td>177.5</td>
</tr>
</tbody>
</table>

2.4.2 Calibrating Trout Lake trap catches to Lake Ottawa trap catches

The mean±1SD trap catch from pre-trawl trapping with minnow traps with exposed bait in Lake Ottawa was 57.6 ±15.6 male crayfish trap$^{-1}$ (more detailed trapping results are presented in the next section); the analogous mean for Trout Lake was 19.0 ± 10.7. In using the population simulations to compare the impact of different trapping methods to that of trawling in Lake Ottawa (below), we therefore multiplied Trout Lake trap catches for each trapping method by 3.03.

2.4.3 Baited traps

Bait protection (3-way repeated measures ANOVA df=1,36, F=8.85, P<0.0001), days of trap soaking (df=1,36, F=28.34, P<0.01) and trap type (df=3,36, F=3.17, P=0.036) all significantly affected male trap catch (Figure 2.1). Additionally, significant interactions existed between days of trap soaking and bait protection (df=1,36, F=6.73,
P=0.01, 2.1a), and trap type and bait protection (df=3,36,F=2.91, P<0.05, Figure 2.1b). The significant interaction between trap type and bait protection was driven by the high catch rates in double bucket traps with protected bait (Figure 2.1b). Protection of bait was effective in reducing the consumption of the bait by captured crayfish. 100% (22 of 22) of traps with exposed bait had the bait completely consumed after 24 hours. In traps with protected bait, only 23% (5/22) had their bait completely consumed after 24 hours.

Figure 2.1: Results from the Trout Lake experiment testing alternative trapping methods. Mean ±SE male crayfish trap catch. a. A significant interaction existed between bait protection and days of trap soaking (repeated measures 3-way ANOVA  df=1,36 F=6.73, P=0.01). b, There was a significant interaction between bait protection and trap type (repeated measures 3-way ANOVA  df=3,36 F=2.91, P<0.05)
To reduce the number of harvest methods in the population simulations, we included only three trapping methods: minnow trap with exposed bait, minnow trap with protected bait, and double bucket trap with protected bait. We chose to model these methods because a minnow trap with exposed bait is the standard method which has been used previously by many researchers and management agencies, and the addition of a bait protection device would be a simple improvement to existing trapping equipment. We also chose to model the double bucket with protected bait because it produced significantly higher catches than the other trapping methods (2.1b). For all three methods, we simulated only two day trap soakings because trap catches were highest for two day soaks (2.1a), and would therefore be more cost effective to implement in a management setting because of lower bait and labor costs. The trap catches for each of the three trapping methods that were simulated fit a normal distribution (Kolmogorov-Smirnov-Lillifores, P>0.08, P>0.9, P>0.2, respectively). For the simulations, we estimated (from our experience) that a crew of two could pull and re-set 150 crayfish traps per eight hours (16 person-hours). Based on these effort estimates we multiplied the male crayfish trap catch by 9.375 (150 traps/16 hours) to get an estimate of harvest in units of male crayfish per person-hour, which was then multiplied by the Trout Lake-to-Lake Ottawa calibration factor (3.03). Final estimates (mean ± SD) used in the simulations were then 469±199 for minnow traps with exposed bait, 1037±263 for minnow traps with protected bait, and 1648 ±469 for double bucket traps with protected bait, all in units of male crayfish per person-hour.

The age composition of all trapping methods was heavily skewed towards older individuals when compared to the age composition of trawling (Table 2.3).
2.4.4 Lake Ottawa crayfish population estimate

Based on our stratified sampling we estimated the population ±SD of Ages 1-3 rusty crayfish in Lake Ottawa to be 5,629,426 ± 3,792,096. Ages 1-3 represent only 43% of the total crayfish population (based on SAD on Leslie matrix without added mortality; Table 2.2). Therefore, we estimate the total population (Ages 0-3) of rusty crayfish in Lake Ottawa to be 13,155,939 (SD=8,862,108).

2.4.5 Elasticity analysis

Population growth rate ($\lambda$) was most sensitive to changes in the transition probability between age 0 and age 1 (Table 2.4).

<table>
<thead>
<tr>
<th>Fecundities</th>
<th>Age 0</th>
<th>Age 1</th>
<th>Age 2</th>
<th>Age 3</th>
</tr>
</thead>
<tbody>
<tr>
<td>Age 1</td>
<td>0.42</td>
<td>0.28</td>
<td>0.12</td>
<td>0.02</td>
</tr>
<tr>
<td>Age 2</td>
<td>-</td>
<td>0.14</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Age 3</td>
<td>-</td>
<td>-</td>
<td>0.02</td>
<td>-</td>
</tr>
</tbody>
</table>

Note: Values represent the sensitivity of population growth rate ($\lambda$) to equal proportion changes in each parameter. The transition between Age 0 and Age 1 (bold) was the most sensitive to changes.
2.4.6 Simulated management regimes using harvest model

Due to differences in age selectivity and CPUE (Table 2.3), the relationship between effort invested and population growth ($\lambda$) rate differed greatly among the four simulated harvest methods (Figure 2.2). The amount of effort needed to cause negative population growth ($\lambda < 1.0$) was approximately 280 person-hours (3.5 weeks of work for a two person crew) for double bucket trap with protected bait, 400 person-hours for minnow traps with protected bait, 1040 person-hours for minnow traps with exposed bait traps, and 3240 person-hours for trawling (Figure 2.2). The shape of the functional relationship between effort and the three trapping methods is very similar because all the traps have very similar age selectivities (Table 2.3). This results in reduction of oldest age classes, which the traps are most selective for, before younger age-classes. The elimination of older age classes had a larger impact on the population growth rate because fecundity is much higher for older individuals (Table 2.1). The trawl on the other hand harvested age classes of one and above in close approximation to their relative abundances. Relative to trapping, trawling therefore led to a much more gradual decrease in population growth rate (Figure 2.2).

The amount of variability in the population growth rate was largest at effort levels near thresholds where the population growth rate drops quickly in response to increasing effort (Figure 2.2). This variability is completely attributable to randomization of the CPUE and selectivity parameters used in each of 100 simulations of a particular removal type regime. For effort levels near thresholds, it was common for some simulations to have CPUEs large enough to cross the threshold causing a large decrease in population.
Figure 2.2: Growth rates ($\lambda$) as a function of person hours and harvest method.

growth rate while others with lesser CPUE did not cross that threshold, leading to increased variability in population growth estimates for those removal regimes.

Simulations where equal proportions of the crayfish population were removed with different methods (to better illustrate the impact of age selectivity alone) produced similar shapes of population responses (Figure 2.3) as simulations with method-specific CPUEs (Figure 2.2). All the baited trap methods produced greater population declines than trawling at the same level of effort. The crayfish population response to increasing harvest was almost identical for all baited trap methods indicating that the small
Figure 2.3: Population growth rates ($\lambda$) as a function of the proportion of population removed and removal method in order to illustrate the impact of age selectivity. All trapping methods produced a very similar response and are therefore condensed into one line.

Differences in selectivity between these methods (Table 2.3) had little effect on their effectiveness.

We also used these simulations to explore the effects of each harvest method on population SADs associated with a range of harvest intensities (Table 2.5). SADs of populations with greater than 20% of the population harvested annually are not shown because they crashed for all harvest methods.
TABLE 2.5

STABLE AGE DISTRIBUTIONS (SAD) OF RUSTY CRAYFISH POPULATIONS AS A FUNCTION OF REMOVAL METHOD AND PROPORTION OF TOTAL POPULATION REMOVED ANNUALLY

<table>
<thead>
<tr>
<th>Removal Method</th>
<th>Proportion of Population Removed Annually</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>0.05</td>
</tr>
<tr>
<td>Minnow Trap w/ Exposed Bait</td>
<td></td>
</tr>
<tr>
<td>Age 0</td>
<td>0.61</td>
</tr>
<tr>
<td>Age 1</td>
<td>0.39</td>
</tr>
<tr>
<td>Age 2</td>
<td>0.00</td>
</tr>
<tr>
<td>Age 3</td>
<td>0.00</td>
</tr>
<tr>
<td>Minnow Trap w/Protected Bait</td>
<td></td>
</tr>
<tr>
<td>Age 0</td>
<td>0.61</td>
</tr>
<tr>
<td>Age 1</td>
<td>0.39</td>
</tr>
<tr>
<td>Age 2</td>
<td>0.00</td>
</tr>
<tr>
<td>Age 3</td>
<td>0.00</td>
</tr>
<tr>
<td>Double Bucket Protected Bait</td>
<td></td>
</tr>
<tr>
<td>Age 0</td>
<td>0.61</td>
</tr>
<tr>
<td>Age 1</td>
<td>0.39</td>
</tr>
<tr>
<td>Age 2</td>
<td>0.00</td>
</tr>
<tr>
<td>Age 3</td>
<td>0.00</td>
</tr>
<tr>
<td>Trawling</td>
<td></td>
</tr>
<tr>
<td>Age 0</td>
<td>0.59</td>
</tr>
<tr>
<td>Age 1</td>
<td>0.31</td>
</tr>
<tr>
<td>Age 2</td>
<td>0.09</td>
</tr>
<tr>
<td>Age 3</td>
<td>0.01</td>
</tr>
</tbody>
</table>
2.5 Discussion

The size selectivity of different removal methods had a large effect on how the simulated crayfish population responded to harvest. Most removal techniques have some size or age bias. For active capture techniques such as trawling, these biases are due to the gear itself (mesh size of nets) or due to the time or location at which the removal is conducted. Active capture techniques with size bias consistently remove a similar size or age composition even as the population is reduced through the removal effort. This leads to a steady decrease in population growth rate with increasing effort because with each additional application of effort, a similar proportion of each age class is removed.

Passive capture methods such as baited traps are often size or age selective due to interactions within the targeted population. The harvests from these removal techniques have a dynamic age composition and lead to dramatic population responses as critical thresholds are met that eliminate certain age classes. Difference in the selectivity between trapping and trawling create the step-like and smooth population responses, respectively, to increasing harvest (Figures 2.2, 2.3).

We explored the effects of size selectivity directly by conducting simulations in which every method removed the same proportion of the crayfish population but with the size selectivity unchanged (Figure 2.3). The result of this set of simulations was opposite of what might have been predicted from the elasticity analysis (Table 2.4). The elasticity analysis indicated that population growth rate ($\lambda$) is most influenced by perturbations to the Age 0 to Age 1 survival probability. However, our simulations show that trapping, which targets the Age 1 to Age 2 and Age 2 to Age 3 transition probabilities, has the greater effect on population growth rate ($\lambda$) than does trawling which more effectively
targets the Age 0 to Age 1 survival probability. The explanation of this difference between the elasticity analysis and our simulations is simple. The elasticity analysis determines the effect of proportionally equal perturbations to each parameter on population growth rate (\( \lambda \)). Removal methods that target large sized crayfish alter transition probabilities that have low elasticity values, but these probabilities are reduced easily because the low number of crayfish in these size classes means that not much effort is necessary to remove a large proportion of an age class. The difference between inferences that might have been drawn from the elasticity analysis and our simulations reinforces the need to evaluate realistic ranges of harvest parameters.

We parameterized the harvest portion of the population model using our population estimate from Lake Ottawa to provide the most realistic model possible. We recognize that our population model omits well documented mechanisms affecting population growth. For example, Leslie matrices like the one used in our analysis do not integrate changing levels of competition and predation. Although Hein et al. (2006) found that rusty crayfish fecundity did not change with declining population, some compensatory or depensatory feedbacks are likely to affect other transition probabilities. We explore these possibilities below.

Our simulations show that harvesting crayfish causes shifts in population age structure (Table 2.5), and previous studies have shown such changes can initiate population feedbacks in crayfish. For example, Momot (1993) found that the removal of large male *Orconectes virilis* crayfish increased the recruitment of crayfish to the age 0 and age 1 size classes. In our study, all trapping methods had very similar age selectivities (Table 2.3) which resulted in similar SADs with very few Age 2 and 3
crayfish (Table 2.5). The shift to a population structure with fewer Age 2 and 3 crayfish may increase recruitment of Age 0 and 1 crayfish, thus mitigating decreases in population growth rate \( (\lambda) \). On the other hand, the increase in young individuals in populations subject to intensive trapping increases the proportion of the population susceptible to predation and thus may lead to depensation (Stein 1977, Kershner and Lodge 1995, Roth et al. 2007).

Compared to trapping, trawling targets smaller individuals (Table 2.3) and therefore leads to SADs similar to those with no harvest (Table 2.5). The feedbacks that result from shifts in population structure would not be as prevalent in populations subjected to trawling because it does not cause as large a change as trapping in population age structure. Although the magnitudes of the feedbacks related to changes in age structure are different between trapping and trawling, we believe that comparisons between trapping and trawling simulations have merit because the feedbacks caused by trapping potentially counteract each other. We hypothesize that the greater feedbacks caused by trapping are more likely to hasten population decline than slow it, because of potentially increased impact by predatory fishes brought on by reduced mean size of crayfish and reduced population abundance.

Decreases in crayfish population size, in addition to changes in age structure, may also initiate depensatory feedback mechanisms which may enhance the effects of harvest. The consumption of macrophytes by crayfish, and the subsequent loss of habitat for *Lepomis* spp. may be a major factor influencing equilibrium densities of crayfish (Roth et al. 2007). Decreasing crayfish populations may allow macrophytes and the associated macroinvertebrate populations to rebound (Lodge et al. 1994, Rosenthal et al. 2006).
Increased macrophytes are likely to increase the recruitment of juvenile predatory fish (Mittelbach 1981, Wener at al. 1983) to sizes where the fishes can consume crayfish. In addition to habitat destruction and competition for food resources, crayfish can directly impact fish populations by consuming fish eggs (Savino and Miller 1991, Dorn and Mittlebach 2004, B. Peters personal observation). Although we do not include any of these feedback mechanisms in our model, the majority of the mechanisms reviewed here are depensatory and would further intensify the effects of harvest. For these reasons, the crayfish population response to harvest in our model is likely to be an underestimate of actual population responses.

The potentially strongest depensatory feedbacks assume the presence of a predatory fish community which is able to respond behaviorally and numerically to crayfish reductions. This reinforces the need for an integrated approach to reducing crayfish populations. Consistent with these lines of logic, Hein et al. (2006) show that predatory fish had a greater impact on rusty crayfish population growth than did an intensive crayfish removal. However, Hein et al. (2006) did not measure any changes to the fish community response to the crayfish removal that could elucidate the possible strength of potentially compensatory and depensatory mechanisms.

The adoption of catch-and-release or other conservative fishing regulations may be crucial to allow a numerical response in crayfish predators or competitors. The depensatory mechanisms discussed above are due to the intra-guild predatory (IGP) relationship between crayfish and predatory fish which can produce the possibility of alternate stable states (Mylius et al 2001, Drury and Lodge 2009). We believe that during the phase of initial rusty crayfish invasions in Wisconsin and Michigan 20-30
years ago, many predatory fish populations were suppressed via liberal recreational fishing regulations (Simonson 2001, Noble 2002) which allowed crayfish to reach a high stable density. With the results of our study, in concert with growing knowledge about the impact of more conservative fishing regulations (Barnhart 1989, Schneider & Juetten 1989, Newman & Hoff 2000, Swenson 2002), managers can now more effectively reduce crayfish populations and possibly initiate a regime shift which would result in crayfish remaining at a low level without perpetual harvesting.

The results of our field experiments and harvest simulations show that the double bucket trap with protected bait is the most effective trap for reducing crayfish populations. Experimental results in particular demonstrate that small improvements to current trapping techniques could greatly increase the effectiveness of efforts to control nuisance rusty crayfish populations. By increasing the soak time of traps from one to two days and protecting the bait, the CPUE of trap catches increased by approximately 270%. By protecting the bait from consumption we were able to increase the effective trapping time and produce higher trap catches with half the bait per day and the same labor. It is likely that the increased trap catches in the double bucket trap are a function of greater volume. Although none of the trap types were ever completely full of crayfish, crayfish were often climbing over each other, a situation that a previous study suggests would decrease the rate at which crayfish entered a trap (Ogle and Kret 2008). Further research is needed to determine if even larger traps and longer soak times would further increase crayfish catch. On the basis of current results, however, managers can more wisely choose trapping methods, parameterize our harvest model with population estimates from a given lake and initial trap catches, and estimate the amount of effort needed to reduce a
rusty crayfish population. Once a manager has reduced a crayfish population to a target level, effort can be relaxed to the point where $\lambda=1$. At this effort level the crayfish population should remain relatively constant. We do not suggest trawling as a method for removing crayfish because other methods are more cost effective in reducing population growth rate. Trawling is also restricted to areas without structure and may risk damaging habitat important to fishes and other organisms.

2.6 Acknowledgments

We thank Gary Czypinski from the U.S. Fish and Wildlife Service for his assistance conducting the experimental trawl in Lake Ottawa. We also thank John Pagel and Jerry Edde from the Ottawa National Forest for the assistance in planning and conducting the experimental trawling in Lake Ottawa. Ashley Baldridge and Jody Peters assisted with the construction and testing of crayfish traps. This research was supported by a cost-share agreement with the USDA Forest Service Ottawa National Forest (contract #03-cs-11090700-013), and a graduate fellowship and research support from the Center for Aquatic Conservation and the University of Notre Dame Environmental Research Center.
CHAPTER 3:

POTENTIAL TO MANAGE INVASIVE CRAYFISHES WITH FISHERIES MANAGEMENT

3.1 Abstract

Most crayfishes are native to North America, but several crayfish species have been translocated outside their native ranges within the continent, and are causing substantial ecological impacts. Previous crayfish control efforts which have employed a combination of traps and enhancement of predatory fish species found that the biocontrol efforts have had a larger impact on crayfish population reduction than did trapping. However, no systematic evaluation exists of which predatory fish species are likely to be most effective in controlling crayfishes. Using a quantitative literature review we estimated the diet composition of eight sportfish species. Using a bioenergetics model, parameterized with literature-derived diet data, we estimated the annual mass of crayfish consumed by each fish species at multiple age classes. Lastly, we used species and age specific consumption rates to estimate how the removal and introduction of piscivores affected the community wide consumption of crayfish. Our analysis revealed that the

---

2 This Chapter will be submitted with coauthor David M. Lodge
response of crayfish consumption to increasing fish age is different in different fish species. Smallmouth bass (*Micropterus dolomieu*) consume the most crayfish when young (ages 2-9), while rock bass (*Ambloplites rupestris*) become the best crayfish predators when old (ages 10+). Community wide crayfish consumption decreases with increasing piscivore abundances, indicating that enhancement of piscivore populations, as commonly practiced by fisheries management, may mitigate crayfish control efforts.

Patterns of crayfish consumption between lakes indicate that smallmouth bass and yellow perch (*Perca flavescens*) may prey heavily on crayfish when alternate prey (small fishes) are scarce, making these species most appropriate for controlling crayfish populations that have achieved high abundance. Our analysis also suggests that *Lepomis* spp. and rock bass will be most effective in controlling incipient crayfish invasions (when crayfish populations are not abundant), and may therefore be the best predators to bolster to prevent future crayfish invasions.

### 3.2 Introduction

Fish predation exerts top down control of lower trophic levels in many aquatic ecosystems, and is especially well demonstrated for planktonic communities (Brooks and Dodson 1965, Carpenter et al. 1987, Murdoch and Bence 1987, Borer et al. 2005). However, similar cascading trophic interactions from fish to benthos also occur (Mittelbach 1988, Lodge et al 1994, Borer et al. 2005), and may provide a rarely used management tool. For example, predatory fish abundances are often inversely related to crayfish abundance (Garvey et al. 2003, Wilson et al. 2005, Roth et al. 2007) suggesting
that predatory fish may be capable of suppressing crayfish populations from reaching high abundances. In turn, crayfish abundance is inversely related to the abundance of many benthic plants, algae, and invertebrates (Wilson et al. 2005, Rosenthal et al. 2006).

In many systems, sportfishes are the major predators on crayfish. The species composition (Rahel 2000) and size structure (Schneider & Juetten 1989, Newman & Hoff 2000, Simonson 2001) of these sportfish communities, and hence their effectiveness at controlling prey (including crayfish) populations, have been altered due to stocking, species control programs, and harvest by anglers.

North America is the global epicenter for crayfish biodiversity (Lodge et al. 2000). Most crayfishes are native to North America, but several crayfish species have been translocated outside their native ranges within the continent, and are causing substantial ecological impacts (Lodge et al. 2000). For example, in the Pacific northwest, non-native signal crayfish (*Pasifasticus lenisculus*) threaten the federally endangered shasta crayfish (*Pasifasticus fortis*) (Light et al. 1995). In the upper midwest, rusty crayfish (*Orconectes rusticus*) are extirpating native virile crayfish (*Orconectes virilis*) and causing drastic changes to the ecosystems in which they invade (Olsen et al. 1991, Lodge et al. 1994, Wilson et al. 2004, Rosenthal et al. 2006). In the southwest, virile crayfish and the red swamp crayfish (*Procambarus clarkii*) are invading stream systems and displacing native fishes and reptiles (Gamradt and Kats 1996). In all these regions, concerned stakeholders and managers are eager to develop strategies to eradicate or control invasive crayfish populations.

Existing control strategies for crayfishes generally fall into two categories: 1) manual removal using traps or other capture methods; and 2) biocontrol using predatory
fishes. Previous crayfish control efforts which have employed a combination of traps and enhancement of predatory fish species found that the biocontrol efforts have had a larger impact on crayfish population reduction than did trapping (Rach and Bills 1989, Hein et al 2006). However, no systematic evaluation exists of which predatory fish species are likely to be most effective in controlling crayfishes.

In this paper we evaluate several sportfishes as possible biological control agents. Sportfishes are ideal candidates for biocontrol because they comprise the majority of the predatory fish communities in The United States and Canada, and abundant information exists on their diet, growth and physiological parameters. Furthermore, sportfishes generally have widespread current distributions, largely due to biotic homogenization (Rahel 2000), minimizing the possible motivation for introduction of novel predators (and their associated risks).

Because many species of invasive crayfish exist throughout the US, we designed our study to inform the management of a variety of crayfish species and predatory fishes across the US and Canada. We conducted a quantitative literature review to estimate the diet composition of different fishes, and bioenergetics modeling to estimate the mass of crayfish consumed by different species and ages of fishes, based on previously published species-specific growth data and physiological parameters, and diet compositions from our literature review. To better inform fisheries management, we scaled up per-capita estimates of crayfish consumption to population and community levels using published population and community composition data for fishes from several water bodies.
3.3 Methods

3.3.1 Determining importance of crayfish to diet of different fishes

We conducted a literature search using ISI Web of Knowledge (search terms in Table 3.1) to extract quantitative metrics on fishes’ diets. Each paper was evaluated to determine if it met our three criteria. First, a study had to be conducted in North America. Second, a study had to contain diet composition data (% by mass or volume, or raw data necessary to calculate % by mass or volume) for smallmouth bass (*Micropterus dolomieu*, because they were the most commonly reported species) and at least one other fish species in the same body of water sampled at the same time. This criterion assured that we could compare consumption patterns by different species across lakes relative to a common species. Lastly, crayfish had to be present in the diet of at least one fish species. This criterion assured that only water bodies which contained crayfish were used.

We divided diet composition into three categories--fish, crayfish, and other--to simplify our analysis and also because many studies report diet compositions in these or other broad categories. For each body of water and fish species, we calculated the mean proportion of each prey category. If a study reported species-specific diet compositions for more than one time period, age, or size class of fish, we determined a weighted average for the species based on the number of fish sampled in each time, age, or size class. If data were only presented in graphical form, sample sizes were not reported, or if crayfish were lumped into other prey categories, the authors of the paper were contacted for necessary data. In several instances, the necessary data were obtained from theses,
### TABLE 3.1
SEARCH TERMS USED IN LITERATURE SEARCH

<table>
<thead>
<tr>
<th>Set A</th>
<th>Set B</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Ambloplites</em></td>
<td>Diet</td>
</tr>
<tr>
<td>Bluegill</td>
<td>Consumption</td>
</tr>
<tr>
<td>Crappie</td>
<td>Gut Contents</td>
</tr>
<tr>
<td>Crayfish</td>
<td>Crayfish</td>
</tr>
<tr>
<td><em>Esox</em></td>
<td>Predation</td>
</tr>
<tr>
<td>Fish Community</td>
<td>Overlap</td>
</tr>
<tr>
<td>Largemouth Bass</td>
<td>Partitioning</td>
</tr>
<tr>
<td><em>Lepomis</em></td>
<td></td>
</tr>
<tr>
<td><em>Micropterus</em></td>
<td></td>
</tr>
<tr>
<td>Muskellunge</td>
<td></td>
</tr>
<tr>
<td>Northern Pike</td>
<td></td>
</tr>
<tr>
<td><em>Perca</em></td>
<td></td>
</tr>
<tr>
<td>Piscivore</td>
<td></td>
</tr>
<tr>
<td><em>Pomoxis</em></td>
<td></td>
</tr>
<tr>
<td>Pumpkinseed</td>
<td></td>
</tr>
<tr>
<td>Rock Bass</td>
<td></td>
</tr>
<tr>
<td><em>Sander</em></td>
<td></td>
</tr>
<tr>
<td>Smallmouth Bass</td>
<td></td>
</tr>
<tr>
<td><em>Stizostedion</em></td>
<td></td>
</tr>
<tr>
<td>Walleye</td>
<td></td>
</tr>
<tr>
<td>Yellow Perch</td>
<td></td>
</tr>
</tbody>
</table>

**NOTE:** Searches were conducted for every combination of terms from set A with set B

dissertations, or other journal articles referenced in the original article. If a paper only reported diet compositions in terms of dry weight, we converted dry weight percentages to percent wet weight using the wet to dry mass ratios from Stein and Murphy (1976) for crayfish and from Hanson et al. (1997) for fish and other diet categories. Species-specific diet proportions were estimated using the weighted mean (based on sample size) of all the studies. To investigate inter-water body effects on diet composition, we used linear
regression to test whether crayfish consumption by smallmouth bass was related to crayfish consumption by other fishes in the same water body.

3.3.2 Bioenergetics

We used a bioenergetics model to estimate the annual consumption of crayfish by each species and age class, based on the basic energy balance equation:

\[ \text{Growth} = \text{Consumption} - \text{Metabolism} - \text{Waste} \]

We estimated consumption of the three dietary components (described above) based on growth and diet, which is the most robust use of bioenergetics models (Kitchell et al. 1977, Bartell et al. 1986). As detailed below, we estimated growth with standard von Bertalanffy (1938) models, diet composition from the literature review (as described above), and metabolism and waste from published literature.

We estimated growth of each age class by developing and using von Bertalanffy (1938) growth models for each fish species, which generated initial and ending weights for each year of growth for each species. We parameterized growth models for all species with length-at-age data from water bodies in northern Wisconsin. We focused on one region so that between-species comparisons would not be biased due to regional differences in fish growth (Beamesderfer and North 1995, Quist et al. 2003); we focused on northern Wisconsin specifically because abundant data exist for this region and control of rusty crayfish is an acute problem there. Following the methods of Quist et al. (2003) we estimated von Bertalanffy growth model parameters using non-linear
regression PROC NLIN (SAS 9.2). We used length-at-age estimates from 55 northeastern Wisconsin lakes to parameterize growth models for black crappie (*Pomoxis nigromaculatus*), northern pike (*Esox lucius*), largemouth bass (*Micropterus salmoides*), sunfish (*Lepomis spp.*), rock bass (*Ambloplites rupestris*), walleye (*Sander vitreus*), and yellow perch (*Perca flavescens*) (Snow 1992). Length-at-age estimates from 20 northeastern Wisconsin lakes were used to estimate smallmouth bass parameters (Bennett 1938). Length-at-age was converted to mass-at-age using species-specific length to mass equations from Schneider et al. (2000).

Daily temperatures used in bioenergetics simulations were the average of daily temperatures from Sparkling Lake and Big Muskellunge Lake (Vilas Co. WI) in 1992, 1998, and 2005 (Trout Lake LTER). Linear extrapolation was used to estimate daily temperatures in between reported temperatures. The energy densities (J g\(^{-1}\) wet mass) used for our simulations were 5328, 3766, 4705 for fish, crayfish and other (modeled as invertebrates), respectively (Hein et al. 2006).

We used species-specific physiological parameters from Bevelheimer et al. (1985) for northern pike, Rice et al (1983) for largemouth bass, Kitchell et al.(1974) for *Lepomis* spp. (modeled as bluegill), Roell and Orth (1993) for rock bass, Whitledge et al. (2003) for smallmouth bass, and Kitchell et al. (1977) for both walleye and yellow perch. Physiological parameters were not available for black crappie so following the suggestion of Raborn et al. (2007) we used bluegill parameters for consumption parameters and smallmouth bass parameters for respiration and excretion parameters.

Using the parameter sources described above, we implemented the standard bioenergetics model by developing a MATLAB (version 7.6) program that operates
similarly to Fish Bioenergetics 3.0 (Hanson et al. 1997), but has the added feature of conducting automated iterations to assess the influence of diet variability on overall consumption. Using our MATLAB bioenergetics model, we assessed how the variability in prey consumption due to diet composition affected annual consumption estimates. For each species and age combination, we conducted 100 independent simulations to estimate consumption. For each simulation, the proportion of a species’ diet made up of each prey category was randomly generated from a multinomial distribution parameterized by the mean proportions from the diet literature review. Consumption estimates made from our MATLAB-based bioenergetics model matched those made by Bioenergetics 3.0 (Hanson et al. 1997) in a series of trials with multiple species and ages.

3.3.3 Estimating community-wide crayfish consumption

We scaled per-capita consumption estimates from the bioenergetics model up to community-wide consumption estimates using fish community composition data from previously published literature. To better inform fisheries management, we also modeled the crayfish consumption of fish communities before and after the introduction or removal of piscivores. We used fish abundance and composition data from before (Kempinger et al. 1978) and after (Engel et al. 1999) piscivore removal from Nebish Lake (Vilas Co. WI, USA) to estimate the community-wide crayfish consumption before and after the removal of northern pike and walleye. We used catch per unit effort (CPUE) for bluegill, yellow perch, and largemouth bass to estimate an index of consumption of crayfish before and after the introduction of northern pike in West Long Lake (Cherry Co. NE, USA) (Debates et al. 2003).
For each of these management scenarios, we multiplied the abundance or CPUE of each fish age or size-class by the corresponding per-capita consumption estimate from our bioenergetics simulations to estimate consumption of crayfish. When fish abundances were reported for age or size categories which encompassed more than one age class, we used the age-specific consumption estimate which minimized the effect of the management action on consumption of crayfish, ensuring that our conclusions about the effect of fish community composition on consumption of crayfish were conservative.

3.4 Results

Our initial Web of Science search yielded 3,625 unique papers. Only 12 papers covering a total of 19 water bodies (10 lakes, 7 rivers, and 2 reservoirs) met the criteria for inclusion into our literature review (Table 3.2). The prevalence of crayfish in fish diets differed greatly between fish species (Figure 3.1). Rock bass relied on crayfish most heavily, with 54% of their diet comprised of crayfish. Yellow perch had the next highest dependence on crayfish (40%), followed by smallmouth bass (37%), *Lepomis* spp. (12%), largemouth bass (7%), walleye (5%), black crappie (5%), and northern pike (<1%).
TABLE 3.2
STUDIES AND WATER BODIES THAT WERE INCLUDED IN LITERATURE REVIEW

<table>
<thead>
<tr>
<th>Study</th>
<th>Water Body</th>
<th>State or Province</th>
<th>Species</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fayram et al. 2005</td>
<td>Crab Lake</td>
<td>Wisconsin</td>
<td>LEP, NP, RB, SMB, WAL, YP</td>
</tr>
<tr>
<td>Fayram et al. 2005</td>
<td>Whitefish Lake</td>
<td>Wisconsin</td>
<td>BC, LMB, LEP, NP, RB, SMB, WAL, YP</td>
</tr>
<tr>
<td>Frey et al. 2003</td>
<td>Big Crooked Lake</td>
<td>Wisconsin</td>
<td>RB, SMB, WAL, YP</td>
</tr>
<tr>
<td>Hein et al. 2006</td>
<td>Sparkling Lake</td>
<td>Wisconsin</td>
<td>SMB, RB</td>
</tr>
<tr>
<td>Liao et al. 2002</td>
<td>Spirit Lake</td>
<td>Iowa</td>
<td>BC, LMB, NP, SMB, WAL, YP</td>
</tr>
<tr>
<td>Mayo et al. 1998</td>
<td>Lake Superior (St. Louis River)</td>
<td>Wisconsin and Minnesota</td>
<td>NP, SMB, WAL, YP</td>
</tr>
<tr>
<td>Olson and Young 2003</td>
<td>Canadarago Lake</td>
<td>New York</td>
<td>LMB, SMB</td>
</tr>
<tr>
<td>Olson and Young 2003</td>
<td>Eaton Brook Lake</td>
<td>New York</td>
<td>LMB, SMB</td>
</tr>
<tr>
<td>Olson and Young 2003</td>
<td>Jamesville Reservoir</td>
<td>New York</td>
<td>LMB, SMB</td>
</tr>
<tr>
<td>Olson and Young 2003</td>
<td>Panther Lake</td>
<td>New York</td>
<td>LMB, SMB</td>
</tr>
<tr>
<td>Probst et al. 1984</td>
<td>2 reaches(19 km apart) of Current River</td>
<td>Missouri</td>
<td>SMB, RB</td>
</tr>
<tr>
<td>Probst et al. 1984</td>
<td>2 reaches(23 km apart) of Jacks Fork River</td>
<td>Missouri</td>
<td>SMB, RB</td>
</tr>
<tr>
<td>Raborn et al. 2003</td>
<td>Norris Reservoir</td>
<td>Tennessee</td>
<td>BC, LMB, SMB, WAL</td>
</tr>
<tr>
<td>Roell and Orth 1993</td>
<td>New River</td>
<td>West Virginia</td>
<td>RB, SMB</td>
</tr>
<tr>
<td>Roth and Kitchell 2005</td>
<td>North Turtle Lake</td>
<td>Wisconsin</td>
<td>LEP, RB, SMB, WAL, YP</td>
</tr>
<tr>
<td>Stephenson and Momot 1991</td>
<td>Kaministiqiuia River</td>
<td>Ontario</td>
<td>NP, SMB</td>
</tr>
<tr>
<td>Zimmerman 1999</td>
<td>Columbia River</td>
<td>Oregon and Washington</td>
<td>SMB, WAL</td>
</tr>
</tbody>
</table>

NOTE: BC= black crappie, LEP= *Lepomis* spp., LMB= largemouth bass, NP= northern pike, RB=rock bass, SMB = smallmouth bass, WAL= walleye, YP= yellow perch
3.4.1 Patterns of consumption by different fishes across lakes

The proportional contribution of crayfish to the diets of walleye (Figure 3.2f) and yellow perch (Figure 3.2g) was positively related to proportional contribution of crayfish to the diet of smallmouth bass, while that of *Lepomis* spp. (Figure 2b) was negatively related to the proportional contribution of crayfish to the diet of smallmouth. No other species showed a significant ($\alpha=0.05$) relationship with smallmouth bass diet (Figure 3.2). These relationships are not incorporated explicitly in our bioenergetics analyses, but we return to them in the Discussion to inform management considerations.
Figure 3.2: Intra-water body comparisons of dependence (proportion of diet) on crayfish by several fishes (y-axis) compared to smallmouth bass dependence on crayfish (x-axis). Linear regression was used to test the null hypothesis of $\beta=0$. 
3.4.2 Bioenergetics analysis

On a per capita basis, smallmouth bass consume more crayfish than any other species when considering ages <9, and rock bass consume the most crayfish when considering ages >10 (Figure 3.3). Yellow perch consume the next most crayfish for all age categories (Figure 3.3). For walleye and largemouth bass, the uncertainty bounds for all ages overlap, and they consume less than yellow perch at all ages. All ages of black crappie, *Lepomis* spp. and northern pike consumed few crayfish, and these three species did not differ statistically from each other. With the exception of smallmouth bass, estimated crayfish consumption increased monotonically with age. The bioenergetics analysis indicated that overall consumption (and hence crayfish consumption) by smallmouth bass stabilized with respect to size because mass-specific respiration decreases allometrically with body mass more for smallmouth bass than for other fishes.

3.4.3 Consumption of crayfish by the fish community

Prior to a piscivore removal in 1966, Nebish Lake had abundant walleye and northern pike populations. After the removal of both species, the lake’s sportfish community consisted of only smallmouth bass and yellow perch. Based on species and age specific population estimates from pre-removal (Kempinger et al. 1978) and post-removal (Engel et al. 1999) data, we estimated that consumption of crayfish by the Nebish Lake fish community increased 242% after the removal of the walleye and northern pike (Table 3.3).
TABLE 3.3

EFFECT OF PISCIVORE REMOVAL OR ADDITION ON POPULATION AND COMMUNITY-WIDE CRAYFISH CONSUMPTION

<table>
<thead>
<tr>
<th></th>
<th>Crayfish Consumption</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Before</td>
</tr>
<tr>
<td>1. Piscivore Removal, Nebish Lake</td>
<td></td>
</tr>
<tr>
<td>Smallmouth bass</td>
<td>119721</td>
</tr>
<tr>
<td>Yellow Perch</td>
<td>95591</td>
</tr>
<tr>
<td>Northern pike</td>
<td>12162</td>
</tr>
<tr>
<td>Walleye</td>
<td>107612</td>
</tr>
<tr>
<td>Rock bass</td>
<td>171806</td>
</tr>
<tr>
<td><em>Lepomis</em> spp.</td>
<td>125739</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td>632631</td>
</tr>
</tbody>
</table>

2. Northern Pike Introduction, West Long Lake                    |             |             |            |
| Bluegill                                                       | 959         | 122         | -87        |
| Largemouth bass                                                | 8257        | 5684        | -31        |
| Yellow perch                                                   | 2624        | 654         | -75        |
| **Total**                                                      | 11840       | 6459        | -45        |

NOTE: Crayfish consumption is in units of grams of crayfish per year for Nebish lake and cpue*grams of crayfish per fish per year for west long lake
In West Long Lake, bluegill, largemouth bass, and yellow perch declined in response to the introduction of northern pike (Debates et al. 2003). Based on species and age specific CPUE data from pre-introduction and post-introduction, we estimated that consumption of crayfish by the West Long Lake fish community decreased by 45% (not including consumption by northern pike) after the introduction of northern pike (Table 3.3). Because we could not estimate consumption by northern pike (due to a lack of comparable data), we may have slightly overestimated this reduction.
3.5 Discussion

Our results provide the first general comparison of consumption of crayfish by different fish species in the same water body, revealing large differences between species and ages of fishes. The patterns between species of fish revealed by our analyses are probably relevant to a wide range of freshwater systems because of the geographically broad, quantitative approach we took to parameterizing the diet composition portion of our bioenergetics model. As discussed below, we believe that our simulations of the impact of past management “experiments” on fishes’ consumption of crayfish provide useful guidance for future attempts to use fisheries management to prevent or control invasions by harmful crayfishes.

Stocking of piscivores for population supplementation and population establishment has been prevalent throughout the United States (Fenton et al. 1996) and can cause dramatic changes in fish community composition, but the impact of these fisheries management actions on crayfish invasions has not been carefully evaluated. For example, the introduction of piscivores can result in decreases in the abundance of smallmouth bass which prey heavily on crayfish (Johnson and Hale 1977, Kempinger and Carline 1977). When we modeled the predatory demand for crayfish in two lakes which had dramatic changes in the piscivore community, we found that in both cases the overall predatory demand for crayfish was greater when there were fewer highly piscivorous fish (walleye and northern pike) in the lakes (Table 3.3).
Previous literature shows that smallmouth bass and rock bass have considerable diet overlap and that both species rely heavily on crayfish as prey (Probst et al. 1984). We expected that reliance on crayfish by both species would be positively correlated and driven by crayfish abundance. Contrary to our expectations, consumption of crayfish by smallmouth bass was unrelated to that of rock bass (Figure 3.2e). The lack of a relationship suggests that these species do not respond similarly to changing prey availability. We hypothesize that the abundance of alternate prey (i.e. not crayfish) drives the diet composition of smallmouth bass. Smallmouth bass are opportunistic generalists and will feed heavily on both small fishes and crayfish, with crayfish having a higher handling time to weight ratio than prey fishes of several morphological categories (Hoyle and Keast 1987). Because of their exoskeleton, crayfish also have lower energy density than prey fishes (Hein et al. 2006). Optimal foraging theory predicts that the combination of these two factors would lead smallmouth bass to prey preferentially on fish over crayfish when possible. This prediction was confirmed by Pflug and Pauley (1984) who found that smallmouth bass preyed heavily on juvenile salmonids and less on crayfish when the salmonids were abundant after hatchery release, and by Carter et al. (2010) who found smallmouth bass negatively selected for crayfish when presented with two other prey fishes. Thus we now hypothesize that smallmouth bass feed heavily on crayfish only when small fishes are not abundant. We were not surprised that walleye and yellow perch dependence on crayfish was positively related to smallmouth bass dependence (Figures 3.2f&g) because both walleye and yellow perch, like smallmouth bass, prefer fish as prey.
We could find no studies on rock bass diet preference, but we hypothesize that rock bass do not prey preferentially on fish because they are not proficient at capturing fish (Keast and Webb 1945). In contrast, rock bass seem to be benthic specialists and probably prefer insect larvae because of high energy content and low handling time relative to fishes.

We were initially surprised to find a negative relationship between *Lepomis* spp. and smallmouth bass dependence on crayfish (Figure 3.2b). Although we interpret this pattern with caution given the low sample size (Figure 3.2b), it is consistent with what we know about the response of these fishes to other dietary categories. Adult bluegills are predators of both littoral zone macroinvertebrates and pelagic zooplankton (Mittelbach 1984). In water bodies with high abundance of small fishes (i.e. where smallmouth bass would consume few crayfish), *Lepomis* spp. may feed primarily in the littoral zone and consequently consume more crayfish due to high competition for zooplankton in the pelagic zone. Also, *Lepomis* spp. change their habitat use to avoid predators (Werner et al. 1983), so they may forage more in the littoral zone near predation refugia when predators are feeding heavily on pelagic fish. We acknowledge that a linear relationship may not best describe the relationship between crayfish consumption by smallmouth bass and other species (Figure 3.2). We used linear regression to estimate the general relationship (positive, negative or none) between species. Although samples size was low for many of these comparisons, the general trends we found agree with previously published studies regarding diet selection by these fishes.

These differences in prey selection by fish species can cause important feedbacks in respect to controlling or reducing invasive crayfish populations. When crayfish reach
high densities, they drastically alter ecosystems by reducing macrophytes (Lodge et al. 1994, Rosenthal et al. 2006), macroinvertebrates (Olsen et al. 1991, Lodge et al. 1994, Wilson et al. 2004, Rosenthal et al. 2006), and fish (Garvey 2003, Wilson et al. 2004, Roth et al. 2007). A stable isotope study by Kreps (2009) found that walleye switched prey base from littoral prey (presumably fish) to benthic prey when crayfish populations reach high levels, suggesting that small fishes are reduced due to crayfish invasions. The negative relationship between crayfish, macroinvertebrates and small fishes could create feedback mechanisms which could enhance or diminish the effectiveness of fishes in controlling crayfish populations. Water bodies with high densities of crayfish will likely not have abundant small fishes or macroinvertebrates (Olsen et al. 1991, Lodge et al. 1994, Roth et al. 2007). We believe that this will cause species such as smallmouth bass, rock bass, and yellow perch to prey heavily on crayfish because their preferred prey (fishes, macroinvertebrates, and fishes, respectively) are scarce. These species may be an important part of an initial effort to reduce abundant crayfish populations when preferred food sources are scarce. As crayfish are reduced, and the ecosystem responds with more available small fish and macroinvertebrates, we believe that these species will decrease their predation on crayfish and become less important as a control mechanism on nuisance crayfish. Diet shifts may thus create a compensatory mechanism (in regard to the crayfish population) which will limit the long term ability of these fish species to control crayfish populations at low density. This feedback will likely be stronger in rock bass since macroinvertebrate populations should recover faster than fish populations. This suggests that smallmouth bass and yellow perch will be the most effective predator
species for decreasing existing high density crayfish populations that have already caused reductions in other ecosystem components.

In an uninvaded water body, managers may find it more cost effective to focus on different fisheries management goals to prevent an invasion (Leung et al. 2002, Keller et al. 2007, 2008). In addition to managing for the prevention of introduction of crayfish, managers could foster a strong first line of predatory defense in case a crayfish introduction does occur. Our results suggest that this might include predators such as *Lepomis* spp., which will readily consume crayfish even when other potential prey are abundant, and rock bass, which will consume crayfish increasingly as macroinvertebrates decline in the face of increasing crayfish abundance. Depletion of macroinvertebrates is the first impact of crayfish invasions, because these organisms are crayfish’s preferred prey (Lodge et al. 1994).

Although smallmouth bass and yellow perch consume many crayfish, we do not believe either species are likely to be effective in maintaining crayfish at low densities, because more preferred prey are available when crayfish are at low abundance. Rather we believe that the loss of forage fishes is necessary for smallmouth bass and yellow perch to switch to preying heavily on crayfish. At that point, the recruitment of smallmouth bass and yellow perch themselves could be impacted by crayfish directly through destruction of habitat and competition. If the feedback from high crayfish abundance to poor smallmouth bass and yellow perch recruitment is strong, these fishes may not be able to suppress crayfish abundance. Ideally, we would like to combine the functional responses (Holling 1959) of each fish with the numerical response to estimate
an overall, community wide predatory response of fish populations to changing crayfish abundance.

If we are correct that rock bass abundance might be important in preventing outbreaks in abundance of invasive crayfish once a crayfish population is established, then it may be important for fisheries managers to consider the management of rock bass. In Wisconsin, for example, the harvest of rock bass is currently not regulated (WI DNR 2009), and in Michigan it is liberally regulated (no closed season, no minimum size limit, and 25 fish creel limit) (MI DNR 2009). In addition to liberal harvest regulations, many Michigan and Wisconsin anglers consider rock bass a “rough fish” and kill all rock bass even if they do not creel them (B. Peters, personal observation). Therefore, if fostering large rock bass populations was a management goal, a public outreach campaign might be necessary to inform anglers about the potential benefits of rock bass in controlling harmful crayfish. Likewise if suppressing nuisance crayfish populations is a management goal, and if smallmouth bass and yellow perch abundance is important in suppressing crayfish, managers may need to reconsider widespread and frequent walleye stocking programs because walleye consume few crayfish and often reduce populations of fishes that prey heavily on crayfish. Walleye abundance is one of the strongest predictors for whether a northern Wisconsin lake would be invaded by rusty crayfish (Keller et al. 2008). The widespread introduction of walleye, coupled with previously lax regulations on smallmouth bass harvest, may therefore have aided the invasion of rusty crayfish throughout the northern lakes regions of the upper Midwest.

Although we did not explicitly model the effects of harvest regulations on crayfish consumption, our analyses may have implications for fisheries management.
when crayfish control is a goal. In both Wisconsin and Michigan, no-kill and 18-inch minimum harvest length regulations for smallmouth bass have been motivated by a desire to reduce invasive rusty crayfish populations (B. Peters, personal observation). These regulations are designed to increase the abundance of large smallmouth bass, but can also have the effect of slowing growth rates, and reducing recruitment of fish to intermediate size classes due to increased competition with larger fish. Due to the rapid increase in crayfish consumption with increasing age (Figure 3.3), smallmouth bass age 4 to 6 (11 to 14 inches) consume nearly as many crayfish as older fish. A protected slot limit (Anderson 1980) of 11-14 inches may be more effective in increasing predation on crayfish because it protects intermediate age classes which prey heavily on crayfish. Slot limits also increase growth rates and recruitment into the protected slot by allowing harvest of fish smaller than the protected slot, and allows harvest of large fish (> 14 inches) which can increase angler satisfaction.

The best management plan for a particular water body is informed by the values of anglers and other stakeholders, and much more local knowledge of regional fisheries managers than is reflected in our analyses. If prevention and/or control of crayfish invasions are among the management goals, our analyses provide managers with a species- and age-specific index of crayfish consumption. These indices will be valuable to managers because empirically estimating species-specific diet and growth of multiple species of fishes in even one water body is very costly. A fisheries manager can instead use our analyses in conjunction with their knowledge of how local fish communities may respond to various management options to promote the fish community that is most likely to prevent or control invasive crayfish.
3.6 Acknowledgments

Kevin Drury and Chris Jerde both provided quantitative assistance. This research was supported by a cost-share agreement with the USDA Forest Service Ottawa National Forest (contract #03-cs-11090700-013), and a graduate fellowship and research support from the Center for Aquatic Conservation and the University of Notre Dame Environmental Research Center.
CHAPTER 4:
CONCLUSION

As the human population and global commerce increase the threat of invasive species will also increase unless improved management of species introductions and impact are instituted. Due to the reactive nature of our society’s response to invasive species, it is likely that many species will become introduced and action will have to be taken to control newly established species and reduce abundant populations (Mack et al. 2000). Crayfish are one taxon with many introduced species that require an integrated approach to control their populations. Crayfish can be controlled using chemical toxicants, but to date no chemical has been found that selectively targets only crayfish (Ray and Stevens 1970, Bills and Marking 1988). Therefore, manual removal and biocontrol are the most promising current strategies for controlling crayfish populations. Developing effective removal and biocontrol programs requires an understanding of crayfish population and community ecology.

My research has shown that minor adjustments are needed to greatly improve manual removal techniques. However, even the most effective removal method we considered still requires a large number of person-hours to implement at the scale necessary to reduce populations of crayfish in most lakes. Future research could improve
upon my trap designs and make control efforts more feasible. Research into crayfish response to chemical compounds could result in identification and synthesis of chemical attractants which are less expensive than current baits and could be delivered in traps in a continuous manner thereby eliminating the need to re-bait traps. Advances in baiting technology will have to be accompanied by advances in trap design to accommodate more crayfish and minimize aggressive interactions which deter uncaptured crayfish from entering traps (Ogle and Kret 2008).

For crayfish control to be most effective, manual removal needs to be combined with biocontrol. My research in chapter 3 illustrates the importance of considering total consumption rather than the traditional assessment of proportional contribution to a diet (Dorn and Mittelbach 1999) when determining the optimal predator for a biocontrol program. Furthermore, I show that common fisheries management practices often decrease the predatory demand for crayfish by the whole fish community within a water body. The optimal fish predator may not be the same in all situations; rather complex interactions among crayfish, macrophytes, macroinvertebrates, zooplankton and fish create feedback mechanisms, which based on initial conditions (crayfish population size), change which fish species is likely to be most effective for biocontrol. As discussed in chapter 3, smallmouth bass and yellow perch will be the most effective biocontrol agents when a manager wishes to reduce the population of an existing abundant crayfish population because they will depend most heavily on crayfish when small fishes are scarce. On the other hand, rock bass and Lepomis spp. are likely to be ideal fishes for preventing a newly established crayfish population from multiplying and causing widespread ecosystem impacts. My results and previous literature suggests that Lepomis
spp. will prey heavily on crayfish when small fishes are abundant and competition for zooplankton is high. Rock bass on the other hand prefer macroinvertebrates and crayfish, but will switch to a diet of mainly crayfish when macroinvertebrates become reduced due to an increasing crayfish population, creating a compensatory mechanism which may prevent an outbreak of crayfish. Similar compensatory mechanisms likely occur with smallmouth bass and yellow perch but these species will switch to consuming crayfish after small fish are depleted (an impact that occurs at higher crayfish densities and longer lag times compared to macroinvertebrate reductions).

Previous authors have noted the inverse relationship between *Lepomis* spp. and crayfish, which they attribute to endogenous feedbacks between crayfish removal of *Lepomis* spp. habitat resulting in a decrease of *Lepomis* spp. abundance and a concurrent reduction in *Lepomis* spp. predation pressure on crayfish (Roth et al. 2007). The combination of these mechanisms creates feedbacks which can produce two stable configurations of high crayfish-low *Lepomis* spp. and low crayfish-high *Lepomis* spp. My results add an additional mechanism influencing the overall strength of depensation between crayfish and *Lepomis* spp. populations.

Depensatory population level mechanisms may also exist between predators such as smallmouth bass and crayfish due to intraguild predation (Drury and Lodge 2009). The mechanisms I found through my literature review which are related to dietary response must be integrated with other mechanisms to determine the overall relationship between fish predators and crayfish to determine which fish species is best for controlling crayfish populations and the ideal size structure and population size of the fish population. Future research should focus on estimating competition and predation
parameters between crayfish and fish to better understand how fish populations will respond numerically to changing crayfish populations. Also, the mechanisms that I hypothesize will drive diet shifts in fishes should also be tested experimentally.

To effectively manage invasive crayfish populations we must develop cost effective removal tools and enhance populations of predatory fish as biocontrol agents. In addition to the development of new management tools we must also learn more about the community and population ecology of crayfish. With this ecological knowledge managers will be able to better design removal tools and predatory fish communities to take advantage of important endogenous feedbacks which can work synergistically with management actions towards the goals.
LITERATURE CITED


