A Multi-Faceted Approach to Understanding Drivers and Consequences of Aquatic Invasive Species Impacts

By

Gretchen Jeanette Anderson Hansen

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The dissertation is approved by the following members of the Final Oral Committee:

M. Jake Vander Zanden, Professor, Zoology

Stephen R. Carpenter, Professor, Zoology

Peter B. McIntyre, Assistant Professor, Zoology

Anthony R. Ives, Professor, Zoology

James F. Kitchell, Professor Emeritus, Zoology

John D. Lyons, Research Scientist, Wisconsin Department of Natural Resources

I dedicate this work to Ada and Jon. Together you are the light of my life.

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Introduction

Invasive species have caused extinctions and extirpations of native species, altered communities and ecosystems, and cost billions to trillions of dollars annually in damages and control costs (Lodge 1993; Vitousek *et al.* 1996; Pimentel *et al.* 2000; Sala *et al.* 2000; Pimentel *et al.* 2005). Freshwater ecosystems are particularly threatened by increasing numbers of invasive species (Moyle & Light 1996; Ricciardi & MacIsaac 2000; Sala *et al.* 2000). Understanding factors regulating the impact of invasive species is a topic of great interest for conservation and management of ecosystems (Lodge *et al.* 1998; Levine *et al.* 2003). Invasive species can influence all levels of ecological organization, from individual organisms to entire ecosystems (Parker *et al.* 1999; Simon & Townsend 2003). Vitousek (1990) proposed that invasive species alter invaded ecosystems when they differ from natives in resource acquisition, alter the trophic structure of invaded communities, or change the frequency or intensity of disturbance. Within these broad and likely oversimplified categories (Davis 2009), there exist many possible mechanisms through which invasive species can act on invaded ecosystems. For example, an invasive species can alter the trophic structure of invaded communities via predation (e.g., Ogutu-Ohwayo 1990), competition (e.g., Vander Zanden et al. 1999), or by altering energy pathways through food webs by serving as a novel prey item (e.g., Steinhart et al. 2004). Unfortunately, the mechanisms underlying the impacts of most invasive species are generally poorly understood (Levine et al. 2003). Invasive species that act upon invaded ecosystems via multiple mechanisms are likely to cause the greatest impacts (Didham et al.

2007), although studies examining the impacts of invasive species on multiple levels of ecological organization are rare (Simon & Townsend 2003).

In this dissertation, I examine invasive species and their impacts on a variety of scales, from landscape level patterns of 10 different invasive species to community interactions among invasive and native littoral species to population dynamics of a single population of rusty crayfish in a single lake. Major themes include variation in invasive species densities and impacts, indirect effects of invasive species, and whole-ecosystem manipulation to understand food web interactions. Although the majority of my research focuses on rusty crayfish (*Orconectes rusticus*) in particular, this research provides insight into the importance of direct and indirect effects of invasive species in general, as well as highlights the importance of using whole-system context for understanding ecosystem disturbances and food web variation.

Despite the drastic impacts of some, the majority of non-native species do not cause detectable adverse effects (Moyle & Light 1996; Williamson & Fitter 1996). As a result, researchers have attempted to identify predictors of invasion success and impact, both in terms of species most likely to be invasive (Rejmanek & Richardson 1996; Ricciardi & Rasmussen 1998; Kolar & Lodge 2001, 2002; Kolar 2004; Marchetti *et al.* 2004) and locations most likely to be adversely affected by invasion (e.g., Buchan & Padilla 2000; Allen & Ramcharan 2001; Vander Zanden *et al.* 2004; Mercado-Silva *et al.* 2006). These studies are predicated on the assumption that invasive species exhibit characteristics that are distinct from species in general, and the majority of focus on the presence-absence of an invader and assume (often implicitly) that the impacts of a given invader are similar in all invaded sites. While these studies represent important progress in directing prevention efforts, they tend to ignore variation in impacts among sites. The impact of a given invasive species depends in part on the density of the species (Parker *et al.* 1999; Thiele *et al.* 2009). Thus, if the population density of a given invasive species varies across landscapes, its impacts are likely to vary as well.

There exists a long history of research on species abundance distributions, and the distribution of abundance *within* a species follows a skewed distribution: a given species is rare in most locations and highly abundant in a few locations (Andrewartha & Birch 1954; Brown *et al.* 1995; Brown *et al.* 1996). In **Chapter 1**, I test whether aquatic invasive species from a variety of taxonomic groups follow distributional patterns that are distinct from the distributions of native species. Such a comparison is valuable from both a basic ecology and an applied perspective. Species abundance distributions are one of the most consistent macroecological patterns, and identifying groups of species that differ in their distributional patterns can provide insight into the mechanisms generating them (Brown 1999; Gaston 1999; McGill *et al.* 2007). Furthermore, an understanding of variation in invasive species abundance patterns could increase the efficacy of future management efforts aimed at preventing invasive species from reaching areas where their impacts are likely to be highest.

Chapters 2-4 focus on invasive rusty crayfish in north temperate lakes. Rusty crayfish are invasive throughout much of North America (Hobbs et al. 1989), and their impacts have been documented at organismal, population, community, and ecosystem levels. Native virile crayfish

(*Orconectes virilis*) become more aggressive and grow faster in lakes containing rusty crayfish (Hayes et al. 2009). Rusty crayfish compete with native crayfish for shelter, thereby increasing predation on native crayfishes (Capelli 1982; Capelli & Munjal 1982). Rusty crayfish reduce invertebrate population densities, particularly gastropods, as a result of predation and competition (Olsen *et al.* 1991; Lodge *et al.* 1994). One of the most significant ways in which invasive species can affect ecosystems is by altering physical attributes of the system, thereby acting as ecosystem engineers (Crooks 2002). When rusty crayfish are abundant, they remove aquatic macrophytes (Magnuson *et al.* 1975; Olsen *et al.* 1991; Lodge *et al.* 1994; Rosenthal *et al.* 2006). This reduction in macrophytes affects native fishes and macroinvertebrates that use macrophytes as a refuge from predation and as a food source (Magnuson *et al.* 1975; Crowder & Cooper 1982). Contrastingly, invasive species can provide a benefit to native species via trophic subsidy, competitive release, or predatory release (Rodriguez 2006). Rusty crayfish are an important food source for native fishes including smallmouth bass (*Micropterus dolomieu*), rock bass (*Ambloplites rupestris*), and sunfishes (Lepomis spp.; Hein *et al.* 2006; Roth *et al.* 2007). By serving as a prey item for these fishes, rusty crayfish may influence their growth rates, as well as release other prey of these species from predation pressure.

I examine rusty crayfish as both passengers and drivers of change in aquatic ecosystems, as illuminated by the experimental removal of rusty crayfish from a north temperate lake. Factors controlling the impacts of invasive species are not well understood, even under constant climate conditions (e.g., Lodge et al. 1998). Rusty crayfish can affect all levels of aquatic food webs; however, at low densities their effects are minimal (Garvey *et al.* 2003; Roth *et al.* 2007).

Rusty crayfish populations may be constrained by both predation and habitat (Hill *et al.* 1993; Lodge & Hill 1994; Garvey *et al.* 2003), and the area of preferred crayfish habitat (cobble) is directly correlated with water level in certain types of seepage lakes where cobble is located within shallow depth contours. Climate projections predict that milder winters and reduced summer precipitation will lower lake levels in the Midwestern United States (Karl 2009). Water levels in seepage lakes in this region are highly affected by drought conditions (Webster et al. 1996), and water levels in north temperate seepage lakes have declined to the lowest levels on record (http://lter.limnology.wisc.edu). These declines in water level could substantially reduce available habitat for rusty crayfish, potentially shifting a lake from one capable of supporting high crayfish densities to one where densities are likely to remain low. In **Chapter 2**, I quantify the relationship between rusty crayfish, water level, *Lepomis*, and other fish predators in two northern lakes that differ in both their response to reduced precipitation and their management history with regards to rusty crayfish. I use multispecies autoregressive models, which are designed to partition drivers of change within complex communities (Ives et al. 2003), to evaluate the effects of predation, trapping, and water level fluctuations on rusty crayfish abundance, while simultaneously evaluating the effects of rusty crayfish on littoral fishes. This model allows identification of conditions that enhance or suppress rusty crayfish abundance and how these might be affected by changing climactic conditions.

Understanding food webs and their multitude of complex interactions is a central goal of ecology. The dynamics of food webs are governed by both biotic (e.g., predator-prey interactions, behavior) and abiotic (e.g., nutrient availability, physical disturbance) processes, and the relative role of each is the subject of extensive debate (e.g., Hairston *et al.* 1960; Paine 1980; Carpenter *et al.* 1987; Pimm *et al.* 1991; Hunter & Price 1992; Power 1992; Polis & Strong 1996). Experimental additions or removals of species have been used to evaluate the role of biotic factors in governing community structure (e.g., Pimm 1980; Sih *et al.* 1985; Carpenter & Kitchell 1988). In this sense, species invasions and removal of established invaders serve as manipulations that can be used to better understand food web dynamics. Rusty crayfish simultaneously exert both positive and negative pressures on native species, and the magnitude and direction of interactions vary with ontogenetic stage of both crayfish and the groups with which they interact. Due to the multitude of interactions between rusty crayfish and invaded ecosystems, predicting their impacts in a whole ecosystem context is difficult. Attempts to break this system down into component parts can provide insights into direct interactions; however, small-scale studies may obscure indirect effects, which are often overlooked but can be important in determining the overall impact of an invasive species (White et al. 2006). To understand both direct and indirect effects of rusty crayfish, a whole system approach is needed.

Rusty crayfish were removed from Sparkling Lake, Wisconsin from 2001-2008, and monitoring of crayfish and other ecosystem parameters continued through 2011. Eradication efforts can produce unexpected results in terms of community dynamics and ecosystem properties, particularly when an invader has been established for long time periods, exhibits strong interactions with other species, or alters physical properties of an ecosystem (Zavaleta et al. 2001). In such cases, invasive species must be viewed in an ecosystem context, particularly when evaluating the effects of an invasive species removal. In **Chapter 3**, I quantify the population and ecosystem-level effects of the removal of the rusty crayfish from Sparkling Lake, with an emphasis on the benthic macroinvertebrate response and how it is influenced by rusty crayfish both directly and indirectly. This chapter provides a unique case study documenting the littoral community response to the removal of a strongly interacting invasive species that had been established for more than two decades. I also use the population dynamics of rusty crayfish at low densities to infer the likelihood of maintained low densities of rusty crayfish following the cessation of trapping. In **Chapter 4**, I use a qualitative food web modeling approach (Levins 1974; Dambacher *et al.* 2002, 2003) to identify interactions between littoral community members that are most important in determining the community response to the rusty crayfish removal, and how these interactions vary among littoral habitat types. Understanding spatial variation in food web structure is an important research need (Holt 1996; Winemiller 1996), and identifying community interactions and how they differ in invaded systems can shed insight into the differential effects of invasive species in systems composed of similar species.

Literature Cited

Allen Y.C. & Ramcharan C.W. (2001) Dreissena distribution in commercial waterways of the US: using failed invasions to identify limiting factors. *Can. J. Fish. Aquat. Sci.*, 58, 898-907

Andrewartha H.G. & Birch L.C. (1954) *The Distribution and Abundance of Animals.* The University of Chicago Press, Chicago, IL.

Brown J.H. (1999) Macroecology: Progress and Prospect. *Oikos*, 87, 3-14

Brown J.H., Mehlman D.W. & Stevens G.C. (1995) Spatial Variation in Abundance. *Ecology*, 76, 2028-2043

Brown J.H., Stevens G.C. & Kaufman D.M. (1996) The Geographic Range: Size, Shape, Boundaries, and Internal Structure. *Annual Review of Ecology and Systematics*, 27, 597-623

Buchan L.A. & Padilla D.K. (2000) Predicting the likelihood of Eurasian watermilfoil presence in lakes, a macrophyte monitoring tool. *Ecol. App.*, 10, 1442-1455

Capelli G.M. (1982) Displacement of Northern Wisconsin Crayfish by *Orconectes rusticus* (Girard). *Limnol. Oceanogr.*, 27, 741-745

Capelli G.M. & Munjal B.L. (1982) Aggressive interactions and resource competition in relation to species displacement among crayfish of the genus Orconectes. *J. Crustacean Biol.*, 2, 486-492

Carpenter S.R. & Kitchell J.F. (1988) Consumer control of lake productivity. *Bioscience*, 38, 764-769

Carpenter S.R., Kitchell J.F., Hodgson J.R., Cochran P.A., Elser J.J., Elser M.M., Lodge D.M., Kretchmer D., He X. & Ende C.N.v. (1987) Regulation of Lake Primary Productivity by Food Web Structure. *Ecology*, 68, 1863-1876

Crooks J.A. (2002) Characterizing ecosystem-level consequences of biological invasions: the role of ecosystem engineers. *Oikos*, 97, 153-166

Crowder L.B. & Cooper W.E. (1982) Habitat Structural Complexity and the Interaction Between Bluegills and Their Prey. *Ecology*, 63, 1802-1813

Dambacher J.M., Li H.W. & Rossignol P.A. (2002) Relevance of community structure in assessing indeterminacy of ecologcial predictions. *Ecology*, 83, 1372-1385

Dambacher J.M., Li H.W. & Rossignol P.A. (2003) Qualitative predictions in model ecosystems. *Ecol. Model.*, 161, 79-93

Davis M.A. (2009) *Invasion Biology.* Oxford University Press, New York.

Didham R.K., Tylianakis J.M., Gemmell N.J., Rand T.A. & Ewers R.M. (2007) Interactive effects of habitat modification and species invasion on native species decline. *Trends Ecol. Evol.*, 22, 489-496

Garvey J.E., Rettig J.E., Stein R.A., Lodge D.M. & Klosiewski S.P. (2003) Scale-dependent associations among fish predation, littoral habitat, and distributions of crayfish species. *Ecology*, 84, 3339-3348

Gaston K.J. (1999) Implications of Interspecific and Intraspecific Abundance-Occupancy Relationships. *Oikos*, 86, 195-207

Hairston N.G., Smith F.E. & Slobodkin L.B. (1960) Community Structure, Population Control, and Competition. *American Naturalist*, 94, 421-425

Hayes N.M., Butkas K.J., Olden J.D. & Vander Zanden M.J. (2009) Behavioural and growth differences between experienced and naive populations of a native crayfish in the presence of invasive rusty crayfish. *Freshwater Biol.*, 54, 1876-1887

Hein C.L., Roth B.M., Ives A.R. & Vander Zanden M.J. (2006) Fish predation and trapping for rusty crayfish (Orconectes rusticus) control: a whole-lake experiment. *Can. J. Fish. Aquat. Sci.*, 63, 383–393

Hill A.M., Sinars D.M. & Lodge D.M. (1993) Invasion of an occupied niche by the crayfish Orconectes rusticus: potential importance of growth and mortality. *Oecologia*, 94, 303-306

Hobbs H.H., Jass J.P. & Huner J.V. (1989) A Review of Global Crayfish Introductions With Particular Emphasis On Two North American Species (Decapoda, Cambaridae). *Crustaceana*, 56, 299

Holt R.D. (1996) Food Webs in Space: An Island Biogeographic Perspective. In: *Food Webs: Integration of Patterns and Dynamics*, pp. 313-323. Chapman & Hall Press, New York

Hunter M.D. & Price P.W. (1992) Playing chutes and ladders: heterogeneity and the relative roles of bottom-up and top-down forces in natural communities. *Ecology*, 73, 723-732

Ives A.R., Dennis B., Cottingham K.L. & Carpenter S.R. (2003) Estimating community stability and ecological interactions from time-series data. *Ecol. Monogr.*, 73, 301–330

Karl T.R.M., J. M.; Peterson, T. C. (2009) *Global Climate Change Impacts in the United States*. Cambridge University Press. Available online at www.globalchange.gov/usimpacts.

Kolar C. (2004) Risk assessment and screening for potentially invasive fishes. *New Zealand Journal of Marine and Freshwater Research*, 38, 391-397

Kolar C.S. & Lodge D.M. (2001) Progress in invasion biology: predicting invaders. *Trends Ecol. Evol.*, 16, 199-204

Kolar C.S. & Lodge D.M. (2002) Ecological predictions and risk assessment for alien fishes in North America. *Science*, 298, 1233-1236

Levine J.M., Vilà M., Antonio C.M.D., Dukes J.S., Grigulis K. & Lavorel S. (2003) Mechanisms underlying the impacts of exotic plant invasions. *Proc. R. Soc. Lond. B. Biol. Sci.*, 270, 775-781

Levins R. (1974) The qualitative analysis of partially specified systems. *Ann. N. Y. Acad. Sci.*, 231, 123-138

Lodge D.M. (1993) Biological invasions: lessons for ecology. *Trends Ecol. Evol.*, 8, 133-137

Lodge D.M. & Hill A.M. (1994) Factors governing species composition, population size, and productivity of cool-water crayfishes. *Nord. J. Freshw. Res.*, 69, 111-136

Lodge D.M., Kershner M.W., Aloi J.E. & Covich A.P. (1994) Effects of an omnivorous crayfish (Orconectes rusticus) on a freshwater littoral food web. *Ecology*, 75, 1265–1281

Lodge D.M., Stein R.A., Brown K.M., Covich A.P., Brönmark C., Garvey J.E. & Klosiewski S.P. (1998) Predicting impact of freshwater exotic species on native biodiversity: challenges in spatial scaling. *Aust. J. Ecol.*, 23, 53–67

Magnuson J.J., Capelli G.M., Lorman J.G. & Stein R.A. (1975) Consideration of crayfish for macrophyte control. In: *The Proceedings of a Symposium on Water Quality Management through Biological Control. Edited by PL Brezonik and JC Fox. University of Florida, Gainesville, Florida. Rep. No. ENV*, pp. 66-74

Marchetti M.P., Moyle P.B. & Levine R. (2004) Invasive species profiling? Exploring the characteristics of non-native fishes across invasion stages in California. *Freshwater Biol.*, 49, 646-661

McGill B.J., Etienne R.S., Gray J.S., Alonso D., Anderson M.J., Benecha H.K., Dornelas M., Enquist B.J., Green J.L., He F., Hurlbert A.H., Magurran A.E., Marquet P.A., Maurer B.A., Ostling A., Soykan C.U., Ugland K.I. & White E.P. (2007) Species abundance distributions: moving beyond single prediction theories to integration within an ecological framework. *Ecol. Lett.*, 10, 995-1015

Mercado-Silva N., Olden J.D., Maxted J.T., Hrabik T.R. & Vander Zanden M.J. (2006) Forecasting the Spread of Invasive Rainbow Smelt in the Laurentian Great Lakes Region of North America. *Conserv. Biol.*, 20, 1740-1749

Moyle P.B. & Light T. (1996) Biological invasions of fresh water: Empirical rules and assembly theory. *Biol. Conserv.*, 78, 149-161

Ogutu-Ohwayo R. (1990) The decline of the native fishes of lakes Victoria and Kyoga (East Africa) and the impact of introduced species, especially the Nile perch, *Lates niloticus*, and the Nile tilapia, *Oreochromis niloticus*. *Environmental Biology of Fishes*, 27, 81-96

Olsen T.M., Lodge D.M., Capelli G.M. & Houlihan R.J. (1991) Mechanisms of impact of an introduced crayfish (*Orconectes rusticus*) on littoral congeners, snails, and macrophytes. *Can. J. Fish. Aquat. Sci.*, 48, 1853-1861

Paine R.T. (1980) Food webs: linkage, interaction strength and community infrastructure. *The Journal of Animal Ecology*, 49, 667-685

Parker I.M., Simberloff D., Lonsdale W.M., Goodell K., Wonham M., Kareiva P.M., Williamson M.H., Von Holle B., Moyle P.B., Byers J.E. & others (1999) Impact: toward a framework for understanding the ecological effects of invaders. *Biol. Invasions*, 1, 3-19

Pimentel D., Lach L., Zuniga R. & Morrison D. (2000) Environmental and Economic Costs of Nonindigenous Species in the United States. *Bioscience*, 50, 53-65

Pimentel D., Zuniga R. & Morrison D. (2005) Update on the environmental and economic costs associated with alien-invasive species in the United States. *Ecological Economics*, 52, 273-288

Pimm S.L. (1980) Food web design and the effect of species deletion. *Oikos*, 35, 139-149

Pimm S.L., Lawton J.H. & Cohen J.E. (1991) Food web patterns and their consequences. *Nature*, 350, 669-674

Polis G.A. & Strong D.R. (1996) Food web complexity and community dynamics. *American Naturalist*, 147, 813-846

Power M.E. (1992) Top-down and bottom-up forces in food webs: do plants have primacy. *Ecology*, 73, 733-746

Rejmanek M. & Richardson D.M. (1996) What Attributes Make Some Plant Species More Invasive? *Ecology*, 77, 1655-1661

Ricciardi A. & MacIsaac H.J. (2000) Recent mass invasion of the North American Great Lakes by Ponto-Caspian species. *Trends Ecol. Evol.*, 15, 62-65

Ricciardi A. & Rasmussen J.B. (1998) Predicting the identity and impact of future biological invaders: a priority for aquatic resource management. *Can. J. Fish. Aquat. Sci.*, 55, 1759-1765

Rodriguez L.F. (2006) Can invasive species facilitate native species? Evidence of how, when, and why these impacts occur. *Biol. Invasions*, 8, 927-939

Rosenthal S.K., Stevens S.S. & Lodge D.M. (2006) Whole-lake effects of invasive crayfish (*Orconectes* spp.) and the potential for restoration. *Canadian Journal of Fisheries & Aquatic Sciences*, 63, 1276-1285

Roth B.M., Tetzlaff J.C., Alexander M.L. & Kitchell J.F. (2007) Reciprocal relationships between exotic rusty crayfish, macrophytes, and Lepomis species in northern Wisconsin lakes. *Ecosystems*, 10, 75–86

Sala O.E., Chapin Iii F.S., Armesto J.J., Berlow E., Bloomfield J., Dirzo R., Huber-Sanwald E., Huenneke L.F., Jackson R.B., Kinzig A. & others (2000) Global biodiversity scenarios for the year 2100. *Science*, 287, 1770-1774

Sih A., Crowley P., McPeek M., Petranka J. & Strohmeier K. (1985) Predation, competition, and prey communities: a review of field experiments. *Annual Review of Ecology and Systematics*, 16, 269-311

Simon K.S. & Townsend C.R. (2003) Impacts of freshwater invaders at different levels of ecological organisation, with emphasis on salmonids and ecosystem consequences. *Freshwater Biol.*, 48, 982-994

Steinhart G.B., Stein R.A. & Marschall E.A. (2004) High growth rate of young-of-the-year smallmouth bass in Lake Erie: A result of the round goby invasion? *Journal of Great Lakes Research*, 30, 381-389

Thiele J., Kollmann J., Markussen B. & Otte A. (2009) Impact assessment revisited: improving the theoretical basis for management of invasive alien species. *Biol. Invasions*, 12, 2025-2035

Vander Zanden M.J., Casselman J.M. & Rasmussen J.B. (1999) Stable isotope evidence for the food web consequences of species invasions in lakes. *Nature*, 401, 464-467

Vander Zanden M.J., Olden J.D., Thorne J.H. & Mandrak N.E. (2004) Predicting occurrences and impacts of smallmouth bass introductions in north temperate lakes. *Ecol. App.*, 14, 132-148

Vitousek P.M. (1990) Biological Invasions and Ecosystem Processes: Towards an Integration of Population Biology and Ecosystem Studies. *Oikos*, 57, 7-13

Vitousek P.M., D'Antonio C.M., Loope L.L. & Westbrooks R. (1996) Biological invasions as global environmental change. *Am. Sci.*, 84, 468-478

Webster K.E., Kratz T.K., Bowser C.J., Magnuson J.J. & Rose W.J. (1996) The influence of landscape position on lake chemical responses to drought in northern Wisconsin. *Limnol. Oceanogr.*, 41, 977-984

White E.M., Wilson J.C. & Clarke A.R. (2006) Biotic indirect effects: a neglected concept in invasion biology. *Diversity& Distributions*, 12, 443-455

Williamson M. & Fitter A. (1996) The varying success of invaders. *Ecology*, 77, 1661-1666

Winemiller K.O. (1996) Factors driving temporal and spatial variation in aquatic floodplain food webs. In: *Food Webs: Integration of Patterns and Dynamics*, pp. 298-312. Chapman & Hall Press, New York

Zavaleta E.S., Hobbs R.J. & Mooney H.A. (2001) Viewing invasive species removal in a whole-ecosystem context. *Trends Ecol. Evol.*, 16, 454-459

CHAPTER ONE

ARE INVASIVE SPECIES MORE ABUNDANT THAN NATIVE SPECIES?

(To be submitted for publication with co-authors M. Jake Vander Zanden, Murray Clayton, Jennifer Hauxwell, Marit Izzo, Matthew S. Kornis, Alison Mikulyuk, Erika Nilsson, Julian D. Olden, Monica Papeş, Sapna Sharma

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ABSTRACT

A central goal of ecology is to characterize and explain spatial patterns in species abundance. A near universal observation is that species are rare in most locations and abundant in a few; that is, abundance distributions are right skewed. Invasive species are widely thought to be exceptions to this pattern, in that they are assumed to become abundant where they occur. Contrary to this conventional wisdom, we report that invasive species from a wide range of aquatic taxonomic groups are present at low densities in most locations where they are present (i.e., their abundance distributions are highly right skewed), similar to their native counterparts. Abundance distributions of invasive and native species exhibited a high degree of overlap, and on average their distributional patterns were remarkably similar. Invasive and native species also exhibited subtle differences; invasive species abundance distributions tended to be *more* right skewed but invasive species on average reached higher densities more often than their native counterparts. Our results challenge the pervasive scientific and public perception that invasive species fundamentally differ from native species by consistently achieving high densities. By recognizing the high degree of spatial heterogeneity in aquatic invasive species

abundance, limited resources can be more effectively targeted to locations where invasive species abundance and impacts are predicted to be high.

INTRODUCTION

Invasive species are powerful agents of global change. Many have produced massive economic and ecological impacts, and invasive species are widely accepted as a leading driver of biodiversity loss and biotic homogenization in many different ecosystem types (Sala *et al.* 2000). Recently, Davis et al. (2011) argued that conservationists, scientists, and the general public hold a pervasive bias against non-native species, and that species should be judged based on their impact rather than their place of origin. The vigorous debate that has followed (e.g, Simberloff 2011) highlights the importance of understanding variation in the impacts of invasive species for both science and resource management, and serves as a reminder of the need to question some of our widely-held assumptions about invasive species.

The invasion biology literature has aimed to make broad generalities, and in doing so, has risked overlooking important sources of heterogeneity (Melbourne *et al.* 2007). It is widely recognized that only a small fraction of introduced species will establish, spread, and cause impacts (Williamson & Fitter 1996). In recognition of this heterogeneity among species, there have been many risk assessments at the species level, classifying species as potentially invasive or not invasive based on life history traits (e.g., Kolar & Lodge 2001). Another research area involves forecasting invasive species spread using ecological niche modeling to classify habitats or sites as either suitable or not suitable for invasion based on environmental characteristics

(Peterson 2003). Furthermore, invasive species monitoring and databases almost universally emphasize occurrence rather than abundance (Online Appendix). The above examples all consider invasions as a binary phenomenon, with the central concern being invasive species occurrence or establishment. But are we missing important insights by ignoring variability in invasive species abundance?

In contrast to the largely binary paradigm of invasive species noted above, it has been long recognized that species abundance is highly variable among sites. For a given species, abundance tends to be low at most locations and high only in a few; that is, the frequency distribution of abundance is right-skewed (Brown *et al.* 1995). This empirical pattern of right-skewed frequency distributions is observed across a wide range of taxonomic groups and spatial scales, and is considered to be central to mainstream ecological theory (Brown 1995; McGill 2010). Surprisingly, virtually no studies have examined whether invasive species follow this same right-skewed frequency distribution of abundance (but see Labra *et al.* 2005).

A basic understanding of the patterns of invasive species abundance and how it compares to that of native species is of obvious importance for both our scientific understanding, as well as resource management. What pattern might we expect? On the one hand, perhaps invasive species play by the same ecological rules and follow abundance frequency distributions similar to those of their native counterparts. On the other hand, invasive species are often viewed as aberrations, and as inherently different from native species, both in terms of biological traits (e.g., high reproductive potential; Kolar & Lodge 2001), and in terms of their community interactions (e.g., lack of natural enemies; Mack *et al.* 2000). Furthermore, the view that invasive species dominate and 'take over' native species and ecosystems (Kolar & Lodge 2001; Valery *et al.* 2008) implies that invasive species commonly (or always) reach high densities. But is this really the case?

In this analysis we compare patterns of species abundance for native and invasive aquatic species, collected simultaneously using the same methods. For each species included in our study, abundance was estimated across many sites, and a Weibull distribution was fit to the frequency distributions. This approach allows direct comparison of the two fitted parameters of the distribution function: k, which represents the degree of skewness of the distribution; and λ, a scaling parameter reflecting the range of abundance values observed (Figure 1). Hence, comparison of these parameters allows us to test (1) whether invasive species are abundant more often than native species (i.e., their abundance frequency distributions are less right-skewed); and (2) whether invasive species reach higher maximum abundances than native species.

APPROACH

We compared cross-site abundance distributions of 12 invasive and 99 native species of aquatic plants, invertebrates (crayfish, mussels, snails) and fishes. According to the United States government (Executive Order 13112) invasive species are defined as " species that are non-native[...]to the ecosystem under consideration and whose introduction causes or is likely to cause economic or environmental harm or harm to human health" (Clinton 1999; Davis &

Thompson 2000). The invasive species included in this analysis are established non-native species that have been classified as invasive by the regional management authorities in the study region, though we recognize that our invasive species differ in the overall magnitude of impacts (Online Appendix Table S1). All invasive species included here have had the opportunity to spread, having been present for at least a decade in the study region.

To examine variability in abundance across sites, our analysis required multiple records of abundance or density for each species collected using the same methods in multiple locations. Invasive species densities at multiple sites are rarely reported in invasive species databases (Online Appendix; Table S2) or the scientific literature. Our data thus derive primarily from our own research in freshwater-rich Wisconsin, USA (169,939 km^2), supplemented with several other data sets from elsewhere in North America and Europe (Online Appendix; Table S3). Our analysis included 23,619 density records (absences excluded), with 20-1,252 records per species (see Online Appendix for specific sampling methods for each taxonomic group). We fit a Weibull distribution to the density data for each species (Figure 1). The Weibull is a flexible distribution used to characterize distributions with rare extreme values. Kolmogorov-Smirnov goodness of fit tests were performed to determine if observed data differed significantly from expected distributions given fitted Weibull parameters. Data which differed significantly (Bonferroni-corrected $\alpha = 0.0045$, $N=112$) from the best-fit Weibull distribution were excluded from analyses reported in main body of text but including these data did not alter conclusions (Table S4). Our objective was to use a distribution that fit the empirical data for most species, and the Weibull fit all but 16 species (see Results and Online Appendix), performing better than either the Gamma (failed to fit 38 species) or the Pareto (failed to fit 77 species) distributions.

RESULTS

All species, regardless of invasive status, had highly right-skewed frequency distributions of abundance and occurred at low densities in the vast majority of sites where they were present (Figure 2). Species varied in the degree of skewness of their distribution of abundance, with the distributional patterns of native and invasive species overlapping considerably (Figure 3a). Contrary to expectation, invasive species distributions were marginally *more* right skewed (i.e., lower *k*) than those of native species (Two-way ANOVA; $F_{1,85}$=3.85, p=0.053; Figure 3b). Because of their right-skewed abundance distributions, the majority of individuals within each sampled population were contained within a small number of sites for both invasive and native species. For example, the top 20% of sites contained from 46-87% of total abundance for invasive species (mean=68%), and from 47-84% of abundance for native species (mean=66%; Figure 3c).

Invasive species distributions also tended to have longer tails (higher λ) than those of native species, indicating a tendency to reach higher densities than native counterparts (Two-way ANOVA; $F_{1,83}$=5.98, p=0.017; Figure 3b). Notably, λ did not differ between invasive and native species when crayfish were excluded from analysis (Two-way ANOVA; $F_{1,82}$=2.06, p=0.155), indicating that differences in λ are driven mainly by a few highly abundant invasive crayfish species. Estimated k and λ values were not correlated (Figure 3b).The statistical differences in fitted distributional parameters translate into small differences between abundance distributions of invasive and native species; exemplar abundance distributions generated using mean *k* and λ values of native and invasive species were remarkably similar, but not identical (Figure 4).   Similar overall patterns emerged when comparing statistical moments (mean, coefficient of variance, skewness, and kurtosis) of invasive and native species – invasive species were on average more abundant than native counterparts, but invasive and native species did not otherwise differ (Online Appendix, Figure S2; Table S5). The abundance distributions of 16 native fishes differed significantly from the Weibull distribution (see Online Appendix) and are not included in statistical analysis of Weibull parameters; however, including them in did not alter conclusions (Online Appendix,Table S4).

We were able to compare abundance distributions for four species in their native and invaded ranges, and three additional invasive species to native congeners or confamilials. Although small sample sizes preclude formal statistical inference, taxa-specific comparisons yielded similar results as overall comparisons between invasive and native species (Table S6).Species were not uniformly less right-skewed in their invaded ranges than in their native ranges: invasive species had higher *k* than native counterparts in only two of seven cases. In some cases invasive species achieved higher densities more regularly in their invaded ranges: invasive species had higher λ than native counterparts in four of six comparisons. However, there are exceptions to both of these conclusions. Signal crayfish (*Pacifastacus leniusculus*) was the only invasive species that was less right skewed (higher *k*) in its invaded range than in its native range. Indeed, signal crayfish had the highest *k* of any species included in this analysis, and the highest λ of any crayfish species (Table S3), indicating that this species is capable of achieving high densities at an unexpectedly large number of sites in its invaded range. Conversely, brook trout (*Salvelinus fontinalis*) was more right skewed and had lower λ values in its invaded range than in its native range, indicating that this species is more abundant more frequently in its native range. These individual comparisons provide revealing case studies and illustrate that a high degree of variability exists both among and within invasive species.

DISCUSSION

Contrary to the perception that invasive species are abnormally abundant, we find that aquatic invasive species are typically found at low densities where they occur, with the majority of invasive species abundance contained in a small number of "hot spots", similar to their native counterparts. However, we also identified subtle differences among invasive and native species (Figure 4); invasive species on average reach higher maximum densities than their native counterparts, with invasive crayfish driving the statistical significance of these differences. Whether the observed differences between aquatic invasive and native species are biologically significant depends on the species-specific relationship between density and ecological impact, knowledge of which is lacking for even the most notorious invaders (Kulhanek *et al.* 2011).

The differences between invasive and native abundance patterns do not necessarily reflect fundamental disparities between them. Species that are widespread tend to be on average more abundant than species restricted small ranges, and the higher average abundance of widespread species is driven by higher maximum abundances, not by any change in the frequency with which they are present at low abundances (Gaston *et al.* 1998). Invasive species by definition have spread outside of their native range and therefore are increasing their range size; one might expect them to achieve higher maximum abundances as their range size increased. Indeed, invasive and native British bird species do not differ in their relationship between range size and abundance, but similar to our findings, invasive species reach higher maximum densities than native counterparts (Labra *et al.* 2005). Invasive terrestrial plants also rarely reach high densities (Kueffer et al. 2010) and do not reach higher abundances in their invaded compared to native ranges (Firn et al. 2011), supporting the idea that invasive and native species do not follow fundamentally different distributional patterns. However, the results of our study and that of Labra and colleagues (2005) indicate that invasive species do tend to fall towards the high end of the observed range of abundance-distribution relationships. Identifying the mechanisms explaining such ecological patterns is a fruitful area of current research (e.g., Gaston *et al.* 1997; McGill & Nekola), and identifying similarities and differences in these patterns among groups of species could provide insight into the forces behind them(McGill *et al.* 2007).

Our results have several implications for the management of biological invasions. Sophisticated modeling techniques are used in invasive species risk assessments that aim to identify which species are likely to become harmful and which sites are likely to be invaded. Our results show that invasive species management would benefit from a more nuanced approach that also considers variation in species abundance among invaded sites, and thus heterogeneity in ecological and economic impacts (Parker *et al.* 1999). Because invasive species occur at low densities in most locations, use of presence/absence data could overestimate landscape-level impacts. Conversely, an invasive species that appears benign at one location could produce unexpected impacts in the few locations where it does reach high densities. Transmissions of infectious diseases follow highly right-skewed distributions similar to what we have shown in this study, and the effectiveness of disease control is improved when this heterogeneity is accounted for by focusing prevention on the most infectious individuals and by predicting the identity of these individuals prior to a disease outbreak (Paull *et al.* 2012). Similarly, invasive species management could be improved by acknowledging heterogeneity in invasive species abundance. Containment efforts should be focused on the small percentage of “hot spots” containing the majority of invasive species abundance, thereby reducing the likelihood of further spread. Future research directed towards understanding and predicting abundance would allow prevention efforts to be more effectively targeted to the small number of locations where abundance and impact are likely to be high.

Conclusion

Our finding that invasive species are at low densities in most locations where they occur challenges the notion of invasive species as ecological aberrations that become exceeding abundant or even dominant (Kolar & Lodge 2001; Valery *et al.* 2008) outside of their native geographic range. Like many other ecological phenomena, invasive species abundance is highly heterogeneous, and like native species, their distribution is highly right skewed. While there is no doubt that invasive species often have harmful ecological and economic impacts, our results call attention to the patchiness of invasive species abundance, and the potential implications of this patchiness for understanding and managing ecological and economic impacts. The overall similarities in abundance distributions of native and invasive species support the notion that applying general ecological and analytical principles to understanding invasive species is likely to advance our understanding of biological invasions more so than the treatment of invasions as idiosyncratic occurrences (Sax & Brown 2000).The fact that we find highly right-skewed species abundance distributions where we would least expect them points to the universality of this general ecological pattern.

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Author Contributions

G.J.A.H. and M.J.V.Z. developed the idea for the analysis and wrote the paper, and M.S.K., S.S., M.P., and M.I. assisted with study design. G.J.A.H. performed statistical analyses and M.C., M.J.V.Z., and J.D.O. provided guidance on statistical analysis. M.S.K., J.D.O., J.H., A.M., E.N. provided primary data. M.I., S.S., and M.P. collated data from other sources. All authors discussed the results and revised the manuscript.

Figure Captions

Figure 1. Probability densities and cumulative distributions (insets) of Weibull distributions described by varying *k* (shape) and λ (scale) parameters. A) *k* describes the degree of right skew of a distribution. When *k*=1, the Weibull distribution is equivalent to the negative exponential distribution. Varying *k* allows the distribution to be more (lower *k*) or less (higher *k*) right skewed than the negative exponential. *k* is unitless, allowing comparisons across sampling methods and taxonomic groups. B) Increasing λ scales the distribution, and increases the length of the tail of the distribution, and higher λ values are a reflection of a species being observed at higher densities.

Figure 2. Abundance distributions for each species used in this analysis. See Table S3 for species identities and fitted λ and *k* values. Colors correspond to taxonomic groups and in every group the darker shade corresponds to invasive species in that group (red=crayfish, blue=North American fish, purple=Swedish fish, green=aquatic plants, yellow=snails, black=zebra mussels). The x-axis scale ranges from 0 to the maximum observed for a given taxonomic group to accommodate different units of measurement, and the y-axis scale varies by species to accommodate different numbers of observations (sites).

Figure 3. A. Cumulative abundance distributions based on empirical data for invasive (black) and native (grey) species. Abundance is presented as percentage of maximum value observed within a taxonomic group to facilitate comparison on a common scale. B. Fitted values of the Weibull parameters *k* and LN(λ) for each species. The *k* parameter is unitless and is comparable across taxonomic groups; lower *k* values correspond with more right-skewed distributions. The

λ parameter depends on the absolute value of sampling units and is only comparable within taxonomic groups; higher λ values correspond with higher maximum abundances. C. Percentage of total abundance contained within the top 20% most abundant sites for all species as a function of the Weibull *k* parameter. As *k* decreases, distributions are more right-skewed and a larger percentage of total abundance of a species is contained within the top 20% of sites. For B. and C, colors indicate taxonomic group (red=crayfish, blue=North American fish, purple=Swedish fish, green=aquatic plants, yellow=snails, black=zebra mussels). Cross-hatched circles are invasive species; solid filled circles are native species.

Figure 4. Probability density and cumulative distributions (inset) of invasive (black) and native (purple) species abundance generated from the Weibull distribution using the fitted mean values of k and LN(λ) for each group ($k_{invasive}$=0.71 , k_{native}=0.78 , LN($\lambda_{invasive}$)= 0.61,LN(λ_{native})=-0.32).

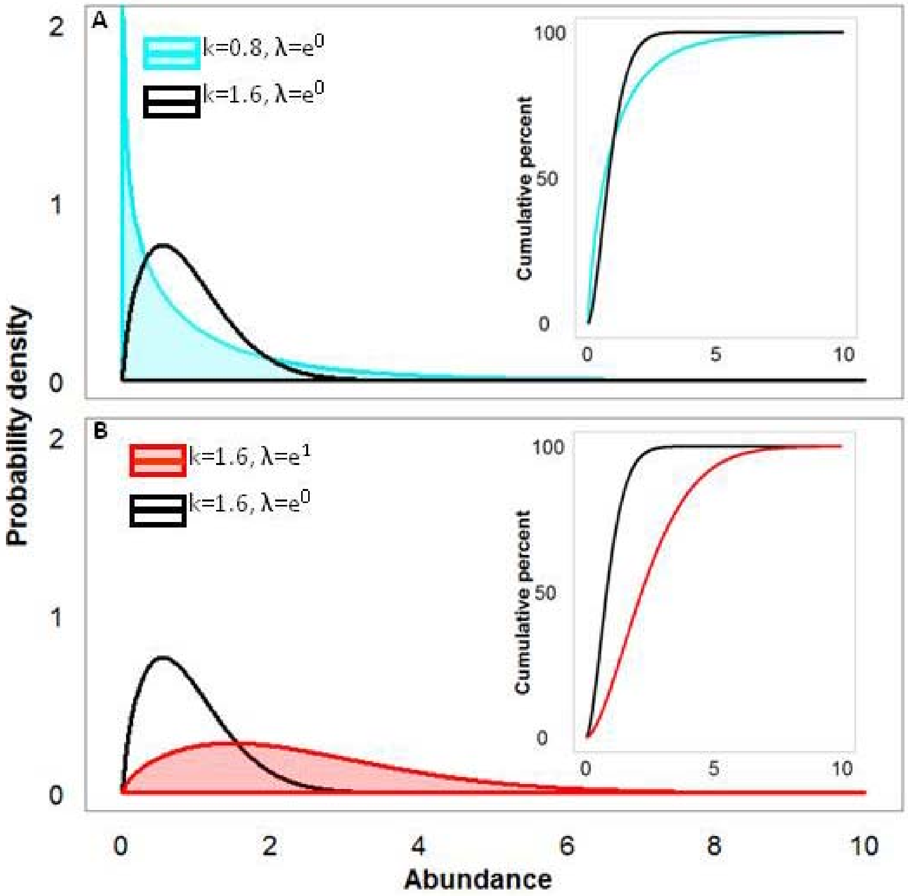
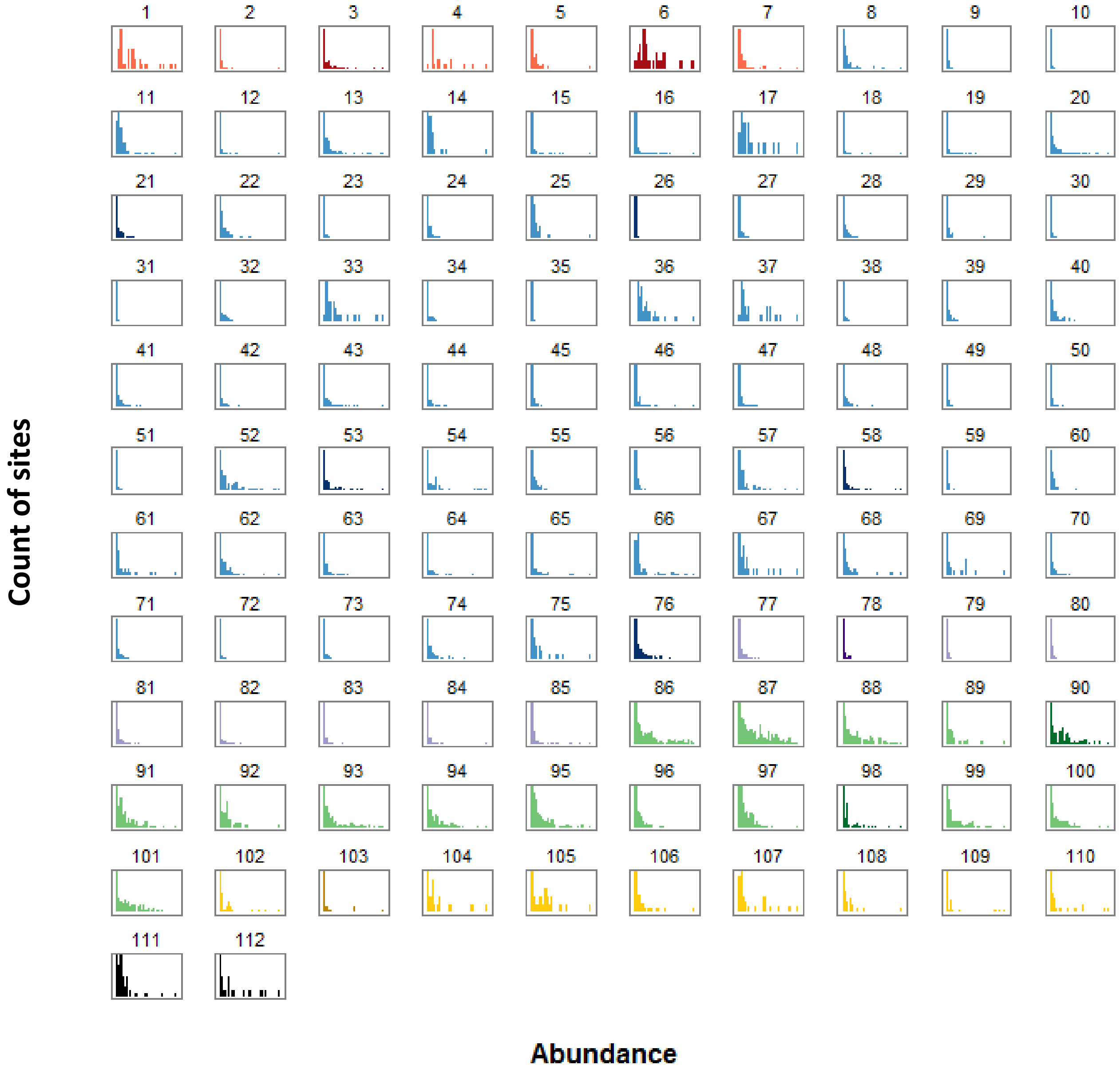

A
k=0.8, $\lambda=e^0$
k=1.6, $\lambda=e^0$
B
k=1.6, $\lambda=e^1$
k=1.6, $\lambda=e^0$
Probability density
0
1
2
Abundance
0
2
4
6
8
10
Cumulative percent
0
50
100
0
5
10

Figure 1.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111
112
Count of sites
Abundance

Figure 2.

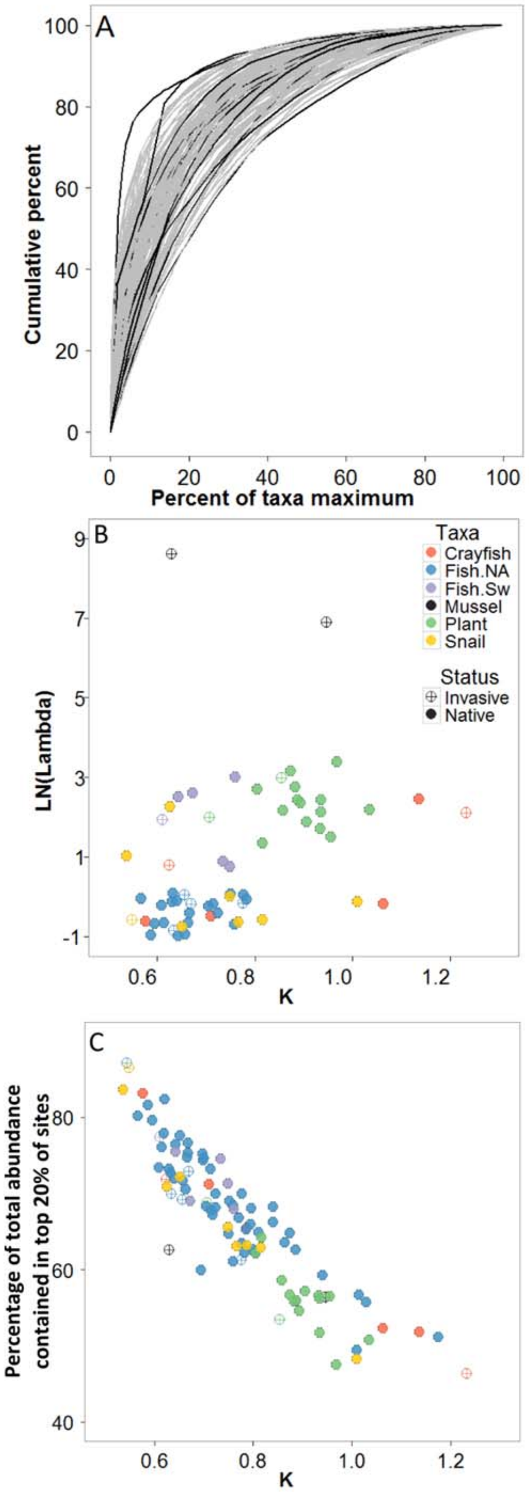
A
Cumulative percent
0
20
40
60
80
100
Percent of taxa maximum
0
20
40
60
80
100
B
Taxa
Crayfish
Fish.NA
Fish.Sw
Mussel
Plant
Snail
Status
Invasive
Native
LN(Lambda)
-1
1
3
5
7
9
K
0.6
0.8
1.0
1.2
C
Percentage of total abundance contained in top 20% of sites
40
60
80
K
0.6
0.8
1.0
1.2

Figure 3.

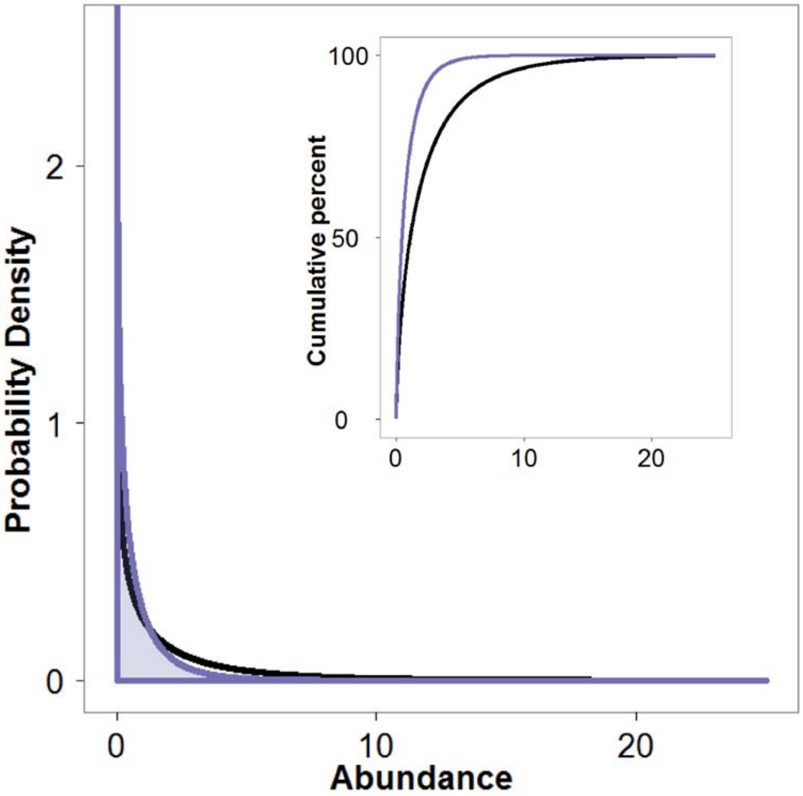
Probability Density
2
1
0
0
10
20
Abundance
Cumulative percent
100
50
0
0
10
20

Figure 4.

Literature Cited

Brown J.H. (1995) *Macroecology*. University of Chicago Press, Chicago, IL.

Brown J.H., Mehlman D.W. & Stevens G.C. (1995) Spatial Variation in Abundance. *Ecology*, 76, 2028-2043

Clinton W.J. (1999) Invasive Species. In, pp. 6183-6186. Federal Register

Davis M.A., Chew M.K., Hobbs R.J., Lugo A.E., Ewel J.J., Vermeij G.J., Brown J.H.R., M. L., Gardener M.R., Carroll S.P., Thompson K., Pickett S.T.A., Stromberg J.C., Del Tredici P., Suding K.N., Ehrenfeld J.G., Grime J.P., Mascaro J. & Briggs J.C. (2011) Don't judge species on their origins. *Nature*, 474, 153-154

Davis M.A. & Thompson K. (2000) Eight ways to be a colonizer; two ways to be an invader: a proposed nomenclature scheme for invasion ecology. *Bulletin of the Ecological Society of America*, 81, 226-230

Firn J., Moore J.L., MacDougall A.S., Borer E.T., Seabloom E.W., HilleRisLambers J., Harpole W.S., Cleland E.E., Brown C.S., Knops J.M.H., Prober S.M., Pyke D.A., Farrell K.A., Bakker J.D., Oâ€™Halloran L.R., Adler P.B., Collins S.L., Dâ€™Antonio C.M., Crawley M.J., Wolkovich E.M., La Pierre K.J., Melbourne B.A., Hautier Y., Morgan J.W., Leakey A.D.B., Kay A., McCulley R., Davies K.F., Stevens C.J., Chu C.-J., Holl K.D., Klein J.A., Fay P.A., Hagenah N., Kirkman K.P. & Buckley Y.M. (2011) Abundance of introduced species at home predicts abundance away in herbaceous communities. *Ecol. Lett.*, 14, 274-281

Gaston K.J., Blackburn T.M., Gregory R.D. & Greenwood J.J.D. (1998) The anatomy of the interspecific abundanceâ€“range size relationship for the British avifauna: I. Spatial patterns. *Ecol. Lett.*, 1, 38

Gaston K.J., Blackburn T.M. & Lawton J.H. (1997) Interspecific Abundance-Range Size Relationships: An Appraisal of Mechanisms. *Journal of Animal Ecology*, 66, 579

Kolar C.S. & Lodge D.M. (2001) Progress in invasion biology: predicting invaders. *Trends Ecol. Evol.*, 16, 199-204

Kueffer C., Daehler C.C., Torres-Santana C.W., Lavergne C., Meyer J.-Y., Otto R.d. & Silva L. (2010) A global comparison of plant invasions on oceanic islands. *Perspectives in Plant Ecology, Evolution and Systematics*, 12, 145-161

Kulhanek S.A., Ricciardi A. & Leung B. (2011) Is invasion history a useful tool for predicting the impacts of the world's worst aquatic invasive species? *Ecol. App.*, 21, 189-202

Labra F.A., Abades S. & Marquet P.A. (2005) Distribution and abundance: scaling patterns in exotic and native bird species. In: *Species Invasions. Insights into Ecology, Evolution and Biogeography* (eds. Sax DF, Stachowicz JJ & Gaines SD), pp. 421-446. Sinauer Associates, Sunderland, MA

Mack R.N., Simberloff D., Lonsdale W.M., Evans H., Clout M. & Bazzaz F.A. (2000) Biotic invasions: Causes, epidemiology, global consequences, and control. *Ecol. App.*, 10, 689-710

McGill B.J. (2010) Towards a unification of unified theories of biodiversity. *Ecol. Lett.*, 13, 627-642

McGill B.J., Etienne R.S., Gray J.S., Alonso D., Anderson M.J., Benecha H.K., Dornelas M., Enquist B.J., Green J.L., He F., Hurlbert A.H., Magurran A.E., Marquet P.A., Maurer B.A., Ostling A., Soykan C.U., Ugland K.I. & White E.P. (2007) Species abundance distributions: moving beyond single prediction theories to integration within an ecological framework. *Ecol. Lett.*, 10, 995-1015

McGill B.J. & Nekola J.C. (2010) Mechanisms in macroecology: AWOL or purloined letter? Towards a pragmatic view of mechanism. *Oikos*, 119, 591-603

Melbourne B.A., Cornell H.V., Davies K.F., Dugaw C.J., Elmendorf S., Freestone A.L., Hall R.J., Harrison S., Hastings A., Holland M., Holyoak M., Lambrinos J., Moore K. & Yokomizo H. (2007) Invasion in a heterogeneous world: resistance, coexistence or hostile takeover? *Ecol. Lett.*, 10, 77

Parker I.M., Simberloff D., Lonsdale W.M., Goodell K., Wonham M., Kareiva P.M., Williamson M.H., Von Holle B., Moyle P.B., Byers J.E. & others (1999) Impact: toward a framework for understanding the ecological effects of invaders. *Biol. Invasions*, 1, 3-19

Paull S.H., Song S., McClure K.M., Sackett L.C., Kilpatrick A.M. & Johnson P.T.J. (2012) From superspreaders to disease hotspots: linking transmission across hosts and space. *Front. Ecol. Environ.*, 10, 75-82

Peterson A.T. (2003) Predicting the geography of species' invasions via ecological niche modeling. *Q. Rev. Biol.*, 78, 419

Sala O.E., Chapin Iii F.S., Armesto J.J., Berlow E., Bloomfield J., Dirzo R., Huber-Sanwald E., Huenneke L.F., Jackson R.B., Kinzig A. & others (2000) Global biodiversity scenarios for the year 2100. *Science*, 287, 1770-1774

Sax D.F. & Brown J.H. (2000) The paradox of invasion. *Global Ecology and Biogeography*, 9, 363-371

Simberloff D. (2011) Non-natives: 141 scientists object. *Nature*, 475, 36

Valery L., Fritz H., Lefeuvre J.-C. & Simberloff D. (2008) In search of a real definition of the biological invasion phenomenon itself. *Biol. Invasions*, 10, 1345-1351

Williamson M. & Fitter A. (1996) The varying success of invaders. *Ecology*, 77, 1661-1666

APPENDIX: SUPPLEMENTARY MATERIAL

Introduction

Invasive species databases

Numerous databases and online resources have been developed in recent years to catalogue and disseminate information on invasive species impacts and distributions at large spatial scales (Table S2). None of these databases contain information on abundance – data are available only in such coarse terms as “established” or “sighted” for a country or state, or at best in terms of species presence (and sometimes presence-absence) on finer spatial scales. Due to the lack of invasive species density data available over broad spatial scales, we used data primarily from our own research to ensure consistent sampling methodology both across sites for a given species and among invasive and native species of the same broad taxonomic groups.

Methods

Data collection and collation

To control for sampling methodology and allow comparisons among native and invasive species, we only included data where both invasive and native species from a taxonomic group were sampled using the same methods across multiple sites. Exceptions were made to include rusty crayfish (*Orconectes rusticus*) in its native range and zebra mussel (*Dreissena polymorpha*) data. Native rusty crayfish data were obtained from (Jezerinac 1982). Zebra mussel data were mainly obtained from a meta-analysis (Naddafi *et al.* 2011) which compiled data from 55 European and 13 North American sites from 1959-2004. Additional densities from North America were compiled from multiple primary literature sources (Table S3). All zebra mussel records were presented as number per m^2 and are from their invaded range; we did not include native mussel data.

Crayfish data were obtained from multiple sources. Crayfish were collected in Wisconsin, USA during summers of 2002-2010 from lakes in the Northern Highlands Lake District following the protocol for crayfish collection described at http://lter.limnology.wisc.edu/. Crayfish were sampled in Wisconsin streams tributary to Lake Michigan from 2007-2010 using 10 gee-style minnow traps per site baited with chicken livers and set overnight. Swedish crayfish were sampled using 30 minnow traps baited with frozen fish in lakes and streams of southern Sweden from 2001-2003 as described in (Nystrom et al. 2006). Washington crayfish were collected from 100 lakes in the Puget Sound Lowlands region of Washington State, USA between 2007 and 2009 from mid-June to early October of each year. At each lake, the investigators set 20 minnow traps baited with fish-based dog food. Traps were deployed in four clusters of five traps each and recovered the following day. All crayfish densities are presented as number per trap per day, with the exception of native range rusty crayfish data, which were reported as number per site (Jezerinac 1982) and excluded from all comparisons that depend on sampling units.

Wisconsin fish data were collected from streams throughout the state from 2005-2010 using either a backpack or towboat electrofisher with pulsed DC current in wadeable (<1m depth) streams for a minimum of 15 minutes. For Wisconsin trout species, locations sampled within 10 years following a stocking event of that species were excluded. Lamprey data were collected from 2008-2010 from Great Lakes tributaries using backpack electrofishers following standardized methods as a part of the sea lamprey assessment program of the United States Fish and Wildlife Service and Department of Fisheries and Oceans, Canada. North American fish densities are presented as number per minute of sampling. Swedish fish data were collected using backpack electrofishing between 1980 and 2010 from streams in Vasterbotten county, northern Sweden, and were obtained from the Swedish Electrofishing REgister (SERS), www.fiskeriverket.se, and are reported as number per 100 m of stream.

Snail data were collected in 2006 from lakes in the Northern Highlands Lake District in Wisconsin as described by (Solomon et al. 2010), and densities are presented as number per two m^2. Aquatic plant data were collected using a systematic grid-based point-intercept sampling methodology to record macrophyte frequency of occurrence in 242 Wisconsin lakes from 2005-2008. Aquatic plant presence/absence was recorded from a boat using a double-sided rake sampler at each point on a sampling grid as described in (Mikulyuk et al. 2010). Density data are presented as proportion of sites within lake littoral zone where a species was present.

For all data, if multiple records existed from the same location, we used the most recent record. If replicate samples existed within the same site on the same sampling date, the mean value was used.

Comparison of invasive and native species

We assessed the statistical significance of differences between the Weibull parameters of invasive and native species while accounting for potential differences among taxonomic groups using two-way analyses of variance (ANOVA; $\alpha = 0.05$). Statistical comparisons of scale (λ) were made using natural log transformed data. Taxonomic group, status (invasive or native), and their interaction were included as predictors. Values reported in text represent the invasive status effect; for full ANOVA tables see Table S4. The interaction between taxonomic group and status was insignificant for both comparisons of k (p-value=0.59) and LN(λ) (p-value=0.14). Zebra mussels had no native counterparts in our dataset and native rusty crayfish were sampled in different units than all other crayfish species, and both were excluded from the λ comparison. Directions of significant differences were assessed visually (Figure S1).

Statistical moments comparison

We compared the mean, coefficient of variation (CV), skewness, and kurtosis of invasive and native species abundance distributions. Zebra mussels and native rusty crayfish were both excluded for the same reasons discussed above. Moments were calculated on raw abundance data for all other species. We assessed the statistical significance of differences in statistical moments of invasive and native species using two-way analyses of variance (ANOVA) with invasive status, taxonomic group, and their interaction included as fixed effects. Statistical moments were natural log transformed due to extreme heteroscedasticity of residuals from untransformed data. Our hypotheses were that invasive species would be on average more abundant (higher mean), less variable (lower CV), less right-skewed (lower skewness), and more uniform (lower kurtosis) than native species. Full ANOVA results for the comparison of k and λ

are presented in Table S5. All analyses were conducted using R v2.12.0 (R Core Development team 2010).

Results

The Weibull distribution

The Weibull distribution described the abundance distribution of most species. A total of 16 native fish species (13 North American fish, 3 Swedish fish) were excluded from our analysis presented in the main text because they failed Bonferroni-corrected Kolmogorov-Smirnov tests when comparing actual data to expected distributions generated from fitted k and λ parameters ($N=112$, $p<0.00045$). The abundance distributions of all excluded species were highly right skewed (low k values, Table S3). Our conclusions remain largely the same when these 16 fish species were included; the k values of invasive species are marginally lower than those of natives, and the λ values of invasive species are higher than those of natives (Table S4).

Supplementary Figures

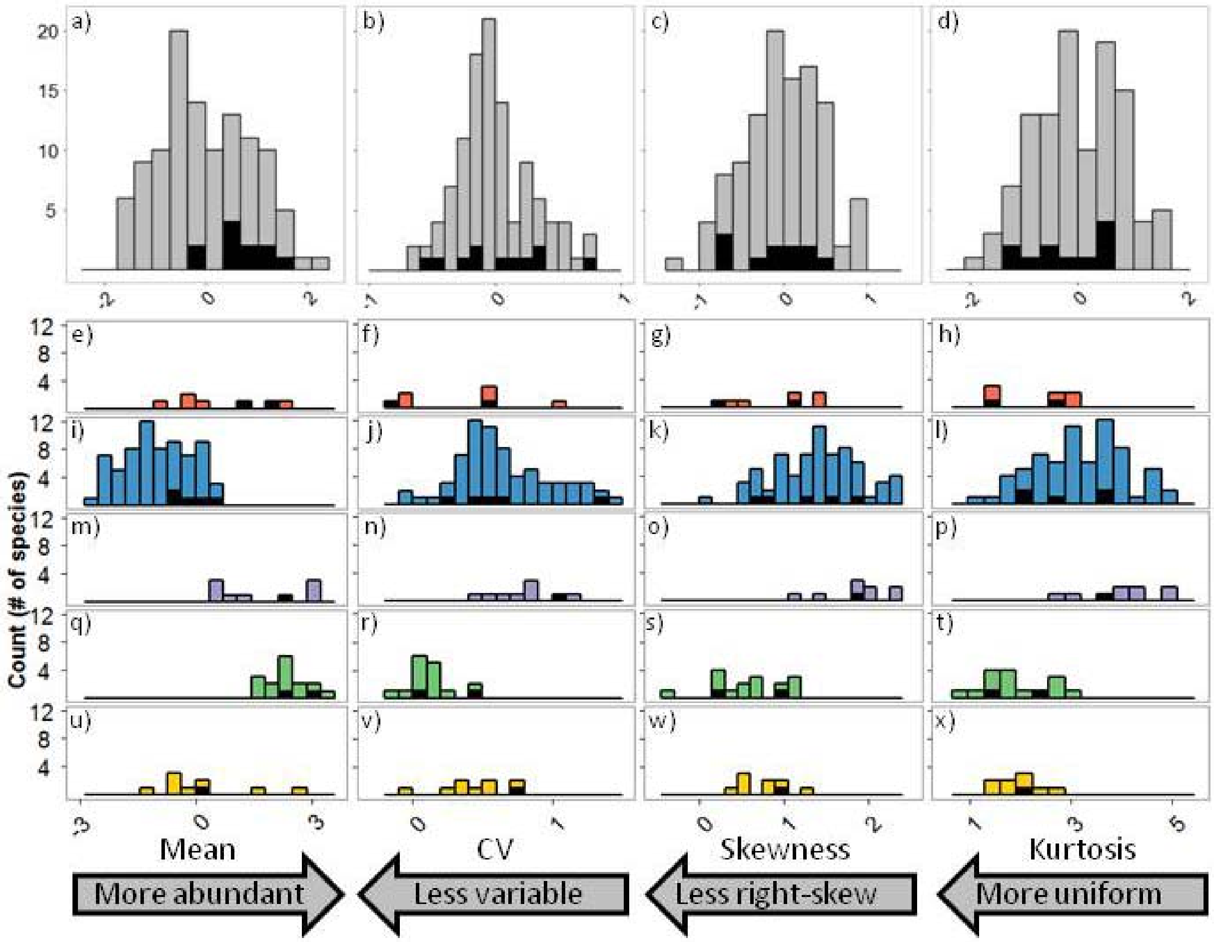

Figure S1. Statistical moments (natural log transformed) of each species used in this analysis. (a-d) all species combined, presented on standardized scale (for graphical purposes only) to facilitate comparison across taxa sampled in different units. Moments were standardized by subtracting the taxa-specific mean value. All other panels present unstandardized moments for (e-h) crayfish; (i-l) North American fish; (m-p) Swedish fish; (q-t) plants; and (u-x) snails. Dark colors indicate invasive species in each group. All species, including those for which the Weibull did not adequately describe abundance distributions, are included, with the exception of one native crayfish excluded due to differences in sampling units and zebra mussels for which no native counterparts existed. Grey arrows indicate expected trend for invasive species relative to native species based on the expectation that invasive species achieve higher abundances and are less right skewed.

Supplementary Tables

Table S1. Invasive species included in this analysis and their ecological impacts. Invasive species are defined as non-native species that are spreading and have demonstrated or perceived ecological impacts. All invasive species included in this analysis are restricted by the regional fisheries management agency in their invaded range (Sweden for signal crayfish and brook trout, www.nobanis.org; Wisconsin for all others, http://dnr.wi.gov/invasives/classification/).

Taxonomic group	Common name	Latin name	Native range	Impacts	Key references
Crayfish	Rusty crayfish	*Orconectes rusticus*	Ohio River valley	Native crayfish, macrophytes, benthic macroinvertebrates, native fishes	Lodge et al. 1994[1]; Wilson et al. 2004[2]; McCarthy et al. 2006[3]
Crayfish	Signal crayfish	*Pacifastacus leniusculus*	Western United States	Native crayfish, macrophytes, benthic macroinvertebrates, amphibians	Nystrom and Strand 1996[4]; Nystrom 1999[5]; Crawford et al. 2006[6]
North American fish	Brown trout	*Salmo trutta*	Europe	Native fishes, invertebrates	Crowl et al. 1992[7]; Townsend 1996[8]; McHugh and Budy 2005[9]
North American fish	Common carp	*Cyprinus carpio*	Asia	Water quality, macrophytes, macroinvertebrates	Zambrano 2001[10]; Miller and Crowl 2005[11]; Matsuzaki et al. 2009[12]
North American fish	Rainbow trout	*Oncorhynchus mykiss*	Western United States	Native fishes, amphibians	Allendorf and Leary 1988[13]; Crowl et al. 1992[7]; Nystrom et al. 2001[14]
North American fish	Round goby	*Neogobius melanostomus*	Ponto-Caspian region	Native fishes, benthic macroinvertebrates	Corkum et al. 2004[15]; Barton et al. 2005[16]; Poos et al. 2010[17]
North American fish	Sea lamprey	*Petromyzon marinus*	Atlantic Ocean	Native fishes	Fetterolf 1980[18]; Pearce et al. 1980[19]; Smith and Tibbles 1980[20]

Swedish fish	Brook trout	*Salvelinus fontinalis*	Eastern North America	Native fishes	Spens et a. 2007[21]; Ohlund et al. 2008[22]
Mussel	Zebra mussel	*Dresseina polymorpha*	Ponto-Caspian region	Native mussels, zooplankton, benthic macroinvertebrates, native fishes, water birds, biofouling	Ludyanskiy et al. 1993[23]; Strayer 2008[24]; Higgins and Vander Zanden 2010[25]
Plant	Curly-leaf pondweed	*Potamogeton crispus*	Europe, Africa, Asia, Australia	Native plants, nutrient cycling	Bolduan et al. 1994[26]; Nichols and Shaw 1986[27]
Plant	Eurasian water milfoil	*Myriophyllum spicatum*	Europe, Asia, Northern Africa	Native plants, macroinvertebrates	Boylen et al. 1999[28]; Madsen et al. 2001[29]; Cheruvelil et al. 2002[30]
Snail	Chinese mystery snail	*Bellamya chinensis*	Asia	Native snails, nutrient cycling, periphyton	Johnson et al. 2009[31]; Solomon et al. 2010[32]

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[1] D.M. Lodge *et al., Ecology* **75**, 1265 (1994).

[2] K.A. Wilson *et al.,* ***Can. J. Fish. Aquat. Sci.*** **61, 2255** (2004).

[3] J.M. McCarthy *et al., Freshwater Biol.* **51**, 224 (2006).

[4] P. Nystrom, J.Strand, *Freshwater Biol.* **36**, 673 (1996).

[5] P. Nystrom, in F. Gherardi, D.M. Holdich, *Crayfish in Europe as alien species: How to make the best of a bad situation* (Balkema Publishers, Rotterdam, The Netherlands, 1999) pp. 63.

[6] L. Crawford *et al. Aquatic Cons.* **16**, 611 (2006).

[7] T.A. Crowl *et al., Rev. Fish Biol. Fish.*, **2**, 217 (1992).

[8] C.R. Townsend, *Biol. Cons.***78**, 13 (1996)

[9] P. McHugh, P. Budy, ***Can. J. Fish. Aquat. Sci.*** **62, 2784** (2005).

[10] L. Zambrano, *et al., Oikos* **94**, 344 (2001)

[11] S.A. Miller, T.A. Crowl, , *Freshwater Biol.* **51**, 85 (2005).

[12] S.S. Matsuzaki *et al., Oecologia* **158**, 673 (2009).

[13] F.W. Allendorf, R.F. Leary, *Cons. Biol.* **2**, 170(1988).

[14] P. Nystrom *et al.*, *Ecology* **82**, 1023 (2001).

[15] L.D. Corkum *et al., Biol. Invasions* **6***,* 173 (2004).

[16] D.R. Barton *et al., J. Great Lakes Res.* **31**, 252(2005).

[17] M. Poos *et al., Biol. Invasions* **12***,* 1269 (2010).

[18] C.M. Fetterolf Jr., ***Can. J. Fish. Aquat. Sci.*** **37, 1588** (1980).

[19] W.A. Pearce *et al.,* ***Can. J. Fish. Aquat. Sci.*** **37, 1802** (1980).

[20] B.R. Smith, J.J. Tibbles, ***Can. J. Fish. Aquat. Sci.*** **37, 1780** (1980).

[21] J. Spens *et al.,* ***Can. J. Fish. Aquat. Sci.*** **64, 654** (2007).

[22] G. Ohlund *et al.,* ***Can. J. Fish. Aquat. Sci.*** **65, 633** (2008).

[23] M.L. Ludyanskiy *et al*. *BioScience* **43**, 533 (1993).

[24] D.L. Strayer, *Front. Ecol. Environ.* **7**, 135 (2008).

[25] S.N. Higgins, M.J. Vander Zanden, *Ecol. Monograph* **80**, 179 (2010).

[26] B.R. Bolduan *et al*. *Lake Reservoir Manage.***10**, 113 (1994).

[27] S.A. Nichols, B.H. Shaw, *Hydrobiologia* **131**, 3 (1986).

[28] C.W. Boylen *et al*. *Hydrobiologia* **415**, 207 (1999).

[29] J.D. Madsen *et al*. *J. Aquat. Plant Manage.* **39**, 67 (2001).

[30] K.S. Cheruvelil *et al*., *J.N. Am. Benthol. Soc.* **21**, 261 (2002).

[31] P.T.J. Johnson *et al*., *Oecologia* **159**, 161 (2009).

[32] C.T. Solomon *et al., Biol. Invasions* **12***,* 1591 (2010).

Table S2. Examples of invasive species databases of invasive species impacts and distribution, none of which report invasive species densities or abundances at multiple sites.

Name	Geographic coverage	Distributional information	URL
Global invasive species database	Global	Presence and status by country/state	http://www.issg.org/database/welcome/
National Biodiversity Network (NBN)	United Kingdom	Presence by $100m^2$ grid	http://data.nbn.org.uk/
Non-indigineous species (NIS) base	Global	Varies (no density information)	http://www.nisbase.org/nisbase/index.jsp
The European network on invasive alien species	Europe	Status by country	http://www.nobanis.org/
United States Geological Survey (USGS) Aquatic gap analysis program	Parts of United States	Presence by watershed	http://www.gapanalysis.usgs.gov/gap-analysis/aquatic-gap
USGS Non-indigenous aquatic species (NAS)	United States	Presence by watershed	http://nas.er.usgs.gov/default.aspx

Table S3. Taxa included in analyses, fitted λ and *k* values (bold face type indicates taxa for which the Weibull distribution failed to fit the observed data based on a Kolmorogov-Smirnov test), mean density and unit of measurement, number of non-zero observations (N) and proportion of sites occupied (only reported if data source included absence data), geographic location of data, and data source. Numeric codes correspond to numbers in figure S1.

Code	Taxa	Common Name	Latin Name	Status	*k*	λ	Mean density (units)	N (prop. sites occupied)	Region	Source
1	Crayfish	Native crayfish	*Procambarus spp., Orconectes spp.*	Native	1.06	0.82	0.8(#/trap)	32(0.47)	Lake Michigan tributaries	1
2	Crayfish	Northern crayfish	*Orconectes propinquus*	Native	0.58	0.54	1.06(#/trap)	26(0.43)	Wisconsin Lakes	2
3	Crayfish	Rusty crayfish	*Orconectes rusticus*	Invasive	0.62	2.20	3.26(#/trap)	76(0.59)	Wisconsin Lakes; Lake Michigan tributaries	1-3
4	Crayfish	Rusty crayfish	*Orconectes rusticus*	Native	1.14	11.63	11.05(#/site)	21(NA)	Ohio and Kentucky streams	4
5	Crayfish	Virile crayfish	*Orconectes virilis*	Native	0.79	0.30	0.36(#/trap)	31(0.52)	Wisconsin Lakes	2,3
6	Crayfish	Signal crayfish	*Pacifastacus leniusculus*	Invasive	1.23	8.30	7.74(#/trap)	34(NA)	Sweden	5
7	Crayfish	Signal crayfish	*Pacifastacus leniusculus*	Native	0.71	0.62	0.81(#/trap)	53(NA)	Washington Lakes	6

8	North American Fish	Banded darter	*Etheostoma zonale*	Native	0.76	0.16	0.2(#/min)	97(0.06)	Wisconsin streams	7
9	North American Fish	Bigmouth shiner	*Notropis dorsalis*	Native	0.62	0.28	0.47(#/min)	94(0.06)	Wisconsin streams	7
10	North American Fish	Black bullhead	*Ameiurus melas*	Native	**0.67**	**0.12**	0.18(#/min)	250(0.16)	Wisconsin streams	7
11	North American Fish	Black crappie	*Pomoxis nigromaculatus*	Native	1.01	0.08	0.08(#/min)	116(0.08)	Wisconsin streams	7
12	North American Fish	Blacknose shiner	*Notropis heterolepis*	Native	0.67	0.19	0.29(#/min)	199(0.13)	Wisconsin streams	7
13	North American Fish	Blackside darter	*Percina maculata*	Native	0.81	0.19	0.22(#/min)	275(0.18)	Wisconsin streams	7
14	North American Fish	Blackstripe topminnow	*Fundulus notatus*	Native	0.75	0.18	0.23(#/min)	28(0.02)	Wisconsin streams	7
15	North American Fish	Bluegill	*Lepomis macrochirus*	Native	**0.65**	**0.18**	0.28(#/min)	362(0.24)	Wisconsin streams	7
16	North American Fish	Bluntnose minnow	*Pimephales notatus*	Native	0.60	0.50	0.85(#/min)	447(0.28)	Wisconsin streams	1,7
17	North American Fish	Bowfin	*Amia calva*	Native	0.94	0.09	0.09(#/min)	21(0.01)	Wisconsin streams	7

18	North American Fish	Brassy minnow	*Hybognathus hankinsoni*	Native	**0.59**	**0.20**	0.39(#/min)	221(0.15)	Wisconsin streams	7
19	North American Fish	Brook stickleback	*Culaea inconstans*	Native	**0.64**	**0.38**	0.58(#/min)	940(0.62)	Wisconsin streams	7
20	North American Fish	Brook trout	*Salvelinus fontinalis*	Native	0.75	1.08	1.3(#/min)	460(0.3)	Wisconsin streams	7
21	North American Fish	Brown trout	*Salmo trutta*	Invasive	0.66	1.04	1.44(#/min)	201(0.13)	Wisconsin streams	7
22	North American Fish	Burbot	*Lota lota*	Native	0.87	0.11	0.12(#/min)	163(0.11)	Wisconsin streams	7
23	North American Fish	Central mudminnow	*Umbra limi*	Native	**0.63**	**0.35**	0.57(#/min)	1015 (0.63)	Wisconsin streams	1,7
24	North American Fish	Central stoneroller	*Campostoma anomalum*	Native	0.64	0.90	1.31(#/min)	267(0.18)	Wisconsin streams	7
25	North American Fish	Channel catfish	*Ictalurus punctatus*	Native	0.86	0.07	0.08(#/min)	32(0.02)	Wisconsin streams	7
26	North American Fish	Common carp	*Cyprinus carpio*	Invasive	0.54	0.25	0.64(#/min)	103(0.07)	Wisconsin streams	7
27	North American Fish	Common shiner	*Luxilus cornutus*	Native	0.63	1.09	1.6(#/min)	743(0.49)	Wisconsin streams	1,7

28	North American Fish	Creek Chub	*Semotilus atromaculatus*	Native	0.78	0.94	1.09(#/min)	1252 (0.82)	Wisconsin streams	1,7
29	North American Fish	Emerald shiner	*Notropis atherinoides*	Native	0.65	0.33	0.48(#/min)	89(0.06)	Wisconsin streams	7
30	North American Fish	Fantail darter	*Etheostoma flabellare*	Native	**0.56**	**0.49**	0.98(#/min)	417(0.27)	Wisconsin streams	7
31	North American Fish	Fathead minnow	*Pimephales promelas*	Native	**0.59**	**0.26**	0.48(#/min)	437(0.29)	Wisconsin streams	7
32	North American Fish	Finescale dace	*Phoxinus neogaeus*	Native	0.80	0.27	0.31(#/min)	158(0.1)	Wisconsin streams	7
33	North American Fish	Freshwater drum	*Aplodinotus grunniens*	Native	1.03	0.16	0.16(#/min)	26(0.02)	Wisconsin streams	7
34	North American Fish	Golden redhorse	*Moxostoma erythrurum*	Native	0.70	0.13	0.18(#/min)	78(0.05)	Wisconsin streams	7
35	North American Fish	Golden shiner	*Notemigonus crysoleucas*	Native	0.62	0.14	0.25(#/min)	142(0.09)	Wisconsin streams	7
36	North American Fish	Grass pickerel	*Esox americanus vermiculatus*	Native	1.17	0.09	0.08(#/min)	40(0.03)	Wisconsin streams	7
37	North American Fish	Greater redhorse	*Moxostoma valenciennesi*	Native	1.01	0.10	0.1(#/min)	24(0.02)	Wisconsin streams	7

38	North American Fish	Green Sunfish	*Lepomis cyanellus*	Native	**0.71**	**0.18**	0.24(#/min)	404(0.25)	Wisconsin streams	1,7
39	North American Fish	Hornyhead chub	*Nocomis biguttatus*	Native	0.71	0.78	1.01(#/min)	453(0.3)	Wisconsin streams	7
40	North American Fish	Iowa darter	*Etheostoma exile*	Native	0.89	0.09	0.1(#/min)	88(0.06)	Wisconsin streams	7
41	North American Fish	Johnny darter	*Etheostoma nigrum*	Native	**0.74**	**0.42**	0.53(#/min)	951(0.59)	Wisconsin streams	1,7
42	North American Fish	Largemouth bass	*Micropterus salmoides*	Native	**0.79**	**0.13**	0.15(#/min)	294(0.19)	Wisconsin streams	7
43	North American Fish	Largescale stoneroller	*Campostoma oligolepis*	Native	0.63	0.88	1.31(#/min)	98(0.06)	Wisconsin streams	7
44	North American Fish	Logperch	*Percina caprodes*	Native	0.70	0.18	0.25(#/min)	183(0.12)	Wisconsin streams	7
45	North American Fish	Longnose dace	*Rhinichthys cataractae*	Native	0.67	0.32	0.46(#/min)	394(0.26)	Wisconsin streams	7
46	North American Fish	Mimic shiner	*Notropis volucellus*	Native	0.70	0.16	0.21(#/min)	39(0.03)	Wisconsin streams	7
47	North American Fish	Mottled sculpin	*Cottus bairdii*	Native	0.67	0.66	0.93(#/min)	628(0.41)	Wisconsin streams	7

48	North American Fish	Northern hog sucker	*Hypentelium nigricans*	Native	0.77	0.30	0.36(#/min)	183(0.12)	Wisconsin streams	7
49	North American Fish	Northern redbelly dace	*Phoxinus eos*	Native	0.59	0.38	0.68(#/min)	273(0.18)	Wisconsin streams	7
50	North American Fish	Pearl dace	*Margariscus margarita*	Native	0.64	0.37	0.57(#/min)	348(0.23)	Wisconsin streams	7
51	North American Fish	Pumpkinseed sunfish	*Lepomis gibbosus*	Native	**0.68**	**0.12**	0.18(#/min)	267(0.18)	Wisconsin streams	7
52	North American Fish	Rainbow darter	*Etheostoma caeruleum*	Native	0.76	0.50	0.59(#/min)	76(0.05)	Wisconsin streams	7
53	North American Fish	Rainbow trout	*Oncorhynchus mykiss*	Invasive	0.63	0.43	0.61(#/min)	43(0.03)	Wisconsin streams	7
54	North American Fish	Redbelly dace	*Phoxinus eos*	Native	0.61	0.80	1.21(#/min)	39(0.03)	Wisconsin streams	7
55	North American Fish	Redside dace	*Clinostomus elongatus*	Native	0.72	0.36	0.45(#/min)	75(0.05)	Wisconsin streams	7
56	North American Fish	Rock Bass	*Ambloplites rupestris*	Native	0.79	0.21	0.24(#/min)	277(0.17)	Wisconsin streams	1,7
57	North American Fish	Rosyface shiner	*Notropis rubellus*	Native	0.80	0.29	0.33(#/min)	92(0.06)	Wisconsin streams	7

58	North American Fish	Round goby	*Neogobius melanostomus*	Invasive	0.67	0.83	1.16(#/min)	60(0.04)	Wisconsin streams	1,7
59	North American Fish	Sand shiner	*Notropis stramineus*	Native	0.61	0.52	0.87(#/min)	114(0.07)	Wisconsin streams	7
60	North American Fish	Shorthead redhorse	*Moxostoma macrolepidotum*	Native	0.78	0.17	0.21(#/min)	159(0.1)	Wisconsin streams	7
61	North American Fish	Silver redhorse	*Moxostoma anisurum*	Native	0.80	0.11	0.13(#/min)	48(0.03)	Wisconsin streams	7
62	North American Fish	Slimy sculpin	*Cottus cognatus*	Native	0.78	1.05	1.24(#/min)	78(0.05)	Wisconsin streams	7
63	North American Fish	Smallmouth bass	*Micropterus dolomieu*	Native	0.71	0.23	0.3(#/min)	238(0.16)	Wisconsin streams	1,7
64	North American Fish	Southern redbelly dace	*Phoxinus erythrogaster*	Native	0.57	0.95	1.7(#/min)	184(0.12)	Wisconsin streams	7
65	North American Fish	Spotfin shiner	*Cyprinella spiloptera*	Native	0.66	0.51	0.72(#/min)	114(0.07)	Wisconsin streams	7
66	North American Fish	Stonecat	*Noturus flavus*	Native	0.84	0.10	0.12(#/min)	111(0.07)	Wisconsin streams	7
67	North American Fish	Suckermouth minnow	*Phenacobius mirabilis*	Native	0.79	0.21	0.25(#/min)	26(0.02)	Wisconsin streams	7

68	North American Fish	Tadpole madtom	*Noturus gyrinus*	Native	0.84	0.08	0.09(#/min)	51(0.03)	Wisconsin streams	7
69	North American Fish	Troutperch	*Percopsis omiscomaycus*	Native	0.69	0.25	0.32(#/min)	24(0.02)	Wisconsin streams	7
70	North American Fish	Western blacknose dace	*Rhinichthys obtusus*	Native	0.72	0.66	0.84(#/min)	803(0.53)	Wisconsin streams	7
71	North American Fish	White sucker	*Catostomus commersonii*	Native	0.71	0.84	1.06(#/min)	1184 (0.74)	Wisconsin streams	1,7
72	North American Fish	Yellow bullhead	*Ameiurus natalis*	Native	**0.71**	**0.10**	0.15(#/min)	144(0.09)	Wisconsin streams	7
73	North American Fish	Yellow perch	*Perca flavescens*	Native	**0.63**	**0.21**	0.34(#/min)	225(0.15)	Wisconsin streams	7
74	North American Fish	American brook lamprey ammocoete	*Lampetra appendix*	Native	0.66	0.39	0.54(#/min)	122(0.45)	North American Great Lakes tributaries	8
75	North American Fish	Ichthyomyzon spp. ammocoete	*Icthyomyzon spp.*	Native	0.72	0.20	0.25(#/min)	26(0.16)	North American Great Lakes tributaries	8
76	North American Fish	Sea lamprey ammocoete	*Petromyzon marinus*	Invasive	0.78	0.85	0.99(#/min)	260(0.97)	North American Great Lakes tributaries	8

77	Swedish fish	Brown trout	*Salmo trutta*	Native	0.67	13.46	18.18(#/100 m^2)	416(0.36)	Vasterbotten county, Sweden	9
78	Swedish fish	Brook trout	*Salvelinus fontinalis*	Invasive	0.61	6.86	11.49(#/100 m^2)	57(0.05)	Vasterbotten county, Sweden	9
79	Swedish fish	Grayling	*Thymallus thymallus*	Native	**0.84**	**1.57**	1.8(#/100 m^2)	352(0.3)	Vasterbotten county, Sweden	9
80	Swedish fish	Northern pike	*Esox lucius*	Native	**0.90**	**1.35**	1.45(#/100 m^2)	343(0.3)	Vasterbotten county, Sweden	9
81	Swedish fish	Burbot	*Lota lota*	Native	**0.89**	**1.59**	1.71(#/100 m^2)	511(0.44)	Vasterbotten county, Sweden	9
82	Swedish fish	Eurasian minnow	*Phoxinus phoxinus*	Native	0.64	12.23	18.44(#/100 m^2)	550(0.47)	Vasterbotten county, Sweden	9
83	Swedish fish	Bullhead	*Cottus gobio*	Native	0.76	20.24	25.09(#/100 m^2)	658(0.57)	Vasterbotten county, Sweden	9
84	Swedish fish	European brook lamprey	*Lampetra planeri*	Native	0.75	2.14	2.78(#/100 m^2)	177(0.15)	Vasterbotten county, Sweden	9
85	Swedish fish	European perch	*Perca fluviatilis*	Native	0.74	2.43	3.16(#/100 m^2)	138(0.12)	Vasterbotten county, Sweden	9
86	Plant	Coontail	*Ceratophyllum demersum*	Native	0.87	23.49	25.08 (Frequency of occurrence)	161(0.73)	Wisconsin Lakes	7

87	Plant	Muskgrass	*Chara spp.*	Native	0.97	29.39	29.75 (Frequency of occurrence)	175(0.69)	Wisconsin Lakes	7
88	Plant	Canadian waterweed	*Elodea canadensis*	Native	0.88	15.62	16.61 (Frequency of occurrence)	140(0.67)	Wisconsin Lakes	7
89	Plant	Quillwort	*Isoetes spp.*	Native	0.82	3.85	4.39 (Frequency of occurrence)	50(0.56)	Wisconsin Lakes	7
90	Plant	Eurasian water milfoil	*Myriophyllum spicatum*	Invasive	0.85	19.76	8.71 (Frequency of occurrence)	100(0.21)	Wisconsin Lakes	7
91	Plant	Shortspike water milfoil	*Myriophyllum sibiricum*	Native	0.94	8.43	21.3 (Frequency of occurrence)	117(0.69)	Wisconsin Lakes	7
92	Plant	Slender water milfoil	*Myriophyllum tenellum*	Native	0.93	5.48	5.67 (Frequency of occurrence)	50(0.5)	Wisconsin Lakes	7
93	Plant	Nodding waternymph	*Najas flexilis*	Native	0.81	15.00	17 (Frequency of occurrence)	165(0.55)	Wisconsin Lakes	7
94	Plant	Stonewort	*Nitella spp.*	Native	0.89	11.44	12.15 (Frequency of occurrence)	132(0.54)	Wisconsin Lakes	7
95	Plant	Varigated yellow pond lily	*Nuphar variegata*	Native	0.96	4.43	4.53 (Frequency of occurrence)	135(0.5)	Wisconsin Lakes	7
96	Plant	Fragrant waterlily	*Nymphaea odorata*	Native	0.91	6.51	6.85 (Frequency of occurrence)	164(0.49)	Wisconsin Lakes	7
97	Plant	Largeleaf pondweed	*Potamogeton ampifolius*	Native	1.04	8.80	8.67 (Frequency of occurrence)	120(0.21)	Wisconsin Lakes	7

98	Plant	Curly leaf pondweed	*Potamogeton crispus*	Invasive	0.71	7.38	9.49 (Frequency of occurrence)	63(0.59)	Wisconsin Lakes	7
99	Plant	Small pondweed	*Potamogeton pusillus*	Native	0.86	8.64	9.39 (Frequency of occurrence)	129(0.26)	Wisconsin Lakes	7
100	Plant	Flatstem pondweed	*Potamogeton zosteriformis*	Native	0.89	10.49	11.09 (Frequency of occurrence)	119(0.42)	Wisconsin Lakes	7
101	Plant	Wild celery	*Vallisneria americana*	Native	0.94	11.28	11.62 (Frequency of occurrence)	128(0.54)	Wisconsin Lakes	7
102	Snail	Mud amnicola	*Amnicola limosa*	Native	0.63	9.52	13.97(#/2 m^2)	36(0.64)	Wisconsin Lakes	10
103	Snail	Chinese mystery snail	*Bellamya chinensis*	Invasive	0.55	0.55	1.1(#/2 m^2)	22(0.45)	Wisconsin Lakes	10
104	Snail	Ponted campeloma	*Campeloma decisum*	Native	0.79	0.27	0.31(#/2 m^2)	20(0.68)	Wisconsin Lakes	10
105	Snail	Flexed gyro snail	*Gyraulus deflectus*	Native	1.01	0.88	0.88(#/2 m^2)	26(0.59)	Wisconsin Lakes	10
106	Snail	Ash gyro snail	*Gyraulus parvus*	Native	0.82	0.56	0.63(#/2 m^2)	28(0.82)	Wisconsin Lakes	10
107	Snail	Two-ridge rams horn	*Helisoma anceps*	Native	0.75	1.00	1.22(#/2 m^2)	29(0.66)	Wisconsin Lakes	10
108	Snail	NA	*Helisoma campanulata*	Native	0.77	0.53	0.63(#/2 m^2)	30(0.66)	Wisconsin Lakes	10
109	Snail	Boreal marstonia	*Marstonia lustrica*	Native	0.54	2.75	5.53(#/2 m^2)	28(0.5)	Wisconsin Lakes	10
110	Snail	Tadpole physa	*Physa gyrina*	Native	0.65	0.47	0.66(#/2 m^2)	29(0.64)	Wisconsin Lakes	10

111	Zebra mussel	Zebra mussel	*Dresseina polymorpha*	Invasive	0.95	983.88	1012.6(#/m^2)	55(NA)	Europe	11
112	Zebra mussel	Zebra mussel	*Dresseina polymorpha*	Invasive	0.63	5500.00	12377.1(#/m^2)	20(NA)	North America	11-15

[1] M. Kornis, unpublished data

[2] North Temperate Lakes Ecological Research, available online at http://lter.limnology.wisc.edu/.

[3] E. Nilsson, unpublished data

[4] R.F. Jezerinac *Ohio J. Sci.* **82**, 181 (1982).

[5] P. Nystrom *et al.,Freshw. Biol.* **51**, 2096 (2006).

[6] E. Larson and J. Olden, unpublished data

[7] Wisconsin Department of Natural Resources

[8] United States Fish and Wildlife Service, Department of Fisheries and Oceans Canada

[9] Swedish electrofishing register, available online at www.fiskeriverket.se

[10] **C.T. Solomon *et al., Biol. Invasions* 12, 1591 (2010).**

[11] R. Naddafi *et al., Hydrobiologia* online, DOI: 10.1007/s10750-011-0689-1 (2011).

[12] R.C. Baily *et al., J. Great Lakes Res.* **25**, 482 (1999).

[13] A.Y. Karatayev, L.E. Burlakova, *Wisconsin DNR Aquatic Invasive Species Grants Program,* pp 67 (2008).

[14] J.L. Mercer *et al., Lake Reservoir Manage.***15**, 310 (1999).

[15] A. Ricciardi *et al., **Can. J. Fish. Aquat. Sci.*** **54, 2596 (1997).**

Table S4. Two-way ANOVA results for comparison of the Weibull parameters *k* and λ among taxonomic groups and invasive and native species. Results were similar when only species for which the Weibull distribution fit were used (Weibull fit only), and when all data were included, including 16 native fishes for which the Weibull distribution failed to describe the data.

Effect	**DF**	**Sum Sq.**	**Mean Sq.**	**F-value**	**p-value**
		k			
Weibull fit only (Adjusted R^2=0.18, p-value=0.003)					
Taxa	5	0.412	0.082	4.718	0.001
Invasive status	1	0.067	0.067	3.851	0.053
Interaction (Taxa*Invasive status)	4	0.050	0.012	0.712	0.586
Residuals	85	1.485	0.017		
All data (Adjusted R^2=0.18, p-value<0.001)					
Taxa	5	0.460	0.092	5.574	<0.001
Invasive status	1	0.064	0.064	3.858	0.052
Interaction (Taxa*Invasive status)	4	0.055	0.014	0.831	0.509
Residuals	101	1.669	0.017		
		λ			
Weibull fit only (Adjusted R^2=0.80, p-value<0.001)					
Taxa	4	186.670	46.668	70.011	<0.001
Invasive status	1	3.987	3.987	5.981	0.017
Interaction (Taxa*Invasive status)	4	4.818	1.205	1.807	0.135
Residuals	83	55.326	0.667		
All data (Adjusted R^2=0.75, p-value<0.001)					
Taxa	4	203.008	50.752	78.668	<0.001
Invasive status	1	5.075	5.075	7.866	0.006
Interaction (Taxa*Invasive status)	4	4.462	1.116	1.729	0.150
Residuals	99	63.870	0.645		

Table S5. Results of two-way ANOVA comparing statistical moments of invasive and native species. Taxa was included as a factor to account for differences in measurement units among taxonomic groups. One species of native crayfish was excluded from the comparison of crayfish means due to differences in measured units, and zebra mussels were excluded because they lacked native counterparts.

Effect	Df	Sum Sq.	Mean Sq.	F-value	p-value
Mean (Adjusted R^2=0.70; p-value<0.001)					
Taxa	4	181.75	45.44	60.39	<0.001
Invasive status	1	7.12	7.12	9.46	0.003
Interaction (Taxa*Invasive status)	4	3.08	0.77	1.02	0.399
Residuals	99	74.49	0.75		
CV (Adjusted R^2=0.27; p-value<0.001)					
Taxa	4	4.26	1.07	11.28	<0.001
Invasive status	1	0.01	0.01	0.09	0.787
Interaction (Taxa*Invasive status)	4	0.39	0.10	1.03	0.398
Residuals	99	9.36	0.09		
Skewness (Adjusted R^2=0.35; p-value<0.001)					
Taxa	4	14.66	3.67	16.37	<0.001
Invasive status	1	0.18	0.18	0.79	0.376
Interaction (Taxa*Invasive status)	4	0.24	0.06	0.27	0.895
Residuals	99	22.17	0.22		
Skewness (Adjusted R^2=0.33; p-value<0.001)					
Taxa	4	41.41	10.35	15.08	<0.001
Invasive status	1	0.71	0.71	1.04	0.31
Interaction (Taxa*Invasive status)	4	0.42	0.10	0.15	0.96
Residuals	99	67.95	0.69		

Table S6. Fitted *k* and standardized λ for native and invasive species of the same species, genus, or subfamily, and whether the comparison supports the hypotheses that invasive species will be less right skewed (higher *k*) and more abundant (higher standardized λ) than their native counterparts. Standardized λ was calculated by subtracting the taxa-specific mean LN(λ) from the fitted LN(λ) for each species for comparison of densities sampled in different units.

	Species (region)		***k***			**Standardized λ**		
Comparison	**Invasive**	**Native**	**Inv.**	**Nat.**	**I>N?**	**Inv.**	**Nat.**	**I>N?**
Brook trout	*Salvelinus fontinalis* (Sweden)	*Salvelinus fontinalis* (Wisconsin)	0.61	0.75	*No*	-0.02	1.28	*No*
Brown trout	*Salmo trutta* (Wisconsin)	*Salmo trutta* (Sweden)	0.66	0.67	*No*	1.25	0.65	*Yes*
Rusty crayfish	*Orconectes rusticus* (Wisconsin)	*Orconectes rusticus* (Ohio)	0.62	1.14	*No*	0.71	NA	
Signal Crayfish	*Pacifastacus leniusculus* (Sweden)	*Pacifastacus leniusculus* (Washington)	1.23	0.71	*Yes*	2.05	-0.55	*Yes*
Pondweeds (*Potamogeton spp.)*	*P. crispus* (Wisconsin)	*P. zosteriformis* (Wisconsin)	0.71	0.89	*No*	-0.32	0.03	*No*
		P. ampifolius (Wisconsin)		1.04			-0.14	
		P. pusillus (Wisconsin)		0.86			-0.16	
Milfoils (*Myriophyllum spp.)*	*M. spicatum* (Wisconsin)	*M. sibiricum* (Wisconsin)	0.85	0.94	*No*	0.67	-0.18	*Yes*
		M. tenellum (Wisconsin)		0.93			-0.61	
Lampreys (Subfamily *Petromyzontinae)*	*Petromyzon marinus* (Great Lakes)	*Lampetra appendix* (Great Lakes)	0.78	0.66	*Yes*	1.05	0.27	*Yes*
		Lampetra planeri (Great Lakes)		0.75			-1.18	
		Ichthyomyzon spp. (Great Lakes)		0.72			-0.42	
Total supporting hypothesis of invasive>native					**2/7**			**4/7**

Supplementary Material Literature Cited

Jezerinac R.F. (1982) Life-history notes and distributions of crayfishes (Decapoda:Cambaridae) from the Chagrin River basin, Northeastern Ohio. *Ohio Journal of Science*, 84, 181-192

Mikulyuk A.M., Hauxwell J., Rasmussen P., Knight S., Wagner K.I., Nault M. & Ridgely D. (2010) Testing a methodology for assessing plant communities in temperate inland lakes. *Lake and Reservoir Management*, 26, 54-62

Naddafi R., Blenckner T., Eklov P. & Pettersson K. (2011) Physical and chemical properties determine zebra mussel invasion success in lakes. *Hydrobiologia*, 669, 227-236

Nystrom P., Stenroth P., Holmqvist N., Berglund O., Larsson P. & Graneli W. (2006) Crayfish in lakes and streams: individual and population responses to predation, productivity, and substratum availibility. *Freshwater Biol.*, 51, 2096-2113

Solomon C.T., Olden J.D., Johnson P.T.J., Dillon R.T. & Vander Zanden M.J. (2010) Distribution and community-level effects of the Chinese mystery snail (*Bellamya chinensis*) in northern Wisconsin lakes. *Biol. Invasions*, 12, 1591-1605

CHAPTER TWO

RAPID TRANSITIONS BETWEEN INVASIVE AND NATIVE SPECIES DOMINANCE DRIVEN BY DROUGHT-MEDIATED HABITAT LOSS

To be submitted for publication with coauthors Anthony. R. Ives, M. Jake Vander Zanden and Stephen R. Carpenter

Abstract

Ecological communities are influenced by both biotic and abiotic drivers, as well as their interaction. As a result, altered environmental conditions can influence the strength of interspecific interactions, potentially resulting in alternative stable states under certain conditions. In this study, we examine the interactions between invasive rusty crayfish (*Orconectes rusticus*) and native fishes and how drought-mediated changes in water level can alter the outcome of species interactions. We also evaluate the empirical evidence for alternative stable states. We use a stage-structured, multi-species time series model fit to 29 years data from two lakes including a 10 year whole lake removal of rusty crayfish. Rusty crayfish density was driven by a combination of sunfish (*Lepomis* spp.) density, water level, and the experimental crayfish removal. The model results predict that a reciprocal negative interaction between rusty crayfish and *Lepomis* spp. can produce alternative stable states under some water level conditions, where each species is capable of excluding the other

contingent upon initial densities. However, alternative states did not occur across the entire range of plausible parameter estimates. Regardless of the existence of alternative states, rapid transitions from rusty crayfish to *Lepomis* spp. domination are possible as a result of changing water levels. Altered precipitation patterns as a result of climate change may indirectly affect the establishment and impact of invasive rusty crayfish in northern lakes.

Introduction

Ecological communities are structured by both biotic and abiotic factors, and community structure can only be fully understood by accounting for both types of drivers (Dunson and Travis 1991). Abiotic conditions can reduce the effects of biotic interactions such as predation (e.g., Savino and Stein 1982, Holt 1984, Leigh et al. 1987, Menge and Sutherland 1987, Diehl 1992, Power 1992, Warfe and Barmuta 2006) and competition (e.g., Menge 1976, Chesson 1986, Wilson and Keddy 1986, Bergelson 1990, Chesson 2000), and as a consequence environmental variation allows the coexistence of species that could not occur in homogenous environments (e.g., Hutchinson 1961, Paine 1966, Chesson 1986, Menge and Sutherland 1987, Svanbã¤Ck and Bolnick 2007). Abiotic factors can also change the outcome of competitive interactions, such that a superior competitor that excludes another species under one set of conditions is inferior and outcompeted under others (e.g., Snaydon 1962, Pigott and Taylor 1964, Tilman 1987, Dunson and Travis 1991, Mason et al. In press). When the range of abiotic conditions favoring one competitor over another is narrow, rapid transitions from one species dominating to another can occur over a very narrow range of environmental parameters (e.g., Park 1962). Such rapid shifts in abundance are characteristic of competitive interactions, since relatively minor changes in performance can shift the balance from one competitor to another due to positive feedbacks (Connell 1961, Frost et al. 1995, Wilson and Nisbet 1997).

Species invasions and climate change are two of the most important drivers of global environmental change (Sala et al. 2000, Tylianakis et al. 2008). When a non-native species invades a community, they can influence biotic interactions via many mechanisms including predation (Ogutu-Ohwayo 1990, Simon and Townsend 2003, Snyder and Evans 2006, Sih et al. 2010) and competition (Spencer et al. 1991, Pace et al. 1998, Courchamp et al. 2000, Orrock et al. 2008, Epanchin et al. 2010). Some invasive species may also act as ecosystem engineers by influencing abiotic conditions (Crooks 2002, Gratton and Denno 2005, Zhu et al. 2006). By definition, climate change alters abiotic conditions which can affect organisms in terms of their physiological tolerances, and in doing so can also influence biotic interactions (Lodge 1993, Loeb et al. 1997, Walther et al. 2002, Winder and Schindler 2004). In some cases the indirect effects of changing climactic conditions can override autecological responses (Suttle *et al.* 2007). Because both can influence biotic and abiotic conditions, climate change and species introductions can interact in complex and non-intuitive ways to alter community structure and function (Hellmann et al. 2008, Selbie et al. 2011).

Rusty crayfish (*Orconectes rusticus*) are invasive in north temperate aquatic ecosystems, and interact strongly with multiple trophic levels (Lodge et al. 1994, Wilson et al. 2004, McCarthy et al. 2006, Roth et al. 2007). However, some systems resist the negative effects of invasion; rusty crayfish establish self-sustaining populations, but persist at low densities with minimal effects (Garvey et al. 2003, Roth et al. 2007). The two distinct lake types of relative rusty crayfish abundance may be the result of variation in predation by native fishes, including bluegill and pumpkinseed sunfish (*Lepomis macrochirus and L. gibbosus, hereafter Lepomis)* (Roth et al. 2007, Tetzlaff et al. 2010) and other fishes such as smallmouth bass (*Micropterus dolomieu*), largemouth bass (*M. salmoides*), rock bass (*Ambloplites rupestris*), walleye (*Sander vitreus*), and yellow perch (*Perca flavescens*) (Mather and Stein 1993, Lodge and Hill 1994, Garvey et al. 2003). Rusty crayfish abundance is also influenced by habitat availability, specifically the abundance of cobble substrate in a lake (Lorman 1980, Capelli and Magnuson 1983), and habitat may interact with predation to determine rusty crayfish abundance. Because crayfish use cobble substrate to avoid predation (Kershner and Lodge 1995), the impact of predators is likely to be lower in structurally complex lakes such as those with abundant cobble than in lakes with less structure (Lodge and Hill 1994, Garvey et al. 2003). In recent years drought has resulted in the lowest water levels on record in north temperate seepage lakes (www.lter.limnology.wisc.edu), dramatically reducing cobble habitat and thus habitat heterogeneity in lakes where cobble is concentrated in shallow areas.

Rusty crayfish act as ecosystem engineers, reducing habitat heterogeneity by destroying macrophytes (Lodge and Lorman 1987, Olsen et al. 1991, Wilson et al. 2004, Rosenthal et al. 2006), thereby negatively affecting the recruitment of *Lepomis* (Dorn and Mittelbach 2004, Wilson et al. 2004). The interaction between *Lepomis* and rusty crayfish is therefore complex: although *Lepomis* prey upon rusty crayfish juveniles, the relationship between the two groups is more akin to a competitive relationship where each negatively affects the recruitment of the other (Chesson 1986). Positive feedbacks between rusty crayfish and *Lepomis* could result in alternative stable states (sensu May 1977, Case 1990, Beisner et al. 2003, Scheffer and Carpenter 2003). Alternative stable states can exist in communities where initial conditions such as the order in which species arrive determine population trajectories and densities of interacting species (Schoener 1974, Paine et al. 1985, Petraitis and Latham 1999). In this case, high densities of rusty crayfish reduce habitat necessary for the survival of one of their main predators (Tetzlaff *et al.* 2010), thus allowing further expansion of their own population and further reduction in macrophyte habitat (Roth *et al.* 2007). Because drought has the potential to increase predation on juvenile rusty crayfish that depend upon cobble for shelter (Lodge and Hill 1994), this positive feedback may be influenced by climate-driven fluctuation in water levels.

The complex interactions between climate, habitat, competition, and predation in systems invaded by rusty crayfish could result in alternative stable states under some climate conditions but not others (e.g., Chase 1999, Mylius et al. 2001, Chase 2003). However, the existence of positive feedbacks does not necessarily generate alternative stable states (Scheffer *et al.* 2001), and patterns predicted to exist under alternative stable states can also result from threshold responses to drivers that do not involve alternative states (Scheffer and Carpenter 2003). Evidence for alternative states can be demonstrated mathematically using time-series data (e.g, Ives et al. 2008, Schooler et al. 2011), and experimental manipulation can greatly increase the probability of detecting alternative stable states (Carpenter *et al.* 2003). We used 29 years of time-series data, including a 10-year experimental crayfish removal, to quantify the effects of climactic conditions on species interactions and to evaluate empirically the evidence for alternative stable states in two lakes invaded by rusty crayfish. Drought conditions resulted in lowered water level and thus substantially reduced cobble habitat during the experimental manipulation. It is unknown which of multiple potential drivers (predation, trapping, or water level) is responsible for the reduction in rusty crayfish observed during the whole-lake manipulation, and how the rusty crayfish population will respond to the cessation of trapping and future water level scenarios. In this study, we (1) quantify empirical relationships between rusty crayfish, fish, trapping, and climate-driven fluctuations in water level; (2) evaluate the evidence for alternate stable states vs. a threshold response that does not include alternative states; and (3) identify the conditions that allow systems to shift between high and low rusty crayfish population densities, regardless of whether alternative states are predicted.

(2) *Materials and methods*

Study Systems

To quantify the relationships between rusty crayfish, fish, water levels, and trapping (Figure 1) we used time-series data collected from 1981-2009 in two north temperate lakes, both part of the North Temperate Lakes Long Term Ecological Research site in Vilas County, Wisconsin, U.S.A. (http://lter.limnology.wisc.edu). Sparkling Lake (46°00’N, 89°42’W) is a 64-ha mesotrophic seepage lake (maximum depth = 20.0 m, shoreline perimeter= 4.3 km). Rusty crayfish invaded Sparkling Lake in the 1970’s (Capelli 1982). Adult rusty crayfish were removed via trapping from 2001-2008, and fishing regulations were changed on smallmouth bass and walleye to increase predation on juvenile crayfish (Hein et al. 2006). The littoral zone habitat of Sparkling Lake is composed primarily of sand, with areas of cobble located in shallow waters (Hein et al. 2006). Water levels declined in Sparkling Lake from 2005-2009 and the water level in 2009 was the lowest on record (http://lter.limnology.wisc.edu). During this period the majority of cobble habitat was exposed as a result of declining water levels. Long-term data collection from Sparkling Lake began after rusty crayfish established. For data on the initial phase of invasion, we used nearby Trout Lake (46°2′N, 89°40′W), a 1608-ha mesotrophic drainage lake (maximum depth 35.7 m, shoreline perimeter 26 km). Rusty crayfish invaded Trout Lake in the 1970's but did not disperse around the entire lake for over two decades (Wilson *et al.* 2004). The majority of littoral zone habitat in Trout Lake consists of cobble (Roth *et al.* 2007), and due to its hydrology and the depth of cobble habitats, neither water levels nor area of cobble have been affected by the recent drought conditions (http://lter.limnology.wisc.edu). No manipulations have occurred to rusty crayfish or fishing regulations in Trout Lake.

Data collection

Data, methods, and equipment descriptions are available online (http://lter.limnology.wisc.edu). Rusty crayfish and fish abundances were indexed in both lakes using annual catch per unit effort (CPUE) of each group from 1981-2009. Annual mean CPUE and standard error were calculated using the catch per trap for rusty crayfish and catch per fyke net of *Lepomis* greater than 80 mm total length. Zero annual counts were replaced by one half of the lowest observed non-zero values, and both rusty crayfish and *Lepomis* CPUE were natural log transformed. Total (non-*Lepomis*) predatory fish abundance was estimated using catch rates of largemouth bass (*Micropterus salmoides*), rock bass (*Ambloplites rupestris*), smallmouth bass, and walleye greater than 80 mm in total length from fyke nets. Crayfish and fish data were standardized to have mean 0 and variance 1. Mean annual water level was calculated from LTER data from 1984-2009. To generate water-level data prior to 1984, we calculated the annual mean from 1978-2009 of the depth of a nearby United States Geological Survey groundwater well (Latitude 45°55'17"N, 89°14'40"W; available online at http://groundwaterwatch.usgs.gov/AWLSites.asp?S=455517089144001&ncd) and estimated the water level of Sparkling Lake by interpolating based on the linear relationship between the USGS data and Sparkling Lake data.

Time-series model

We used an age-structured time-series model to quantify drivers of change in rusty crayfish and *Lepomis* abundance from 1981-2009, and fit a single model to the data from Trout and Sparkling lakes simultaneously. Our model has the potential to produce alternative stable states but their existence depends on the combination of parameter estimates; the model thus provides an opportunity to evaluate the possibility that alternative stable states explain observed dynamics. The model has a non-linear state space form (Harvey 1989) and therefore allows us to account for process errors (due to poor model fit) and observation errors (due to sampling variability). The model is based on three sets of equations: one for the biological processes driving rusty crayfish dynamics, one for the biological processes driving *Lepomis* dynamics, and one to describe the sampling used to generate observed data. All variables were modelled on a one-year time step.

To model the dynamics of rusty crayfish, we used the set of equations

$$x_1(t) = x_3(t-1)e^{r_x - k_x x_3(t-1) - a_x y_2(t-1) - c_{lake} u_2(t) - v u_3(t)}$$

$$x_2(t) = x_1(t-1)$$

$$x_3(t) = \left(x_2(t-1) + d_x x_3(t-1)\right)e^{-m u_1(t) + \varepsilon_x(t)} \qquad (1)$$

where $x_1(t)$, $x_2(t)$ and $x_3(t)$ denote the densities of young-of-year, juvenile, and adult (trappable) crayfish in year t. The predictor variables $u_1(t)$, $u_2(t)$ and $u_3(t)$ give the trapping pressure on adult rusty crayfish, lake level, and the density of predatory fish in year t. The trapping pressure $u_1(t)$ was measured as the number of adult crayfish removed during the manipulation divided by the abundance index of rusty crayfish caught in the same year, with the parameter m translating the trapping pressure into the survival of adult crayfish, $e^{-m u_1(t)}$. Lake level, $u_2(t)$, reduces the number of crayfish recruited by the proportion $e^{-c_{lake} u_2(t)}$, although this is treated differently between lakes. For Sparkling Lake the value of $u_2(t)$ is the height of the lake standardized to have variance 1 and maximum value 0. The coefficient $c_{\text{Sparkling}}$ measures the possible dependence of crayfish recruitment on lake level. For Trout Lake, we assumed that variation in lake level had no effect on habitat suitability for crayfish, and we therefore set lake level to a constant value of $u_2(t) = 1$ to reflect differences in overall habitat suitability between lakes. Thus, the coefficient c_{Trout} measures differences between lakes in overall crayfish recruitment. The recruitment of young-of-year crayfish in a given year, $x_1(t)$, depends on the density $x_3(t–1)$ of adults from the previous year multiplied by $e^{r_x - k_x x_3(t-1)}$, where r_x sets the maximum per capita recruitment rate, and k_x scales the strength of adult-density-dependent reduction in recruitment. The negative effects of *Lepomis* (via predation) occur on juvenile crayfish, with $e^{-a_x y_2(t-1)}$ giving the proportion of young-of-year that survive predation; as the parameter a_x increases, the per capita predation rate on crayfish increases. Similarly, the effect of total predatory fish density (excluding *Lepomis*) on crayfish recruitment is given by $e^{-v u_3(t)}$, where v scales the strength of predation.

The density of adults in year t depends on the density of juveniles and adults in year t–1, with the adult density discounted by the parameter d_x giving adult survival. Adults experience lognormal process error described by the Gaussian random variable $\varepsilon_x(t)$ that has zero mean and standard deviation σ_x. The survivals of young-of-year and juveniles are subsumed within the recruitment of juveniles, r_x, because only adult densities were estimated. Similarly, we did not include an effect of random environmental fluctuation on young-of-year and juvenile density, because we included environmental variation in adult density $\varepsilon_x(t)$.

The *Lepomis* dynamics were modeled by the equations

$$y_1(t) = y_2(t-1)e^{r_y - k_y y_2(t-1) - a_y x_3(t-1)}$$
$$y_2(t) = \left(y_1(t-1) + d_y y_2(t-1)\right)e^{\varepsilon_y(t)} \qquad (2)$$

where $y_1(t)$ and $y_2(t)$ denote the densities of juvenile and adult fish in year t. The structure of these equations is similar to those for crayfish. The recruitment of juvenile fish, $y_1(t)$, depends on the density $y_2(t–1)$ of adults in the previous year multiplied by $e^{r_y - k_y y_2(t-1)}$, where r_y sets the maximum per capita recruitment rate, and k_y scales the strength of adult-density-dependent reduction in recruitment. The negative effect of adult rusty crayfish on *Lepomis* recruitment leads to a proportion of $e^{-a_y x_3(t-1)}$ juveniles that survive. Although rusty crayfish have the potential to influence Lepomis survival via both trophic (egg predation) and non-trophic (macrophyte habitat destruction) pathways, data on macrophyte abundance was not available for the full time series and thus both types of negative effects are encompassed in the single term a_y. The density of adults in year t depends on the density of juveniles and adults in year t–1, with the adult density discounted by the parameter d_y giving adult survival. Adults experience lognormal process error described by the Gaussian random variable $\varepsilon_y(t)$ that has zero mean, standard deviation σ_y, and correlation ρ with the variation for crayfish, $\varepsilon_x(t)$. As with crayfish, the model does not include a parameter for the survival of juveniles to adulthood or environmental variation in juvenile survival, because we only have observations of adult densities.

In the state-space model, the set of equations that describes the sampling (measurement) process are

$$\begin{aligned} X_3(t) &= \log x_3(t) + \alpha_x(t) \\ Y_2(t) &= \log y_2(t) + \alpha_y(t) \end{aligned} \qquad (3)$$

where $X_3(t)$ and $Y_2(t)$ are the observed log densities of adult crayfish and *Lepomis*, respectively, and $\alpha_x(t)$ and $\alpha_y(t)$ are Gaussian random variables with mean zero and standard deviations $\sigma_{sx}(t)$ and $\sigma_{sy}(t)$, respectively. We computed the standard errors of the observed log densities of crayfish and fish in each year to give estimates of $\sigma_{sx}(t)$ and $\sigma_{sy}(t)$ for each year t. Preliminary analyses suggested that the modelled estimates of measurement standard errors did not fit the observed estimates well, so we fit scaling parameters s_x and s_y in the time-series analysis to give the time-dependent measurement error variances of $s_x\ \sigma^2_{sx}(t)$ and $s_y\ \sigma^2_{sy}(t)$.

The maximum log likelihood (MLL) of the model fit to the data on crayfish and *Lepomis* dynamics in both lakes was calculated using an extended (non-linear) Kalman filter (Harvey 1989). Adult population values at the first time point for each lake were set to the observed values, and juvenile values (that were not measured) were back-calculated assuming the population size of adults was not changing. Initial values of the variance in population values for crayfish and *Lepomis* were assumed to be σ^2_x and σ^2_y, with correlation ρ between crayfish and *Lepomis*.

Parametric bootstrapping

Following selection of the model that best fit the observed data, we performed parametric bootstrapping to approximate the distributions of the parameter estimates. Using parameter values estimated from the MLL model fit to observed data (MLL parameters), the dynamics of crayfish and *Lepomis* were simulated 1000 times using the full state-space model, including process and measurement error (Eqs 1-3). The state-space model was subsequently fit to each of the 1000 simulated data sets to give 1000 sets of bootstrapped parameter values. The distributions of these parameter values approximate the distributions of the estimators of the parameters. We also examined the distribution of the MLLs obtained from the 1000 simulations. As an informal check on the fit of the model to the data, the MLL for the data should be similar to the MLL values computed for the simulated data set. If the MLL for the data is lower than the values for the simulations, this would suggest that the model does not fit the data well.

Alternative stable states

We used the MLL parameters and the 1000 bootstrapped parameter sets to evaluate the strength of evidence for alternative stable states in the crayfish-*Lepomis* system. Specifically, for each parameter set we performed an invasibility analysis in which one species was assumed to reach equilibrium abundance, and then the per capita population growth rate of the second species was computed mathematically as it invaded the first species (May 1973). Performing this invasibility analysis reciprocally for both species allowed us to categorize the parameter set as: (i) crayfish always win, (ii) *Lepomis* always win, (iii) both species coexist, and (iv) alternative stable states exist in which either species once established can thwart the invasion of the other.

We performed the invasibility analysis for a range of fixed values of water level, $u_2(t)$. Trapping pressure, $u_1(t)$, and standardized abundance of predatory fish, $u_3(t)$, were set to zero.

We performed an additional invasibility simulation study to evaluate the likelihood of predicting alternative stable states when they do not exist. We set the values of interspecific interactions a_x and a_y to equal the corresponding intraspecific interactions k_x and k_y. With these changes in parameter values (and leaving all other parameters as estimated from the MLL model), the two species coexist (barely) at intermediate water levels, and alternative stable states should not be present. We then simulated 1000 datasets and estimated the corresponding 1000 parameter sets. Finally, we repeated this procedure but set k_x and k_y equal to a_x and a_y (rather than the other way around).

Regardless of whether alternative stable states exist in this system, the range of water levels over which the system transitions from domination of one species to domination of the other is of both practical and theoretical interest. We simulated rusty crayfish and *Lepomis* abundance using equations 1 and 2 given steadily changing water levels using the MLL parameters and the bootstrapped parameter sets. Two scenarios were explored; the transition from rusty crayfish to *Lepomis* domination as water levels decline, and the transition from *Lepomis* to rusty crayfish domination as water levels rise. Simulations were run for 100 years with mean water level changing from 0 to -3 or -3 to 0 over the course of the simulation. In both cases water level was simulated as a stochastic variable (SD = 0.61; estimated from an AR(1) model fit to observed water level data where the AR coefficient = 0.83, (Box *et al.* 1994)). A small number of rusty crayfish (0.1; 0.5% of equilibrium value in the absence of *Lepomis*) and *Lepomis* (0.02; 1% of equilibrium value in absence of rusty crayfish) were added each year to simulate invasion pressure and to prevent the model from becoming “trapped” in a state where one species had been extirpated.

(3) *Results*

Rusty crayfish abundance varied over three orders of magnitude in Trout Lake and two orders of magnitude in Sparkling Lake from 1981-2009 (Figure 2A, B). In Trout Lake rusty crayfish increased over time, while in Sparkling Lake the lowest numbers were observed from 2003-2009, during and following the experimental removal. The trajectories of rusty crayfish and *Lepomis* abundance in Trout Lake and pre- and post- manipulation in Sparkling Lake follow distinct paths (Figure3).

The state-space model was able to capture the crayfish dynamics well. *Lepomis* populations exhibited high levels of inter-annual variation, with a general decreasing trend in Trout Lake and increasing trend in Sparkling Lake (Figure 2A, B). The model ascribed much of the inter-annual variability in *Lepomis* abundance to measurement error, so that the fitted line appears to average over this variability. This is consistent with the large standard errors of estimates of *Lepomis* populations. Predatory fish exhibited inter-annual variation but no strong directional trend (Figure 2C, D). Water level in Sparkling Lake declined from 2005 to 2009, with the lowest observed value in 2009 (Figure 2C).

The parameter estimates from the MLL model contained a negative effect of rusty crayfish on *Lepomis* and a negative effect of *Lepomis* on rusty crayfish (a_x and a_y, respectively), as well as a negative effect of water level on rusty crayfish recruitment (*c*; Table 1). Removal trapping had a strong negative effect on adult rusty crayfish (*m*). The estimated effect of predatory fish on rusty crayfish (*v*) was zero. The MLL value estimated from the observed data (-91.0) fell well within the range of MLL values of the bootstrap simulations (mean = -91.3, 95% inclusion interval = -32.8 to -118.1), indicating that the dynamics produced by the model are qualitatively similar to those observed in the data; that is, the model was able to capture reality well. However, bootstrapped parameter estimates indicate that the estimators for some parameters are skewed (mean vs. median values) and biased (estimates vs. mean values from the bootstrapping; Table 1); this is not unexpected given the short length of the data sets (e.g., Cheang and Reinsel 2000, Dennis et al. 2006, Ziebarth et al. 2010).

Alternative stable states

Alternative stable states were predicted to exist for rusty crayfish and *Lepomis* given the maximum likelihood parameter estimates, depending on water level. We characterized water level in terms of the observed standard deviation in Sparkling Lake over the course of the study. In the parameterized model, if water level was 0.75 standard deviations below the maximum observed value or lower, then *Lepomis* always excluded rusty crayfish. Conversely, if water level was 0.5 standard deviations below the maximum or higher, then rusty crayfish always excluded *Lepomis*. However, in the range from 0.75 to 0.5 standard deviations below the maximum, alternative stable states existed in which either rusty crayfish or *Lepomis* excluded the other, depending on their relative initial abundances (i.e., who arrived first, Figure 4A).

Because uncertainty exists in parameter estimates (Table 1), we performed an invasibility analysis using the bootstrapped parameter sets to assess the uncertainty in the existence of alternative stable states. For all sets of bootstrapped parameters, sufficiently low water levels led to *Lepomis* excluding rusty crayfish, and sufficiently high water levels led to rusty crayfish excluding *Lepomis*. At intermediate water levels, there were two possibilities: alternative stable states where the species that arrives first will persist (Figure 4A) or coexistence (Figure 4B). The range of water levels giving either of these outcomes was very narrow for 15% of the bootstrapped parameter sets. Of the remaining parameter sets, 35% predicted alternative stable states and 50% predicted coexistence for some range of water levels (Figure 5). In a similar analysis in which water level was treated as a stochastic rather than a fixed variable, rusty crayfish were predicted to exclude *Lepomis* in more parameter sets and over a wider range of mean water level values, yet there was similar uncertainty in whether intermediate water levels gave alternative stable states or coexistence (results not shown).

The equivocal evidence for alternative stable states from the parameters estimated from the data led us to evaluate the likelihood of predicting alternative stable states when they do not exist. Of the 1000 parameter sets estimated from data simulated when we set k_x and k_y equal to a_x and a_y, respectively (which should produce coexistence), alternative stable states were predicted in 43% of parameter sets, while coexistence was predicted in 37%. When we set k_x

and k_y equal to a_x and a_y, respectively (rather than the other way around), alternative stable states were predicted in 40% and coexistence in 51% of parameter sets. These simulations show that even when alternative stable states cannot occur, the estimated parameters may nonetheless predict alternative stable states.

Regardless of whether alternative stable states or coexistence are predicted at intermediate water levels, the transition from domination by rusty crayfish to domination by *Lepomis* took place over a narrow range of water levels. Of the 1000 bootstrap parameter sets, the median range of water levels separating exclusion of *Lepomis* from exclusion of rusty crayfish was 0.2 standard deviations (the median range for parameter sets predicting alternative stable states was 0.5 standard deviations; for those predicting coexistence it was 0.2 standard deviations). To investigate crayfish/*Lepomis* dynamics at the transition between domination of one or the other, we simulated rusty crayfish and *Lepomis* abundance for 100 years under conditions of either increasing or decreasing mean water levels using two parameter sets: one predicting alternative stable states (estimated from the data) and one predicting coexistence (from the bootstrapped parameter estimates; Figure 6). In both cases the transition between the dominant species was driven by water level and occurred rapidly. The switch generally occurred at an earlier time step (i.e., as a result of smaller changes in mean water level) in the coexistence scenario (Figure 6B and D) compared to the alternative stable states scenario (Figure 6A and C), and in the alternative stable states scenario the transitions between species occurred at different water level values when approached from opposite directions, illustrating hysteresis (Scheffer *et al.* 2001). Finally, more variability existed in the alternative stable states scenario than in the coexistence scenario. However, coexistence still led to abrupt shifts between states, and coexistence and alternative stable states produced similar qualitative results.

(4) *Discussion*

Strong feedbacks exist between invasive rusty crayfish and native *Lepomis*, where each negatively affects the recruitment of the other (Roth et al. 2007). Our results support the hypothesis that these feedbacks can result in alternative stable states, but we find that the ability of *Lepomis* to control rusty crayfish populations is contingent upon water level, which serves as a proxy for available habitat. At low water levels the most likely outcome is *Lepomis* excluding rusty crayfish; at high water levels the most likely outcome is rusty crayfish excluding *Lepomis;* and at intermediate water levels it is possible for either coexistence or alternative stable states. Interestingly, the maximum likelihood parameter estimate for the effect of other fish predators (smallmouth bass, largemouth bass, rock bass, and walleye) was zero, indicating that these species exert very little population level effect on rusty crayfish. This result was somewhat surprising, as these fish species are known to consume rusty crayfish at high rates (Garvey et al. 1994, Lodge and Hill 1994, Garvey et al. 2003), and have been implicated as the drivers of alternative states in crayfish dynamics (Horan et al. 2011). Juvenile crayfish are the most vulnerable to predation (Didonato and Lodge 1993), and as a result juveniles are likely to benefit more from shelter provided by cobble than adults (Lodge and Hill 1994). *Lepomis* prey mainly on juvenile crayfish, and juvenile mortality produces a greater effect on rusty crayfish populations than the adult mortality (Hein *et al.* 2006). Thus it stands to reason that declining water levels and reduced shelter availability should increase the population-level effects of *Lepomis* predation more so than predation by other fishes.

Alternative stable states are possible only under certain environmental conditions of moderate water levels and cobble availability in our model. However, the evidence for alternative stable states is equivocal given the uncertainty in parameter estimates. Over a broad range of water levels, any of the four outcomes of rusty crayfish-*Lepomis* interactions are possible within the joint distribution of the parameter estimates (Figure 5). When accounting for uncertainty in the parameters, there is a 35% chance of alternative stable states and a 50% chance of coexistence at intermediate water levels, with the remaining 15% of cases showing a very rapid transition between rusty crayfish and *Lepomis* exclusion. Trajectories of rusty crayfish and *Lepomis* densities follow different paths in Trout Lake and in Sparkling Lake pre- and post-manipulation (Figure 3). The two Sparkling Lake trajectories are consistent with what would be observed under alternative state dynamics, with different initial conditions leading to different final states (Scheffer et al. 2003). However, environmental conditions also changed between these two periods with lower habitat availability in the post-manipulation time series, and the differential trajectories could be a reflection of the water level effect. Similiarly, despite low initial densities of rusty crayfish and moderate Lepomis densities, the Trout Lake trajectory moved consistently towards higher crayfish abundance. This could be a reflection of the abundant cobble habitat in Trout Lake providing refuge from predation for rusty crayfish.

Overall, we conclude that alternative stable states are possible but by no means certain in this system.

Our results highlight the difficulty associated with identifying alternative stable states in field settings at spatial scales relevant to management (Scheffer and Carpenter 2003, Schröder et al. 2005) and when a realistic range of parameter estimates are examined (Fung *et al.* 2011). We provide a rigorous quantitative test of the existence of alternative stable states in a real system by using 29 years of observations from two lakes combined with a whole-system manipulation. Previous evidence from long-term study, cross-site comparison, and ecological theory supports the possibility of alternative stable states governing the outcome of rusty crayfish invasions (Roth et al. 2007, Horan et al. 2011). However, we were unable to prove statistically that rusty crayfish invasions are governed by alternative states. While long-term from an ecological standpoint, our data were short relative to the number of relevant drivers in this system. We benefited from the contrast provided by the rusty crayfish invasion in Trout Lake and removal in Sparkling Lake; however, in both lakes we essentially observed a “one way trip” in opposite directions. These characteristics of our data contributed to the uncertainty in identifying alternative stable states from observed data. This uncertainty was underscored by our simulation studies of the model parameterized so that alternative stable states could not occur; alternative stable states were nonetheless predicted to occur in more than 40% of parameter sets.

The differential outcome of competitive interactions between invasive and native species as a result of changing abiotic conditions has important implications for the management of invasive species under climate change (e.g., Mason et al. In press). Because transitions between invasive and native species dominance can occur rapidly as a result of external events, they can be viewed as “opportunities” and “hazards” (sensu Westoby et al. 1989), and research and management can be designed accordingly to manage these transitions favorably and to take advantage of thresholds and feedbacks to push lakes into desirable states (Holmgren and Scheffer 2001, Horan et al. 2011, Schooler et al. 2011). In our study, water level was a critical determinant of the outcome of a rusty crayfish invasion. Low water periods may present opportunities for eradication of rusty crayfish populations, while high water periods could increase the likelihood of invasion or population growth in some lakes. Prevention is the most effective mode of invasive species management (Lodge *et al.* 2006); lakes with abundant cobble and low *Lepomis* densities are at highest risk of adverse effects of rusty crayfish and should be a focus of prevention efforts. Conversely, protection or stocking of *Lepomis* could reduce the likelihood of rusty crayfish establishment in lakes with low to moderate cobble. Although the study region experienced record-breaking drought conditions from 2005-2009, other regions of Wisconsin experienced higher than average precipitation over this same period, and future climate projections predict wetter overall conditions but more frequent droughts (WICCI 2009). Rusty crayfish are therefore expected to continue to be a management challenge in north temperate lakes.

There is growing recognition that the impacts of climate change extend beyond the direct effects of altered abiotic regimes to changes in species interactions (Stenseth and Mysterud 2002, Winder and Schindler 2004, Suttle et al. 2007, Tylianakis et al. 2008, Gilman et al. 2010). Invasive species interact strongly with invaded communities via numerous trophic links, and climate change could alter the strength and outcome of these interactions with potentially unexpected outcomes (Dukes and Mooney 1999, Walther et al. 2002, Hellmann et al. 2008, Rahel and Olden 2008) We have demonstrated that the transition between invasive rusty crayfish and native *Lepomis* domination occurs abruptly as a result of small changes in climate-driven water level. This rapid transition is due to the strongly negative effects of lowered water level on rusty crayfish recruitment, allowing *Lepomis* to gain a competitive edge over rusty crayfish under drought conditions that are then compounded by positive feedbacks. The interaction of climate change and invasive species is a topic of critical importance, and this represents one of only a few studies have looked examined this interaction on the scale relevant to management (but see Selbie et al. 2011).

(5) *Acknowledgements*

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Literature Cited

Beisner, B. E., D. T. Haydon, and K. Cuddington. 2003. Alternative stable states in ecology. Frontiers in Ecology and the Environment **1**:376-382.

Bergelson, J. 1990. Life after death: Site pre-emption by the remains of poa annua. Ecology **71**:2157-2165.

Box, G. E. P., G. M. Jenkins, and G. C. Reinsel. 1994. Time series analysis: Forecasting and control, Third edition. Prentice Hall, Englewood Cliffs, NJ.

Capelli, G. M. 1982. Displacement of northern Wisconsin crayfish by *Orconectes rusticus* (Girard). Limnology and Oceanography **27**:741-745.

Capelli, G. M., and J. J. Magnuson. 1983. Morphoedaphic and biogeographic analysis of crayfish distribution in northern Wisconsin. Journal of Crustacean Biology **3**:548-564.

Carpenter, S. R., O. Kinne, and W. Wieser. 2003. Regime shifts in lake ecosystems: Pattern and variation. International Ecology Institute, Oldendorf/Luhe.

Case, T. J. 1990. Invasion resistance arises in strongly interacting species-rich model competition communities. Proceedings of the National Academy of Sciences of the United States of America **87**:9610-9614.

Chase, J. M. 1999. Food web effects of prey size refugia: Variable interactions and alternative stable equilibria. The American Naturalist **154**:559-570.

Chase, J. M. 2003. Experimental evidence for alternative stable equilibria in a benthic pond food web. Ecology Letters **6**:733-741.

Cheang, W. K., and G. C. Reinsel. 2000. Bias reduction of autoregressive estimates in time series regression model through restricted maximum likelihood. Journal of the American Statistical Association **95**:1173-1184.

Chesson, P. 2000. General theory of competitive coexistence in spatially-varying environments. Theoretical Population Biology **58**:211-237.

Chesson, P. L. 1986. Environmental variation and the coexistence of species. Pages 240-256 *in* J. Diamond and T. J. Case, editors. Community ecology. Harper & Row, New York.

Connell, J. H. 1961. Effects of competition, predation by *thais lapillus*, and other factors on natural populations of the barnacle *balanus balanoides*. Ecological Monographs **31**:61-104.

Courchamp, F., M. Langlais, and G. Sugihara. 2000. Rabbits killing birds: Modelling the hyperpredation process. Journal of Animal Ecology **69**:154-164.

Crooks, J. A. 2002. Characterizing ecosystem-level consequences of biological invasions: The role of ecosystem engineers. Oikos **97**:153-166.

Dennis, B., J. M. Ponciano, S. R. Lele, M. L. Taper, and D. F. Staples. 2006. Estimating density dependence, process noise, and observation error. Ecological Monographs **76**:323-341.

DiDonato, G. T., and D. M. Lodge. 1993. Species replacements among Orconectes crayfishes in Wisconsin lakes: The role of predation by fish. Canadian Journal of Fisheries and Aquatic Sciences **50**:1484-1488.

Diehl, S. 1992. Fish predation and benthic community structure: The role of omnivory and habitat complexity. Ecology **73**:1646-1661.

Dorn, N. J., and G. G. Mittelbach. 2004. Effects of a native crayfish (Orconectes virilis) on the reproductive success and nesting behavior of sunfish (Lepomis spp.). Canadian Journal of Fisheries and Aquatic Sciences **61**:2135–2143.

Dukes, J. S., and H. A. Mooney. 1999. Does global change increase the success of biological invaders? Trends in Ecology & Evolution **14**:135-139.

Dunson, W. A., and J. Travis. 1991. The role of abiotic factors in community organization. The American Naturalist **138**:1067-1091.

Epanchin, P. N., R. A. Knapp, and S. P. Lawler. 2010. Nonnative trout impact an alpine-nesting bird by altering aquatic-insect subsidies. Ecology **91**:2406-2415.

Frost, T. M., S. R. Carpenter, A. R. Ives, and T. K. Kratz. 1995. Species compensation and complementarity in ecosystem function. Pages 224-239 *in* C. G. Jones and J. H. Lawton, editors. Linking species and ecosystems. Chapman and Hall, New York, New York.

Fung, T., R. Seymour, and C. Johnson. 2011. Alternative stable states and phase shifts in coral reefs under anthropogenic stress. Ecology **92**:967-982.

Garvey, J. E., J. E. Rettig, R. A. Stein, D. M. Lodge, and S. P. Klosiewski. 2003. Scale-dependent associations among fish predation, littoral habitat, and distributions of crayfish species. Ecology **84**:3339-3348.

Garvey, J. E., R. A. Stein, and H. M. Thomas. 1994. Assessing how fish predation and interspecific prey competition influence a crayfish assemblage. Ecology **75**:532-547.

Gilman, S. E., M. C. Urban, J. Tewksbury, G. W. Gilchrist, and R. D. Holt. 2010. A framework for community interactions under climate change. Trends in Ecology & Evolution **25**:325-331.

Gratton, C., and R. F. Denno. 2005. Restoration of arthropod assemblages in a spartina salt marsh following removal of the invasive plant *phragmites australis*. Restoration Ecology **13**:358-372.

Harvey, A. C. 1989. Forecasting structural time series models and the kalman filter.Cambridge University Press, Cambridge, U.K.

Hein, C. L., B. M. Roth, A. R. Ives, and M. J. Vander Zanden. 2006. Fish predation and trapping for rusty crayfish (*Orconectes rusticus*) control: A whole-lake experiment. Canadian Journal of Fisheries and Aquatic Sciences **63**:383–393.

Hellmann, J. J., J. E. Byers, B. G. Bierwagen, and J. S. Dukes. 2008. Five potential consequences of climate change for invasive species. Conservation Biology **22**:534-543.

Holmgren, M., and M. Scheffer. 2001. El niño as a window of opportunity for the restoration of degraded arid ecosystems. Ecosystems **4**:151-159.

Holt, R. D. 1984. Spatial heterogeneity, indirect interactions, and the coexistence of prey species. American Naturalist:377-406.

Horan, R. D., E. P. Fenichel, K. L. S. Drury, and D. M. Lodge. 2011. Managing ecological thresholds in coupled environmental-human systems. Proceedings of the National Acadamy of Sciences, USA **108**:7333-7338.

Hutchinson, G. E. 1961. The paradox of the plankton. The American Naturalist **95**:137-145.

Impacts, W. I. o. C. C. 2009. Maps of recent and projected climate change in Wisconsin. *in*, Madison, WI.

Ives, A. R., A. Einarsson, V. A. A. Jansen, and A. Gardarsson. 2008. High-amplitude fluctuations and alternative dynamical states of midges in lake myvatn. Nature **452**:84-87.

Kershner, M. W., and D. M. Lodge. 1995. Effects of littoral habitat and fish predation on the distribution of an exotic crayfish, Orconectes rusticus. Journal of the North American Benthological Society **14**:414–422.

Leigh, E. G., R. T. Paine, J. F. Quinn, and T. H. Suchanek. 1987. Wave energy and intertidal productivity. Proceedings of the National Academy of Sciences **84**:1314-1318.

Lodge, D. M. 1993. Species invasions and deletions: Community effects and responses to climate and habitat change. Pages 367-387 *in* P. M. Kareiva, J. G. Kingsolver, and R. B. Huey, editors. Biotic interactions and global change. Sinauer Associates Inc., Sunderland, MA.

Lodge, D. M., and A. M. Hill. 1994. Factors governing species composition, population size, and productivity of cool-water crayfishes. Nordic Journal of Freshwater Research **69**:111-136.

Lodge, D. M., M. W. Kershner, J. E. Aloi, and A. P. Covich. 1994. Effects of an omnivorous crayfish (*Orconectes rusticus*) on a freshwater littoral food web. Ecology **75**:1265–1281.

Lodge, D. M., and J. G. Lorman. 1987. Reductions in submersed macrophyte biomass and species richness by the crayfish *Orconectes rusticus*. Canadian Journal of Fisheries and Aquatic Sciences **44**:591-597.

Lodge, D. M., S. Williams, H. J. MacIsaac, K. R. Hayes, B. Leung, S. Reichard, R. N. Mack, P. B. Moyle, M. Smith, D. A. Andow, J. T. Carlton, and A. McMichael. 2006. Biological invasions: Recommendations for u.S. Policy and management. Ecological Applications **16**:2035-2054.

Loeb, V., V. Siegel, O. Holm-Hansen, R. Hewitt, W. Fraser, W. Trivelpiece, and S. Trivelpiece. 1997. Effects of sea-ice extent and krill or salp dominance on the antarctic food web. Nature **387**:897.

Lorman, J. G. 1980. Ecology of the crayfish Orconectes rusticus in northern Wisconsin. University of Wisconsin–Madison.

Mason, T. J., K. French, and K. Russell. In press. Are competitive effects of native species on an invader mediated by water availability? Journal of Vegetation Science.

Mather, M. E., and R. A. Stein. 1993. Direct and indirect effects of fish predation on the replacement of a native crayfish by an invading congener. Canadian Journal of Fisheries and Aquatic Sciences **50**:1279-1288.

May, R. M. 1973. Stability and complexity in model ecosystems, First edition. Princeton University Press, Princeton, NJ.

May, R. M. 1977. Thresholds and breakpoints in ecosystems with a multiplicity of stable states. Nature **269**:471-477.

McCarthy, J. M., C. L. Hein, J. D. Olden, and M. Jake Vander Zanden. 2006. Coupling long-term studies with meta-analysis to investigate impacts of non-native crayfish on zoobenthic communities. Freshwater Biology **51**:224–235.

Menge, B. A. 1976. Organization of the new england rocky intertidal community: Role of predation, competition, and environmental heterogeneity. Ecological Monographs **46**:355-393.

Menge, B. A., and J. P. Sutherland. 1987. Community regulation: Variation in disturbance, competition, and predation in relation to environmental stress and recruitment. The American Naturalist **130**:730-757.

Mylius, S. D., K. Klumpers, A. M. de Roos, and L. Persson. 2001. Impact of intraguild predation and stage structure on simple communities along a productivity gradient. The American Naturalist **158**:259-276.

Ogutu-Ohwayo, R. 1990. The decline of the native fishes of lakes victoria and Kyoga (east Africa) and the impact of introduced species, especially the Nile perch, *Lates niloticus*, and the Nile tilapia, *Oreochromis niloticus*. Environmental Biology of Fishes **27**:81-96.

Olsen, T. M., D. M. Lodge, G. M. Capelli, and R. J. Houlihan. 1991. Mechanisms of impact of an introduced crayfish (*Orconectes rusticus*) on littoral congeners, snails, and macrophytes. Canadian Journal of Fisheries and Aquatic Sciences **48**:1853-1861.

Orrock, J. L., M. S. Witter, and O. J. Reichman. 2008. Apparent competition with an exotic plant reduces native plant establishment. Ecology **89**:1168-1174.

Pace, M. L., S. E. G. Findlay, and D. Fischer. 1998. Effects of an invasive bivalve on the zooplankton community of the hudson river. Freshwater Biology **39**:103-116.

Paine, R. T. 1966. Food web complexity and species diversity. American Naturalist **100**:65-75.

Paine, R. T., J. C. Castillo, and J. Cancino. 1985. Perturbation and recovery patterns of starfish-dominated intertidal assemblages in chile, new zealand, and washington state. The American Naturalist **125**:679-691.

Park, T. 1962. Beetles, competition, and populations. Science **138**:1369-1375.

Petraitis, P. S., and R. E. Latham. 1999. The importance of scale in testing the origins of alternative community states. Ecology **80**:429-442.

Pigott, C. D., and K. Taylor. 1964. The distribution of some woodland herbs in relation to the supply of nitrogen and phosphorus in the soil. JOURNAL OF ECOLOGY **52**:175-185.

Power, M. E. 1992. Habitat heterogeneity and the functional signifiance of fish in river food webs. Ecology:1675-1688.

Rahel, F. J., and J. D. Olden. 2008. Assessing the effects of climate change on aquatic invasive species. Conservation Biology **22**:521–533.

Rosenthal, S. K., S. S. Stevens, and D. M. Lodge. 2006. Whole-lake effects of invasive crayfish (*Orconectes* spp.) and the potential for restoration. Canadian Journal of Fisheries & Aquatic Sciences **63**:1276-1285.

Roth, B. M., J. C. Tetzlaff, M. L. Alexander, and J. F. Kitchell. 2007. Reciprocal relationships between exotic rusty crayfish, macrophytes, and Lepomis species in northern Wisconsin lakes. Ecosystems **10**:75–86.

Sala, O. E., F. S. Chapin Iii, J. J. Armesto, E. Berlow, J. Bloomfield, R. Dirzo, E. Huber-Sanwald, L. F. Huenneke, R. B. Jackson, A. Kinzig, and others. 2000. Global biodiversity scenarios for the year 2100. Science **287**:1770-1774.

Savino, J. F., and R. A. Stein. 1982. Predator-prey interaction between largemouth bass and bluegills as influenced by simulated, submersed vegetation. Transactions of the American Fisheries Society **111**:255-266.

Scheffer, M., S. Carpenter, J. A. Foley, C. Folke, and B. Walker. 2001. Catastrophic shifts in ecosystems. Nature **413**:591–596.

Scheffer, M., and S. R. Carpenter. 2003. Catastrophic regime shifts in ecosystems: Linking theory to observation. Trends in Ecology & Evolution **18**:648-656.

Scheffer, M., S. Szabó, A. Gragnani, E. H. Van Nes, S. Rinaldi, N. Kautsky, J. Norberg, R. M. M. Roijackers, and R. J. M. Franken. 2003. Floating plant dominance as a stable state. Proceedings of the National Academy of Sciences of the United States of America **100**:4040-4045.

Schoener, T. W. 1974. Resource partitioning in ecological communities. Science **185**:27-39.

Schooler, S. S., B. Salau, M. H. Julien, and A. R. Ives. 2011. Alternative stable states explain unpredictable biological control of *salvinia molesta* in kakadu. Nature **470**:86-89.

Schröder, A., L. Persson, and A. M. De Roos. 2005. Direct experimental evidence for alternative stable states: A review. Oikos **110**:3-19.

Selbie, D. T., J. N. Sweetman, P. Etherton, K. D. Hyatt, D. P. Rankin, B. P. Finney, and J. P. Smol. 2011. Climate change modulates structural and functional lake ecosystem responses to introduced anadromous salmon. Canadian Journal of Fisheries and Aquatic Sciences **68**:675-692.

Sih, A., D. I. Bolnick, B. Luttbeg, J. L. Orrock, S. D. Peacor, L. M. Pintor, E. Preisser, J. S. Rehage, and J. R. Vonesh. 2010. Predator-prey naivete antipredator behavior, and the ecology of predator invasions. Oikos **119**:610-621.

Simon, K. S., and C. R. Townsend. 2003. Impacts of freshwater invaders at different levels of ecological organisation, with emphasis on salmonids and ecosystem consequences. Freshwater Biology **48**:982-994.

Snaydon, R. W. 1962. Micro-distribution of *trifolium repens* l. And its relation to soil factors. JOURNAL OF ECOLOGY **50**:133-143.

Snyder, W. E., and E. W. Evans. 2006. Ecological effects of invasive arthropod generalist predators. Annual Review of Ecology, Evolution, and Systematics **37**:95-122.

Spencer, C. N., B. R. McClelland, and J. A. Stanford. 1991. Shrimp stocking, salmon collapse, and eagle displacement. Bioscience **41**:14-21.

Stenseth, N. C., and A. Mysterud. 2002. Climate, changing phenology, and other life history traits: Nonlinearity and match-mismatch to the environment. Proceedings of the National Academy of Sciences **99**:13379-13381.

Suttle, K. B., M. A. Thomsen, and M. E. Power. 2007. Species interactions reverse grassland responses to changing climate. Science **315**:640-642.

SvanbÃ¤ck, R., and D. I. Bolnick. 2007. Intraspecific competition drives increased resource use diversity within a natural population. Proceedings of the Royal Society B: Biological Sciences **274**:839.

Tetzlaff, J. C., B. M. Roth, B. C. Weidel, and J. F. Kitchell. 2010. Predation by native sunfishes (*centrarchidae*) on the invasive crayfish *Orconectes rusticus* in four northern Wisconsin lakes. Ecology of Freshwater Fish **20**:133-143.

Tilman, D. 1987. On the meaning of competition and the mechanisms of competitive superiority. Functional Ecology **1**:304-315.

Tylianakis, J. M., R. K. Didham, J. Bascompte, and D. A. Wardle. 2008. Global change and species interactions in terrestrial ecosystems. Ecology Letters **11**:1351-1363.

Walther, G. R., E. Post, P. Convey, A. Menzel, C. Parmesan, T. J. C. Beebee, J.-M. Fromentin, O. Hoegh-Guldberg, and F. Bairlein. 2002. Ecological responses to recent climate change. Nature **416**:389-395.

Warfe, D., and L. Barmuta. 2006. Habitat structural complexity mediates food web dynamics in a freshwater macrophyte community. Oecologia **150**:141-154.

Westoby, M., B. Walker, and I. Noy-Meir. 1989. Opportunistic management for rangelands not at equilibrium. Journal of Range Management **42**:266-274.

Wilson, K. A., J. J. Magnuson, D. M. Lodge, A. M. Hill, T. K. Kratz, W. L. Perry, and T. V. Willis. 2004. A long-term rusty crayfish (Orconectes rusticus) invasion: Dispersal patterns and community change in a north temperate lake. Canadian Journal of Fisheries and Aquatic Sciences **61**:2255–2266.

Wilson, S. D., and P. A. Keddy. 1986. Measuring diffuse competition along an environmental gradient: Results from a shoreline plant community. The American Naturalist **127**:862-869.

Wilson, W. G., and R. M. Nisbet. 1997. Cooperation and competition along smooth environmental gradients. Ecology **78**:2004-2017.

Winder, M., and D. E. Schindler. 2004. Climate change uncouples trophic interactions in an aquatic ecosystem. Ecology **85**:2100-2106.

Zhu, B., D. G. Fitzgerald, C. M. Mayer, L. G. Rudstam, and E. L. Mills. 2006. Alteration of ecosystem function by zebra mussels in oneida lake: Impacts on submerged macrophytes. Ecosystems **9**:1017-1028.

Ziebarth, N. L., K. C. Abbott, and A. R. Ives. 2010. Weak population regulation in ecological time series. Ecology Letters **13**:21-31.

Table 1: Maximum likelihood parameter estimates and mean, median, and 95% confidence intervals of the 1000 parameter sets generated from parametric bootstrapping.

Parameter	Description	MLL estimate	Median	Mean	Lower 95% CI	Upper 95% CI
r_x	Maximum per capita recruitment rate (crayfish)	1.01	1.51	3.28	0.18	6.08
r_y	Maximum per capita recruitment rate (*Lepomis*)	0.52	0.76	2.13	0.00	9.83
k_x	Rate of adult-density-dependent reduction in recruitment (crayfish)	0.09	0.10	0.29	0.02	1.09
k_y	Rate of adult-density-dependent reduction in recruitment (*Lepomis*)	1.02	1.18	4.66	0.14	26.23
a_x	*Lepomis* effect on juvenile crayfish	0.49	0.24	1.15	0.00	5.74
a_y	Crayfish effect on juvenile *Lepomis*	0.36	0.45	1.21	0.00	6.10
d_x	Adult survival (crayfish)	0.80	0.82	0.82	0.60	1.00
d_y	Adult survival (*Lepomis*)	0.91	0.89	0.86	0.25	1.00

$c_{Sparkling}$	Water level effect on crayfish recruitment (Sparkling)	2.44	2.77	6.53	0.51	15.14
c_{Trout}	Difference between crayfish recruitment in Trout vs. Sparkling Lake	1.01	0.01	-0.22	-6.22	6.96
m	Effect of trapping on adult crayfish	0.14	0.16	0.16	0.06	0.26
v	Effect of predatory fish on juvenile crayfish	0	0.03	0.11	0.00	0.75
σ_x	Process error standard deviation in adult crayfish survival	0.22	0.15	0.14	0.00	0.42
σ_y	Process error standard deviation in adult *Lepomis* survival	0	0.02	0.05	0.00	0.35
ρ	Correlation between process errors	-0.20	-0.17	-0.03	-1.00	1.00
s_x	Measurement error rescaling for crayfish CPUE	4.74	5.05	5.27	9.41	1.88
s_y	Measurement error rescaling for *Lepomis* CPUE	2.85	3.00	3.10	1.88	4.93

Figure Captions

Figure 1. Conceptual diagram of time-series model. Arrows indicate drivers included in state-space model. Filled shapes indicate life-stages for which we had no data. Predatory fish include smallmouth bass, largemouth bass, rock bass, and walleye.

Figure 2: Time series of data used in the state-space model. (A&B) Standardized log CPUE of rusty crayfish (black open circles) and *Lepomis* (grey filled triangles) in (A) Sparkling Lake and (B) Trout Lake; error bars are standard errors. Values from the fitted model (lines) are the updated estimates of population abundances from the extended Kalman filter. (C&D) Standardized values of predatory fish CPUE (smallmouth bass, rock bass, and walleye; open black triangles), removal trapping effort (filled black squares), and water level (open grey circles) in (C) Sparkling Lake and (D) Trout Lake. In (C&D) lines connect observed data points. Water level was standardized to have a maximum value of 0 and standard deviation of 1, water level for Trout Lake was assumed to be constant and set to 1 for the entire time series. All other data were standardized to have a mean of 0 and standard deviation of 1.

Figure 3. Trajectories of rusty crayfish and *Lepomis* CPUE over time tended to different final states depending on initial conditions and environmental variables. Sparkling Lake (pre-manipulation; black circles) and Trout Lake (light grey diamonds) both had abundant cobble habitat and moved from low to high rusty crayfish abundance and low *Lepomis* abundance, while Sparkling Lake (post-manipulation; dark grey triangles) lacked cobble habitat due to lowered water levels and moved from low to high *Lepomis* abundance and low rusty crayfish

abundance. Mean values across several years are shown; for Trout Lake, values are from 1981-1985, 1986-1990, 1991-1995, 1996-2001, 2001-2005, and 2006-2009. For Sparkling Lake (pre-manipulation), values are from 1981-1984, 1985-1988, 1989-1992, 1993-1996, and 1997-2000. Sparkling Lake (post-manipulation) values are from 2003-2004, 2005-2006, 2007-2008, and 2009.

Figure 4. Proportion of rusty crayfish (predicted rusty crayfish CPUE/predicted rusty crayfish CPUE + predicted *Lepomis* CPUE) predicted from invasibility analysis (see text) under different water levels. Water levels were standardized to have a maximum value of 0 and standard deviation of 1. Predicted abundances were generated from invasibility analysis (see text) using (A) the maximum likelihood parameter estimates, which produce alternative stable states for water levels from -0.75 to -0.5 (grey dotted line), and (B) one of the 1000 bootstrapped parameter sets for which no alternative stable states exist and both species coexist for water levels -1.42 to -0.22 (grey solid line). Under both parameter sets, rusty crayfish always win at high water levels and Lepomis always win at low water levels (black lines).

Figure 5. Dynamical outcomes of crayfish-Lepomis interactions for invasibility analysis using parameters estimated from 1000 simulated datasets across a range of water levels when water level $u_2(t)$ is constant. Proportions of parameter sets giving the 4 possible outcomes are labeled: "crayfish" = crayfish always exclude *Lepomis*; "*Lepomis*" = *Lepomis* always exclude crayfish; "coexistence" = both species coexist; and "ASS" = there are alternative stable states in which either species once established can thwart the invasion of the other species.

Figure 6. Proportion of rusty crayfish (predicted rusty crayfish CPUE/predicted rusty crayfish CPUE + predicted *Lepomis* CPUE) simulated as mean water level (dashed line) declined (A and B) and increased (C and D). Simulated data were generated using parameters predicting alternative stable states estimated from the data (A and C) and using one set of parameters predicting coexistence estimated from simulated data (B and D). Symbols within a panel represent multiple simulations using the same parameter set; differences are a result of stochasticity in water level and process error in model (see text).

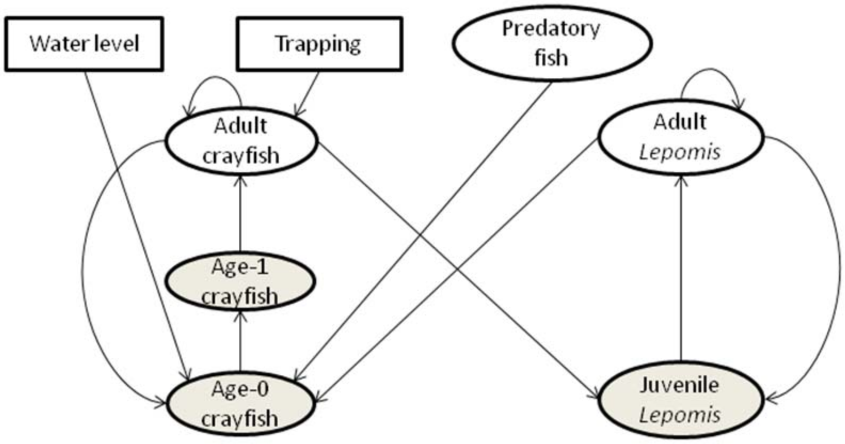

Water level
Trapping
Predatory fish
Adult crayfish
Adult *Lepomis*
Age-1 crayfish
Age-0 crayfish
Juvenile *Lepomis*

Figure 1.

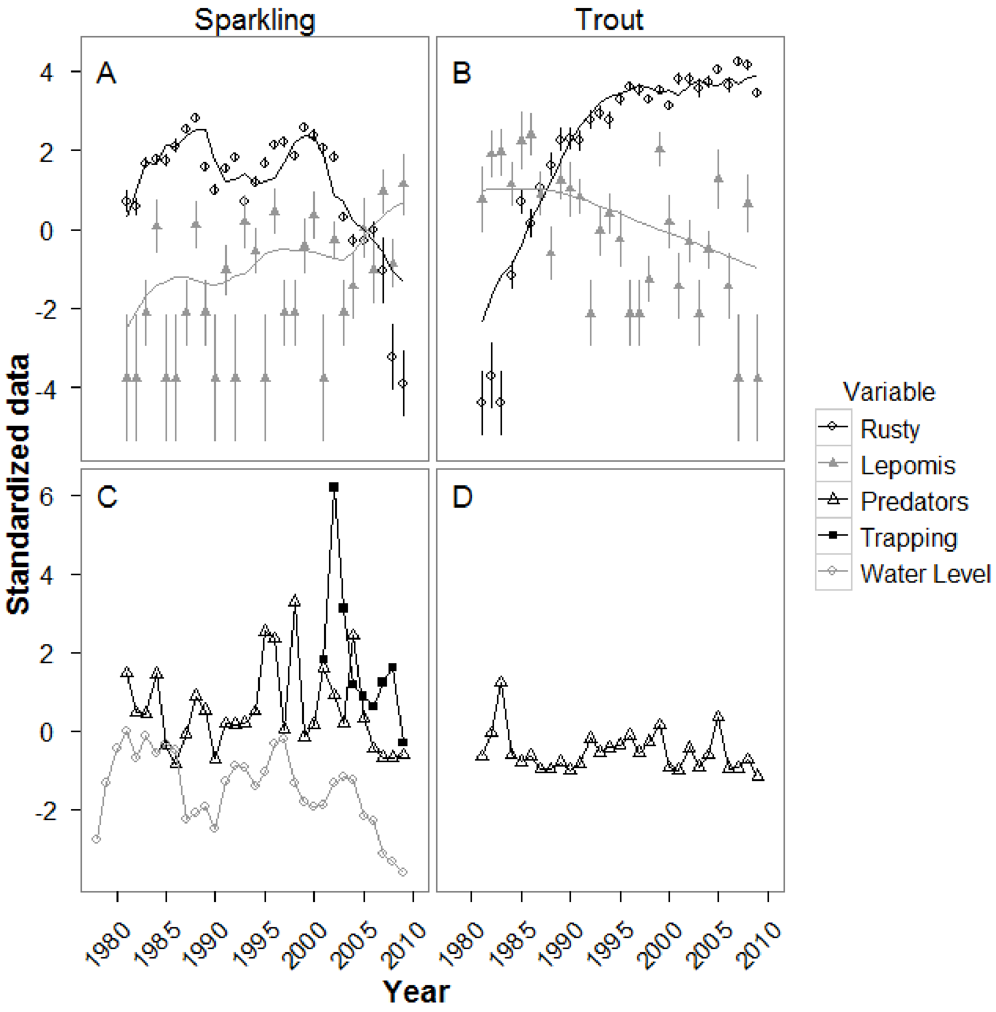

Sparkling
Trout
A
B
C
D
4
2
0
-2
-4
6
4
2
0
-2
Standardized data
1980
1985
1990
1995
2000
2005
2010
Year
Variable
Rusty
Lepomis
Predators
Trapping
Water Level

Figure 2.

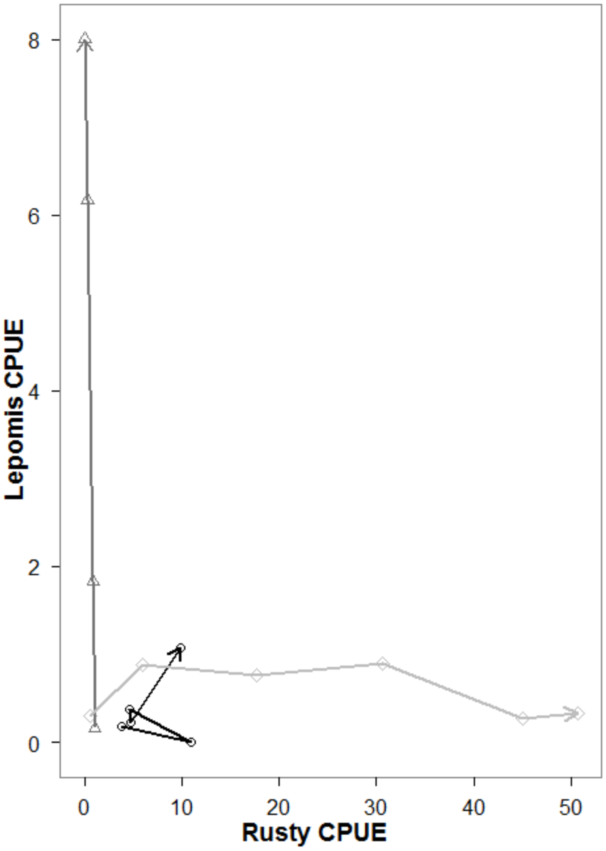


Figure 3.

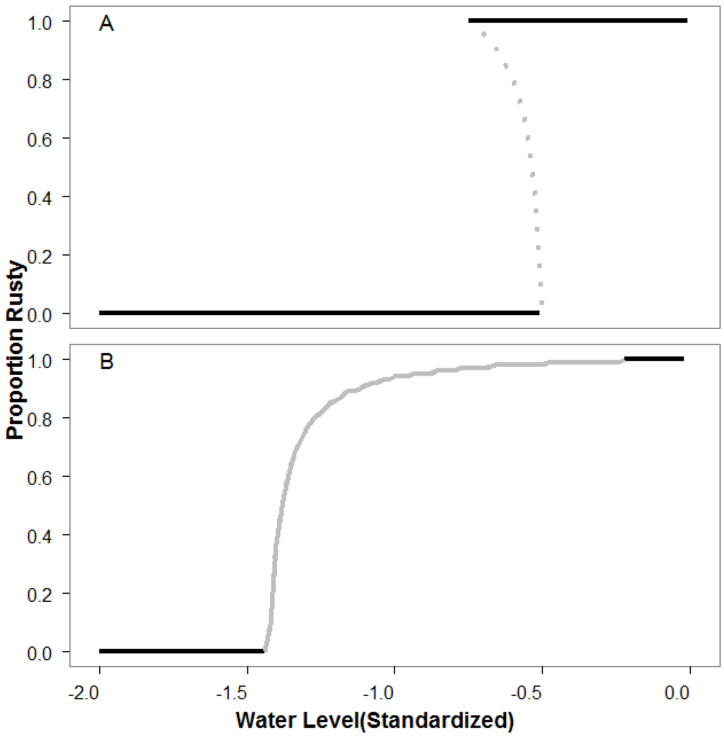
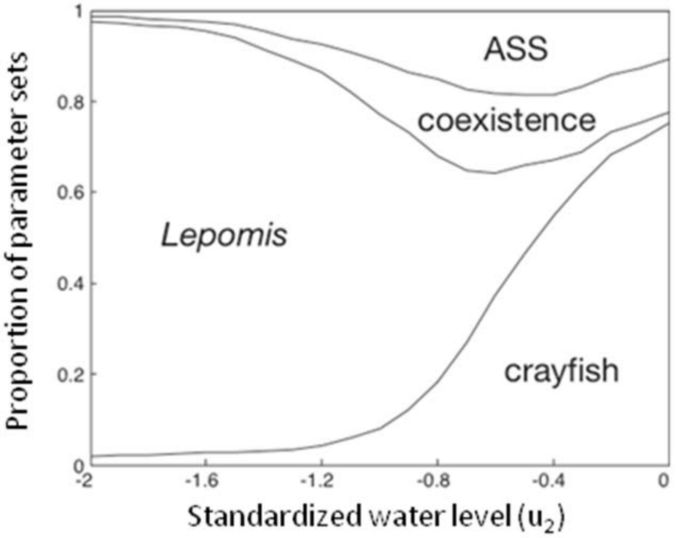

A
B
Proportion Rusty
1.0
0.8
0.6
0.4
0.2
0.0
-2.0
-1.5
-1.0
-0.5
0.0
Water Level(Standardized)

Figure 4.



ASS
coexistence
Lepomis
crayfish
Proportion of parameter sets
0
0.2
0.4
0.6
0.8
1
-2
-1.6
-1.2
-0.8
-0.4
0
Standardized water level (u_2)

Figure 5.

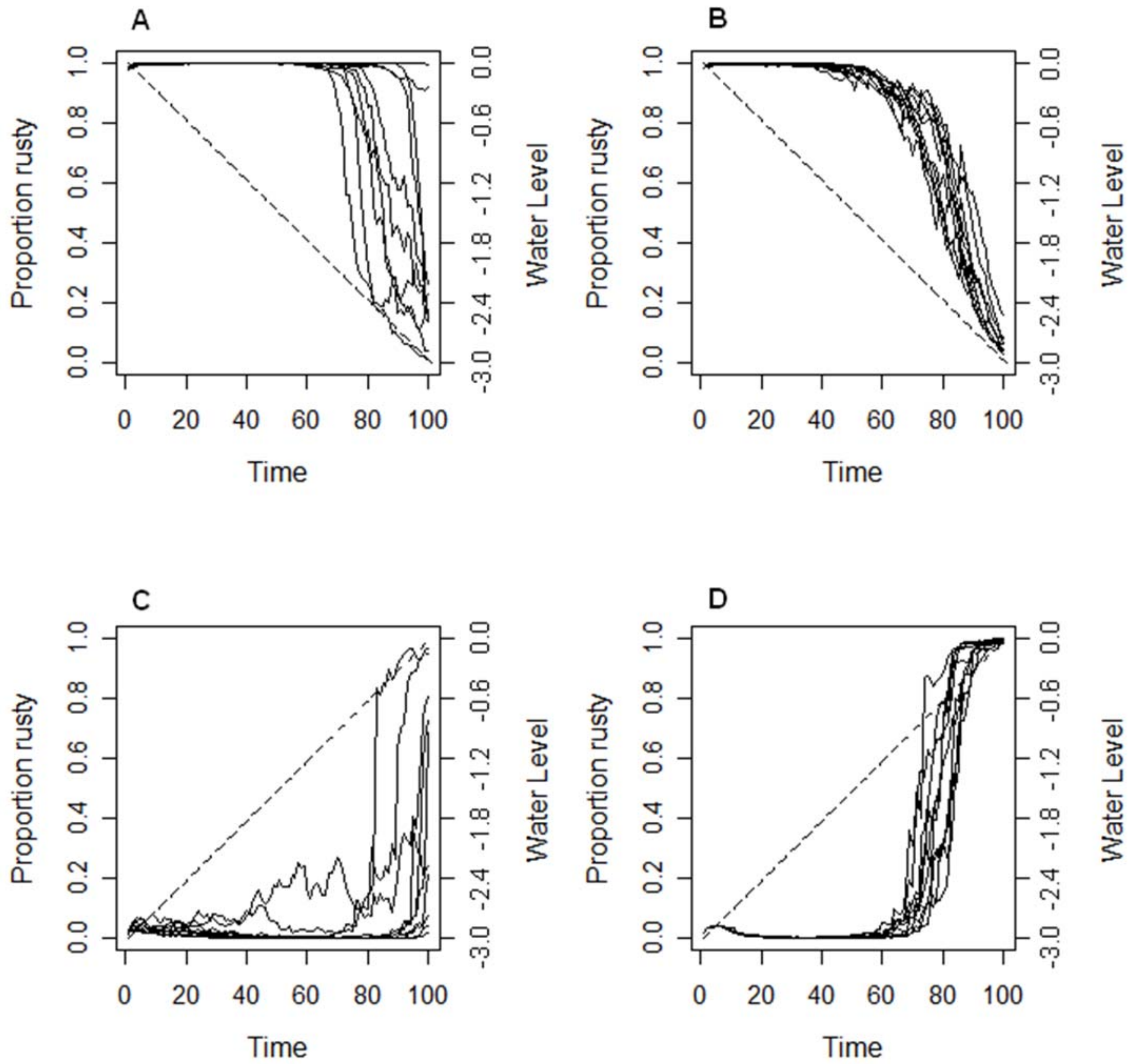

A
Proportion rusty
0.0
0.2
0.4
0.6
0.8
1.0
Water Level
0.0
-0.6
-1.2
-1.8
-2.4
-3.0
Time
0
20
40
60
80
100
B
Proportion rusty
0.0
0.2
0.4
0.6
0.8
1.0
Water Level
0.0
-0.6
-1.2
-1.8
-2.4
-3.0
Time
0
20
40
60
80
100
C
Proportion rusty
0.0
0.2
0.4
0.6
0.8
1.0
Water Level
0.0
-0.6
-1.2
-1.8
-2.4
-3.0
Time
0
20
40
60
80
100
D
Proportion rusty
0.0
0.2
0.4
0.6
0.8
1.0
Water Level
0.0
-0.6
-1.2
-1.8
-2.4
-3.0
Time
0
20
40
60
80
100

Figure 6.

CHAPTER THREE

Littoral community response to a decade-long removal of invasive rusty crayfish from a north temperate lake.

To be submitted for publication with coauthors Catherine L. Hein, Brian M. Roth, M. Jake Vander Zanden, Jereme Gaeta, Alexander W. Latzka, Stephen. R. Carpenter

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Abstract

Invasive species are leading drivers of biodiversity loss in aquatic systems. Removing established invasive species can restore native communities and ecosystem function, and can reveal unexpected connections between invasive species and other community members via indirect effects. In this study we quantify the littoral food web response to a decade long, whole-lake removal of invasive rusty crayfish (*Orconectes rusticus*) density. Rusty crayfish populations declined by two orders of magnitude and remained low for three years following the cessation of the removal. No compensatory response in rusty crayfish recruitment was observed, and fecundity was lower at low population densities, indicating a potential for sustained low densities. Native virile crayfish (*O. virilis*) increased by two orders of magnitude, and littoral macrophyte cover, most Gastropod families, and native sunfishes (*Lepomis spp*.) also increased. Contrary to expectation, some benthic macroinvertebrate taxa declined in abundance or showed no significant response to the crayfish removal, and for many groups the response in cobble differed from that in macrophytes. Bioenergetics modeling showed that consumption of the majority of invertebrate orders by littoral fishes increased, providing a possible explanation for the counterintuitive invertebrate response. However, some invertebrate groups increased in abundance despite increased consumptive pressure by littoral fishes, indicating that the effects of crayfish predation and increased macrophyte habitat may outweigh the effects of increased fish consumption in determining the response of some macroinvertebrate groups. Overall, the manipulation revealed the myriad ways in which rusty crayfish interact with invaded food webs via both direct and indirect effects. This study highlights the importance of indirect effects in determining the ecosystem impacts of invasive species, and demonstrates that reversal of the negative effects of invasive species is possible over relatively short timescales.

Introduction

Species within ecological communities interact via multiple pathways both directly and indirectly. As a result, the effects of perturbations to one species can be difficult to predict (Wootton 1994a), even in such coarse terms as the direction of responses and which species are likely to be most affected (Yodzis 1988; Zavaleta *et al.* 2001; Brown *et al.* 2011). Experimental additions or removals of species have been used to evaluate the relative strength of species interactions (Pimm 1980; Sih *et al.* 1985; Carpenter & Kitchell 1988). In this sense, species invasions serve as whole-system “experiments” that can be used to better understand food-web structure.

Invasive species are a major threat to biodiversity worldwide, particularly in aquatic ecosystems (Vitousek *et al.* 1997; Ricciardi & Rasmussen 1999; Sala *et al.* 2000). While prevention is the cornerstone of any invasive species management program, eradication or control (maintaining at low densities) of invasive species can sometimes be successful when prevention fails (Myers *et al.* 2000). Removal via harvesting has often been discounted as impossible for most species due to the high cost and low probability associated with removing all individuals (Dahlsten *et al.* 1989). However, eradication or control does not necessarily require that 100% of the population be killed by management interventions. Practitioners of fisheries science and conservation biology are well aware that the dynamics of small populations can result in the long-term maintenance of a population at low numbers or even extinction, even when major factors of mortality have been removed (Hilborn & Walters 1992; Liebhold & Bascompte 2003). A depensatory response, where population growth is reduced at low densities, is possible, in which case reducing the mortality of a population will not necessarily result in increased population growth (Myers *et al.* 1995; Myers *et al.* 1999; Liermann & Hilborn 2001; Walters & Kitchell 2001). In contrast, a compensatory response of increased survival or recruitment can result in population increases following removal efforts and thus failures of eradication efforts (Zipkin *et al.* 2009).

Invasive species that interact with multiple species and/or physically alter invaded systems cause the greatest impacts (Didham *et al.* 2007), and thus are the most likely target of removal efforts. The removal of such species can produce unexpected responses, and must be viewed in a whole-ecosystem context (Zavaleta *et al.* 2001; Hulme 2006). Indirect effects, where one species affects another through an intermediary species or modifies the strength of interaction between other species, can be critical in determining the overall impact of an invasive species (White *et al.* 2006; Brown *et al.* 2011). A whole-system manipulation is a powerful way to quantify the overall responses of various groups to direct and indirect effects (Sih *et al.* 1985; Yodzis 1988), and can provide unique insight into ecosystem level responses to perturbations on the relevant scale, even in the absence of replication (Carpenter *et al.* 1995; Carpenter 1998; Schindler 1998). Removals of established invasive species can thus serve two purposes: restoring native biodiversity and function and quantifying the effect of food-web interactions on ecosystem dynamics (Donlan *et al.* 2002; Hulme 2006; Vander Zanden *et al.* 2006).

Invasive species can strongly influence ecosystem processes, acting as ecosystem engineers (Crooks 2002) by removing aquatic macrophytes used by other species as a refuge from predation and/or a food source (Magnuson *et al.* 1975; Crowder & Cooper 1982; Olsen *et al.* 1991; Lodge *et al.* 1994; Rosenthal *et al.* 2006), altering sediment dynamics (Statzner *et al.* 2000; Crooks 2002; Wright & Jones 2006), reducing clogging of interstitial spaces (Nogaro *et al.* 2006), and increasing the depth of oxygenation in sediments (Revsbech *et al.* 1980) via their burrowing behaviors. Rusty crayfish (*Orconectes rusticus*) are invasive throughout much of North America (Hobbs *et al.* 1989) and are one of the best documented examples of the pervasive negative impacts of invasive crayfish (Lodge *et al.* 2000). Their impacts have been documented at organismal (Hayes *et al.* 2009), population (Capelli 1982; Capelli & Munjal 1982), community (Olsen *et al.* 1991; Wilson *et al.* 2004; McCarthy *et al.* 2006), and ecosystem (Lodge *et al.* 1994) levels.

Crayfish are omnivores and have been considered keystone predators of particular importance in shaping community dynamics, as they interact with multiple food web components simultaneously (Momot *et al.* 1978; Diehl 1995; Dorn & Wojdak 2004). Rusty crayfish can simultaneously exert both positive and negative pressures on native species, as they interact with members of the littoral community via numerous direct and indirect pathways (Figure 1). One of the most cited impacts of invasive crayfish is their negative effect on benthic macroinvertebrates (Hanson *et al.* 1990; Olsen *et al.* 1991; Lodge *et al.* 1994; Perry *et al.* 1997; Nyström *et al.* 1999; Nyström *et al.* 2001; Usio & Townsend 2004; Nystrom *et al.* 2006; Correia & Anastácio 2008; Usio *et al.* 2009). Macroinvertebrates are important diet items of omnivorous crayfish (Capelli 1980; Whitledge & Rabeni 1997; Roth *et al.* 2006), but the effects of rusty crayfish on non-gastropod macroinvertebrates in whole-lake studies are highly variable (Wilson *et al.* 2004; McCarthy *et al.* 2006; Rosenthal *et al.* 2006; Nilsson *et al.* 2012). This variation could be due to direct and indirect effects acting in opposition in some cases and synergistically in others. For example, the effects of habitat modification can either augment or cancel out the direct effects of predation on invertebrates (Crowder & Cooper 1982; Peckarsky 1985; Parkyn *et al.* 1997; Helms & Creed 2005). Furthermore, rusty crayfish may indirectly reduce predation pressure on some invertebrate taxa through their effects on littoral fishes. Rusty crayfish negatively affect bluegill (*Lepomis macrochirus*) and pumpkinseed (*L. gibbosus*) (hereafter *Lepomis*) sunfish (Wilson *et al.* 2004; Roth *et al.* 2007), which are known to affect invertebrate populations via predation (e.g., Bohanan & Johnson 1983; Gilinsky 1984; Osenberg *et al.* 1992). Additionally, fishes such as rock bass (*Ambloplites rupestris*) and smallmouth bass

(*Micropterus dolomieu*) prey upon both crayfish and other benthic invertebrates (Becker 1983; Hein *et al.* 2006). Thus, an increase in crayfish abundance could reduce predation on invertebrates by providing an alternative prey source (Abrams 1987; Abrams 1991; Wootton 1994b), or conversely could increase predation on invertebrates via apparent competition (Holt & Lawton 1994). Moreover, trophic interactions among non-crayfish macroinvertebrates also play a role in determining macroinvertebrate community structure (e.g., Cooper *et al.* 1985; Robinson & Wellborn 1987; Blois-Heulin *et al.* 1990; Hart 2002).

Rusty crayfish were removed from a north temperate lake to promote recovery of the native littoral food web. The removal was successful in reducing rusty crayfish catch rates by over 95% from 2001-2005 (Hein *et al.* 2007); removal trapping ceased in 2008 and monitoring continued through 2011. The objectives of this paper are: (1) To document changes in rusty crayfish abundance and population dynamics over the entire removal experiment plus three post-removal years; (2) to quantify the native community response, including native crayfish, macrophytes, benthic macroinvertebrates, and littoral fishes; and (3) to use the community responses to infer the relative strength of crayfish predation, habitat, and fish predation in shaping benthic macroinvertebrate densities.

Methods

Study site

Sparkling Lake is a 64 ha mesotrophic seepage lake in Vilas County, WI, USA (46.008°, -89.701°) with a maximum depth of 20 m. Sparkling Lake is a study lake of the North Temperate Lakes Long Term Ecological Research (NTL-LTER) program, which has monitored physical, chemical, and biological variables since 1981 (http://lter.limnology.wisc.edu). Rusty crayfish invaded Sparkling Lake in the 1970's. A whole-lake manipulation was initiated in Sparkling Lake in 2001 (Hein *et al.* 2007); rusty crayfish were manually removed via trapping from 2001-2008. Fishing regulations were also changed in 2001 with the intention of reducing angler harvest and increasing fish predation on juvenile crayfish (Hein *et al.* 2006); the length limits of smallmouth bass and walleye were increased to 457 and 711 mm, respectively, and bag limits were decreased to 1 for both species (compared to a statewide bag limit of 5 and length limits of 356 and 381 mm, respectively. These regulations were in effect for the duration of this study.

Crayfish

Adult rusty crayfish were trapped in August of 2001 and from June-August of 2002-2011 using Gee-style minnow traps modified by widening the openings and baited with beef liver or frozen fish following (Capelli & Magnuson 1983). Between 30-313 (mean=149) traps were set at 43 sites around the perimeter of the lake at the 1 m depth contour, with higher concentrations of traps in locations of higher crayfish abundance (Hein *et al.* 2007). Traps were emptied daily from 2001-2003 and every 1–4 days from 2004-2011 as catch rates declined. From 2001-2008 all trapped rusty crayfish were removed, and all native virile crayfish (*Orconectes virilis*) were released. From 2009-2011 trapping continued but all crayfish were released. Catch per unit effort (CPUE) of each crayfish species is used as an index of adult crayfish abundance, and was calculated daily (total crayfish caught/total trap days) and presented as mean annual CPUE (+/- SE). For several analyses described below, rusty crayfish density was categorized as "high", representing the early years of the crayfish removal when $CPUE \geq 1$, and "low", representing the later years of the crayfish removal when $CPUE<1$.

Rusty crayfish densities were estimated in mid-July of 2002-2004 and 2007-2010 shortly following the release of juvenile crayfish from brooding females. Adult (age 1+) and juvenile (age 0) rusty crayfish were sampled with SCUBA in cobble using hand collections and an airlift suction sampler, respectively, following methods described by Hein and colleagues (2007). Additionally, populations (>age 0) of both rusty and virile crayfish were estimated using the Chapman modification of the Schnabel mark-recapture method (Krebs 1999) in 2009 and 2010 for comparison to the rusty crayfish population estimate from 2003 (Hein *et al.* 2006). Crayfish for mark-recapture were collected using traps and by hand while snorkeling to increase numbers of small (<25 mm carapace length) individuals. All captured crayfish of both species were individually marked using visual implant elastomer tags (Northwest Marine Technologies) embedded in abdominal flexor muscles.

Stock recruitment

The relationship between adult female density and juvenile (age 0) density was examined in Sparkling Lake over time and in 10 nearby lakes sampled in 2002-2004 representing a range of rusty crayfish densities (Appendix 1). Adult and juvenile crayfish were sampled concurrently in cobble using the methods described above for density surveys, and crayfish were identified to species and sex. Preliminary analysis of the stock-recruitment relationship indicated that the data followed a linear form; non-linear stock-recruitment models (Beverton-Holt and Ricker) that exhibit negative density dependence at high adult densities (Hilborn & Walters 1992) were fit to data, but best fit parameter estimates for both non-linear models included zeros and as a result the models reduced to linear form. Linear models predicting juvenile density as a function of female density were subsequently fit to stock-recruitment data, and we tested whether the relationship differed in Sparkling Lake from the cross-lakes surveys by comparing models with and without terms for Sparkling Lake (intercept and interaction with female density). The best fit model was selected using Akaike's Information Criterion, or AIC (Akaike 1973), with extra parameters included for Sparkling Lake if they reduced the AIC value by more than 2 (Burnham & Anderson 2002).

Fecundity

Gravid females were collected from Sparkling Lake in June of 2002-2004 and 2008-2009, and from seven additional lakes in June of 2009 representing a range of rusty crayfish densities (Appendix 1, Appendix 2). Our goal was to collect at least 30 gravid females from each lake, but this was not possible in two low density lakes due to the difficulty associated with finding rusty crayfish. Gravid females were measured to the nearest mm carapace length (CL) and eggs were removed and enumerated. Size distributions of gravid females for years/lakes of high (≥1 CPUE) or low (<1 CPUE) rusty crayfish densities were compared both across lakes and across years in Sparkling Lake using Kolmogorov-Smirnov tests. The relationship between egg number and female CL was assessed using multi-level mixed effects models (Gelman & Hill 2006) with random effects for lake and year to account for non-independence of samples. Fixed effects for CL (centered about the mean for analysis; Gelman & Hill 2006), crayfish density (high or low), and its interaction were included in the full model, and the most parsimonious set of fixed effects was determined by selecting the best fit model using AIC using the criteria described above. Fixed effects were chosen using AIC values generated using the maximum likelihood (ML) method of parameter estimation (Pinheiro & Bates 2000). Both slope (CL) and intercept were allowed to vary as a function of each random effect.

Macrophytes

Macrophyte cover was assessed in the third or fourth week of July from 2002-2004 and from 2007-2010. Eight transects were selected to correspond to trap survey sites for rusty crayfish and represent the range of macrophyte communities in the lake. These transects stretched from the waterline to a depth of 4 meters, running perpendicular to shore. Circular quadrats ($1m^2$) were placed along each transect at 1 m longitudinal intervals, and observers using SCUBA estimated visually the percent cover of each macrophyte species within the quadrat. The sum of percent cover of all species within a quadrat does not necessarily add to 100; rather, this sum reflects the percentage of bottom substrate covered by macrophytes. Total percent cover in each quadrat (+0.5, half of the minimum non-zero observed value) was natural log transformed to correct for heteroscedasticity of residuals and modeled as the independent variable. Macrophyte data were grouped into years of high crayfish abundance (2002-2003) and years of low crayfish abundance (2004; 2007-2010) for statistical analysis. Differences in percent cover for these groups was assessed using a multi-level general linear model with crayfish abundance index (high or low), depth range (0-1m, 1-2m, 2-3m, 3-4m), and their interactions as fixed effects, and transect and year as random effects. *See Statistical Analysis: Hierarchical Modeling* (below) for more details on statistical analysis of macrophyte data.

Benthic macroinvertebrates

Benthic macroinvertebrates were sampled from 2002-2003 and from 2008-2010 along 5 transects that corresponded to crayfish survey sites and represented a range of habitat types and crayfish abundance in 2002 when sampling began. Samples were collected at 1, 3, and 5 m depths, although not all depths were sampled for all transects in all years. Three replicate samples were collected at each site/depth combination in each year using an underwater vacuum air-lift sampler (Wahle & Steneck 1991; Butkas *et al.* 2010). The sampler consists of a length of PVC attached to a SCUBA tank with a 500 µm mesh bag attached to the top of the PVC. We sampled a 0.09 m2 area delimited by a circular quadrat and placed haphazardly at the appropriate depth perpendicular from shore at the transect location.

All surfaces potentially available as macroinvertebrate habitat were sampled within a quadrat. For example, macrophytes contained within the quadrat were placed inside the PVC tube prior to opening the SCUBA tank to sample invertebrates living on macrophyte surfaces. In cobble habitat, the upper surface of the rocks were suctioned and then all rocks contained inside the quadrat were picked up, suctioned on all surfaces, and placed outside of the quadrat. Substrate exposed when cobble was removed was also suctioned. Samples were sealed in plastic bags with lake water, placed on ice, and separated live within 48 hours. Invertebrates were separated from substrate, preserved in 95% EtOH, and later identified to the lowest practical taxonomic level (genus in most cases).

Habitat for each sample was classified based on substrate contained within the quadrat as soft substrates (mainly sand), cobble, or macrophyte. All sites classified as sand in 2002-2003 were subsequently covered with macrophytes in 2008-2009; therefore, for analysis substrates were classified as either macrophyte/soft or cobble. The effect of crayfish CPUE and habitat on individual invertebrate taxa was evaluated using multi-level models similar to those used to evaluate macrophyte percent cover. Crayfish abundance was classified as high (2002-2003) or low (2008-2009), and this crayfish abundance factor, habitat, and their interaction were evaluated as fixed effects. Sample site (transect*depth combination) nested within year were included as random effects to account for non-independence of samples from the same site and same year. Invertebrate density (+5, one half of the minimum non-zero observed value) was natural log transformed to resolve heteroscedasticity of residuals and modeled as the independent variable. Analyses were conducted on total invertebrate density, orders, and for families that appeared in at least 10% of samples. See *Statistical Analysis: Hierarchical Modeling* (below) for more information on statistical analysis of macroinvertebrate data and assessment of statistical significance.

Fish

Relative abundance of *Lepomis* was indexed from 1981-2011 using catch rates from LTER sampling (data available online at http://lter.limnology.wisc.edu). Catch per unit effort was calculated for each gear type (beach seine, electrofishing, fyke net, trammel net) in each year, and due to high within-year variability in catch rates we calculated the sum of CPUE from all gear types to avoid bias introduced by any single gear type (Weaver *et al.* 1993; Wilson *et al.* 2004).

We sampled the Sparkling Lake littoral fish community bimonthly during summer months from 2001-2004 and from 2009-2010 using electrofishing. Fyke nets were also used to sample fish in 2009-2010. All fish were measured (total length, mm), weighed (g), and tagged with Floy tags or fin clips. Adult population size of smallmouth bass, rock bass, bluegill sunfish, and pumpkinseed sunfish were estimated in each year using the Chapman modification of the Schnabel mark-recapture method (Ricker 1975; Krebs 1999). Diets were collected from each species at each electrofishing sampling event using gastric lavage (Seaburg 1957) and preserved in 95% EtOH. Diet items were identified to order for non-crayfish invertebrates and to species (when possible) for fish and crayfish, enumerated, dried at 57°C for 48 hours, and weighed.

Similarity of smallmouth bass and rock bass diets between each pair of years from 2001-2004 and 2009-2010 was quantified using Morisita's index of diet overlap (Smith & Zaret 1982). We used non-parametric bootstrapping to assess whether diets of a given species were significantly different in any two years of study (Guy *et al.* 2007). For each year of study, we sampled with replacement the same number of fish contained in the original sample from the entire population of individuals from all years. We re-calculated Morisita's index for each pair of years in the study using the resampled data, and repeated 1000 times to generate a distribution of similarities between all sets of years. We then calculated the proportion of times that the bootstrapped index was lower (more dissimilar) than the actual index for each pair of years, and values more dissimilar than 95% or more of the resampled values were considered statistically significant.

Bioenergetics

Total annual consumption (kg) of major prey items of each fish species was estimated using Bioenergetics 3.0 (Hanson *et al.* 1997) modified to be run in R version 2.14.1 (R Development Core Team 2011). Bioenergetic parameters for rock bass and smallmouth bass were obtained from Roell and Orth (1992) and Whitledge and colleagues (2003), respectively. Bioenergetics analysis requires data on fish growth, diets, and water temperature. Age-specific growth rates were estimated from scales using the Fraser-Lee back-calculation model (Appendix 3) (Ricker 1975). Age-length keys with semi-random age assignment to were used to estimate population sizes at age in each year; this approach explicitly assigns an age to each individual in a sample based on a subsample of aged fish (Isermann & Knight 2005). Separate age samples were used for 2001-2003 and 2009-2010, as preliminary analysis showed differences in growth rates in these year groups (Appendix 3), and sample sizes of aged individuals were insufficient to generate separate age-length keys for each year. Average daily surface water temperatures for each year were obtained from the NTL-LTER (http://lter.limnology.wisc.edu) and used in Bioenergetics simulations. Diet proportions (% by mass) specific to each sampling date were used for each species subdivided into length classes (<150, 151-250, >250 mm TL) to reflect ontogenetic diet changes. Diet items were grouped for analysis and/or display according to diet item descriptions in Table 1. The "Fish" category consisted mostly of mimic shiners (*Notropis volucellus*) but also included rainbow smelt (*Osmerus mordax*), bluntnose minnow (*Pimephales notatus*), *Lepomis* spp., and rock bass. Energy densities ($J{\cdot}g^{-1}$ wet weight) of prey items were obtained from various sources (Table 1). When reported energy density values were in $J{\cdot}g^{-1}$ dry weight they were converted to wet weight using percent water for the same taxa used for energy density (when available; Cummins & Wuycheck 1971).

Consumption and prey density effect size

We calculated changes in consumption of invertebrates from years of high crayfish to years of low crayfish abundance for comparisons with changes in invertebrate density. Mean of total consumption by all fish species from Bioenergetics was calculated for 2001-2003 (high) and 2009-2010 (low), which were compared with invertebrate densities measured in 2002-2003 and 2008-2010, respectively. Consumption data from 2004 were not included as rusty crayfish CPUE was <1, but invertebrate densities were not measured in a low crayfish year until 2008. Similarly, prey density changes were calculated for each non-crayfish benthic invertebrate taxa as the difference between the restricted maximum likelihood (REML; see *Statistical analysis: Multi-level modeling*) estimate of taxa density in low crayfish years (2002-2003) and that in high crayfish years (2008-2010). Invertebrate density was modeled on the natural log scale, so effect sizes are in the same natural log units as the consumption effect size. For crayfish, effect size was calculated as the difference between mean rusty crayfish density in 2007-2010 and 2001-2003 on the natural log scale. Changes in consumption represent whole-lake changes, changes in non-crayfish invertebrate density were calculated separately for cobble and macrophyte/soft habitats, and changes in crayfish density were calculated for cobble only.

Statistical analysis: Multi-level modeling

For analysis of macrophyte percent cover and benthic macroinvertebrate densities, we used a multi-level modeling approach (Gelman & Hill 2006). We estimated fixed effects and their confidence intervals from the full model (all potential fixed effects, interactions, and random effects included), which results in higher variance within groups but avoids problems of "data snooping", and is thus a conservative test (Bolker *et al.* 2009). Full models included a small number (2-3) of fixed effects expected to influence results based on biological knowledge of the system, and random effects to account for non-independence of samples from the same sites or years similar to classical blocked experimental designs (see *Macrophyte* and *Benthic macroinvertebrate* sections above for details of fixed and random effects for each analysis). Effects are reported as restricted maximum likelihood (REML) estimates of fixed effects from the lme4 package (Bates & Sarkar 2007) in R v2.14 (R Development CoreTeam 2011). Confidence intervals were estimated using the languageR package using Bayesian highest posterior density (HPD) confidence intervals of parameter estimates generated from Markov

Chain Monte Carlo (MCMC) simulations (Baayen *et al.* 2008). The HPD intervals of fixed effects from MCMC simulations incorporate variation in random effects (Baayen *et al.* 2008). Statistically significant differences are based on non-overlapping 95% HPD intervals of fixed effect estimates (Gelman & Hill 2006; Qian & Shen 2007). Adjusted R^2 values for mixed effects models were calculated as the likelihood ratio test R^2 (Magee 1990; Kramer 2005).

Results

Crayfish

We removed a total of 91,930 rusty crayfish with traps from 2001-2008. Rusty crayfish CPUE decreased by two orders of magnitude from its peak in 2002 of $11.8 \cdot \text{trap}^{-1}$ to $0.1 \cdot \text{trap}^{-1}$ in the final year of the crayfish removal in 2008, and did not increase following cessation of removal trapping (Figure 2A). Catch rates differed significantly among years (ANOVA, $F_{10, 303}=49.7$, $p<0.001$), although Tukey post-hoc tests showed no significant differences in catch rates of rusty crayfish from 2004-2011 (all pair wise comparisons $p>0.99$). Native virile crayfish CPUE increased by two orders of magnitude from a low of $0.001 \cdot \text{trap}^{-1}$ in 2004 to a peak of $0.165 \cdot \text{trap}^{-1}$ in 2010 (Figure 2A). Virile catch rates differed significantly among years (ANOVA, $F_{10,303}=44.6$, $p<0.001$), and Tukey post-hoc tests showed significant differences in catch rates of virile crayfish in 2010 and 2011 compared to all other years (all pair wise comparisons $p<0.001$), and significant differences between virile catch rates in 2009 compared to 2002-2004 ($p<0.003$). Both adult and juvenile rusty crayfish density decreased by approximately 1.5 orders of magnitude from the early years of the crayfish removal to the final year of sampling

(Figure 2B). Total number marked (recaptured) in 2009 and 2010 for rusty crayfish was 767(85) and 1,258(227), and for virile crayfish was 124(4) and 656(165), respectively. Mark-recapture population estimates (95% confidence interval) of adult rusty crayfish were 4,032 (3,229-5,367) in 2009 and 4,420 (3,876-5,142) in 2010. This is a two order of magnitude decrease from the population estimate of 578,790 in 2003 (Hein *et al.* 2006). The population estimate for virile crayfish was 1,397 (621-3,343) in 2009 and 1,904 (1,636-2,277) in 2010. No comparable estimates for virile crayfish exist from 2003 due to low catches (only 21 individuals were captured over 6,403 trap days).

The relationship between female rusty crayfish density and juvenile density was linear, and the stock-recruitment relationship for Sparkling Lake did not differ from that of the cross-lakes survey (Appendix 4, Figure 3). No density dependent effects on juvenile density as a function of female density were discernible. The size distribution of gravid females from Sparkling Lake differed from that of the cross-lakes survey (Two-sample Kolmogorov-Smirnov test, $D=0.26$, $p<0.001$). Additionally, size distributions differed between high and low crayfish densities, compared between high and low years in Sparkling Lake (Two-sample Kolmogorov-Smirnov text, $D=0.27$, $p<0.001$), and among high and low lakes in the cross-lake surveys (Two-sample Kolmogorov-Smirnov text, $D=0.50$, $p<0.001$). Carapace length of gravid females was on average 3-4 mm lower in lakes/years with low crayfish density than in lakes/years with high crayfish density (Figure 4) in both Sparkling Lake (Two sample t-test, $t=-5.25$, $df=318.6$, $p<0.001$) and cross-lakes samples (Two sample t-test, $t=-6.099$, $df=106.2$, $p<0.001$) . The number of eggs per female increased exponentially with increasing carapace length, and the best fit model contained an interaction between length and crayfish density (Appendix 4), meaning that fewer eggs were produced at smaller sizes when crayfish density was low (Figure 4D,C).

Macrophytes

Macrophyte percent cover increased significantly in the 2-4m depth range in years of low crayfish CPUE compared to years of high crayfish CPUE (Figure 5C, D). In 0-2 m depths percent cover increased, but was more variable and the change was not statistically significant (Figure 5A, B). The change in macrophyte cover was driven primarily by changes in *Najas flexilis, Potomogeton gramineus, and Chara spp*. (Appendix 5).

Benthic macroinvertebrates

The benthic macroinvertebrate response to the crayfish removal differed among taxonomic groups and among habitat types (Figure 6). Effects were highly variable in cobble habitat, with Gastropoda exhibiting a strong positive response to the crayfish removal and most Ephemeroptera families exhibiting a strong negative response (with the exception of Caenidae). In macrophyte/soft substrates, most invertebrate groups responded negatively to the crayfish removal with the exception of Mollusca and Megaloptera. Amphipoda, Odonata, and Physidae (Gastropoda) all declined significantly following the crayfish removal. The difference in density of most invertebrate groups was not statistically significant based on overlapping 95% confidence intervals (Appendix 6).

Fish

Lepomis abundance increased during the experimental period. The six highest CPUE values from the LTER record (1981-2011) were observed in 2006-2011 (Figure 7A). Mark-recapture population estimates of *Lepomis* were not possible in 2001-2004 due to low sample sizes (a total of 23 pumpkinseed and 0 bluegill collected in these 4 years), but by 2009-2010 the population size was estimated to be between 2,000-3,000 individuals (Figure 7B). Rock bass and smallmouth bass populations fluctuated but did not show a directional trend during the experimental period (Figure 7C and Figure 7D).

Diets of littoral fishes changed from early in the crayfish removal (2001-2003) to post-crayfish removal (2009-2010; Figure 8). In particular, during the first year of study crayfish constituted more than 30% and 20% by number of rock bass and smallmouth bass diets, respectively (Figure 8). Following the crayfish removal, crayfish made up less than 1% of rock bass diets and just over 1% of smallmouth bass diets. Ephemeroptera also made up a smaller proportion of the diets of both rock bass and smallmouth following the cessation of the crayfish removal, but the proportion of rock bass and smallmouth diets comprised of Diptera, Odonata, and Trichoptera increased in the years following the crayfish removal. Both rock bass and smallmouth bass diets changed over time (Figure 9). Smallmouth bass diets in 2010 differed significantly from smallmouth bass diets in all other years (Figure 9B) while rock bass diets from years with low crayfish abundance only differed significantly from those in 2001 and 2002 (Figure 9A).

Lepomis were not present in sufficient numbers to sample for diets in 2001-2003, and thus diet data are presented only for 2009-2010 for bluegill and pumpkinseed sunfishes (Figure 10). Both sunfish species consumed high numbers of Diptera, and bluegill consumed high numbers of zooplankton while pumpkinseed consumed high numbers of Gastropoda.

Bioenergetics

Estimated total annual consumption of most prey groups increased over time (Figure 11). Crayfish, Ephemeroptera, and terrestrial items were exceptions; total annual consumption of these groups declined. Increases in total consumption of most invertebrate taxa in later years were due to the appearance of substantial *Lepomis* populations that previously had exerted negligible predation pressure (e.g., Amphipoda, Bivalva, Diptera, Isopoda), although diet shifts in rock bass and smallmouth bass contributed to increases in consumption of some groups (Figure 11).

Total consumption by fish of most invertebrate groups increased from years of high crayfish abundance to years of low crayfish abundance (Figure 12). Ephemeroptera and crayfish were the only taxa for which total consumption declined. The density of most invertebrate groups increased in cobble habitat (Figure 12B). In macrophyte/soft habitat, the density of some groups increased, some decreased, and some remained the same (Figure 12C). The magnitude of density changes was smaller than changes in consumption for most groups. Consumption changes were calculated on whole-lake basis, and therefore x-axis values for taxa in Figure 12B and 12C are identical.

Discussion

Rusty crayfish population

Our whole-lake manipulation successfully reduced invasive rusty crayfish CPUE by two orders of magnitude. We observed declines of similar magnitude in both density surveys of juveniles and adults and in mark-recapture population estimates, indicating that the reduction in rusty crayfish numbers has occurred in all age classes and both sexes. Although others have argued that without total eradication, controlling invasive species will require ongoing management to avoid the system reverting to a degraded state (Norton 2009), rusty crayfish densities remained low even three years after cessation of removal, and recovery of native species continued in post-trapping years.

The success of invasive species control depends critically on density-dependent population effects. On one hand, a compensatory response of increased reproduction or survival at low densities is possible and can result in *increased* abundance of the target species following removal efforts (Zipkin *et al.* 2008; Zipkin *et al.* 2009). The stock-recruitment relationship of rusty crayfish exhibited no compensatory response; in fact, recruitment appeared to be a constant proportion of adult density (Figure 3). This density-independent relationship between adult and juvenile density is common among exploited species, and could be a reflection that even at their highest abundance, rusty crayfish did not fully saturate available habitat (Hilborn & Walters 1992). On the other hand, Allee effects (positive density dependence and reduced population growth rates at low densities) can be created or taken advantage of by removal efforts, and can lead to extirpation of populations or maintenance of low densities in the long term (Tobin *et al.* 2011). Notably, in their review of the role of Allee effects in controlling invasive populations, Tobin and colleagues (2011) identified culling and augmentation of generalist predators as strategies to control invasive aquatic invertebrates, particularly when culling preferentially targets males. Both strategies were employed here, and fecundity was reduced as a result of both lower mean size at reproduction for females and lower number of eggs produced at a given size.

Intensive size-selective harvest is known to decrease size at maturity and to reduce the overall reproductive potential of populations, resulting in reductions in yield (Kuparinen & Merila 2007; Allendorf *et al.* 2008; Fenberg & Roy 2008). Reductions in fecundity due to intensive harvest have been documented not only due to the strong relationship between female size and reproductive output, but also because relative fecundity (fecundity per gram of body weight)is higher in older and larger individuals (Goni *et al.* 2003; Longhurst 2006). Furthermore, harvest selects for younger, smaller, slower growing individuals by removing the largest members of a population, and can increase the vulnerability of the non-harvested survivors to predation (Kuparinen & Merila 2007), further reducing the harvested population. Whether harvest-induced life history changes are caused by genetics or phenotypic plasticity is a topic of debate in the literature , and has important implications for the reversal of the effects (Kuparinen & Merila 2007). Harvest-driven selection has been implicated in the sustained collapse of exploited populations even after harvest mortality has been discontinued (Hutchings 2000; Hutchings & Reynolds 2004). Continued monitoring of the rusty crayfish population will reveal if the changes in size at maturity and fecundity are sustained, suggesting a genetic basis, or rapidly recover, suggesting a phenotypic plasticity basis. It is interesting to note that while some have argued for the potential of recruitment overfishing of European crayfish (Skurdal & Taugbol 1994), population studies of virile crayfish in northern systems revealed a compensatory response to harvest in juvenile production (Momot 1998) and the belief that high levels of harvest were sustainable (Momot 1991). However, these studies only harvested males and harvest rates were substantially lower than the harvest in this study.

Native food web recovery

In response to the reduction of rusty crayfish to a small fraction of their former densities, native crayfish, macrophytes, gastropods, and *Lepomis* all increased. These results are consistent with what would be expected following the removal of the negative direct effects of rusty crayfish. While restoration of native species has been observed following the eradication of established invaders in some systems (Berger 1993; Simberloff 2003; Hulme 2006), the rate at which native species recovered in this system in the absence of further restorative actions is notable. For example, both *Lepomis* and virile crayfish populations began to increase 5 years into the removal experiment, in spite of being reduced to nearly undetectable levels prior to the removal. Previous research predicted that reseeding of macrophytes may be needed to restore macrophytes in lakes invaded by rusty crayfish (Rosenthal *et al.* 2006); we find that such action is not needed in Sparkling Lake. Although the macrophyte recovery in Sparkling Lake was dominated by *N. flexilis and Chara spp*. as observed by Rosenthal and colleagues, we also documented increases in other caulescent or long-leaved species such as *Potomogeton gramineus and Vallisneria americana*, indicating that even species that reproduce clonally are able to rapidly increase in abundance following reductions in crayfish herbivory. These species-specific responses may also explain the greater increase in macrophyte cover at 2-4 m depths compared to 0-2 m depths; shallow waters of Sparkling lake are dominated by short statured isoetid species, while deeper waters contain more single stemmed or long leaved species that are likely targets of crayfish destructive activities (Lodge & Lorman 1987; Olsen *et al.* 1991).

Benthic invertebrates

While the responses of many littoral community members were consistent with what would be expected based on a reduction of the direct negative effects of rusty crayfish, the benthic macroinvertebrate community response was much more variable and likely reflects the myriad pathways through which rusty crayfish interact with other benthic macroinvertebrates. Suppression or removal of invasive species that are integrated into invaded ecosystems in complex ways can produce unexpected results (Zavaleta *et al.* 2001; Donlan *et al.* 2002; Hulme 2006; Bergstrom *et al.* 2009), and the response of many macroinvertebrate groups reflect the complexity of interactions between rusty crayfish and their prey.

The invertebrate response differed among habitat types. Rusty crayfish are associated with cobble habitat (Garvey *et al.* 2003) and their direct effects were likely the strongest in this substrate. Gastropoda and Ephemeroptera densities both significantly changed in response to the crayfish removal in cobble, although in opposite directions. Negative effects of rusty crayfish on Gastropods have been demonstrated much more consistently than on other invertebrate groups (Lodge *et al.* 1994; Perry *et al.* 1997; Wilson *et al.* 2004; McCarthy *et al.* 2006). Gastropod density increased approximately 20-fold as crayfish density declined, consistent with the removal of predation pressure of rusty crayfish. However, the Gastropod response varied among families and among habitat types. The densities of two pulmonate snail families (*Lymnaeidae and Planorbidae*) significantly increased in cobble. These increases are likely a reflection of the preference of crayfish for thin-shelled pulmonate snails which are more easily crushed than Caenogastropoda (Stein *et al.* 1984; Brown 1998). The third pulmonate family (*Physidae*) increased but not significantly. Physids are capable of avoiding crayfish predation both by altering their behavior and their life history strategy(Crowl & Covich 1990; Covich *et al.* 1994; DeWitt *et al.* 2000), and were perhaps less affected by rusty crayfish. Gastropods are also the preferred prey of pumpkinseed sunfish (Mittelbach 1984), and consumption of Gastropods by fishes increased by an order of magnitude in the years following the crayfish removal. Additionally, many Gastropods are found at the highest densities in macrophyte habitats (Brown & Lodge 1993), as macrophytes provide refuge from fish predation (Crowder & Cooper 1982; Osenberg & Mittelbach 1989). The complexity of these interactions are reflected in the variable responses of Gastropod families in macrophytes where direct predation effects of crayfish are the lowest, predation pressure by pumpkinseed is likely the highest, and the beneficial effects of macrophyte complexity are also the highest. Physidae decreased and was the only family whose response was statistically significant. The negative response of Physids to the crayfish removal in macrophyte habitat could be an indication that they are ill-adapted to avoid predation by fishes, perhaps as a result of shell morphology adapting to avoid crayfish consumption (DeWitt *et al.* 2000).

Overall, Ephemeroptera densities decreased in cobble habitat, indicating that the direct effect of predation by rusty crayfish is not major determinant of Ephemeroptera abundance. Indeed, rusty crayfish may have indirectly facilitated high densities of Ephemeroptera in cobble. Many possible mechanisms for this facilitation are possible, and examination of the differential responses of the life histories of the three major Ephemeroptera families and how their responses differed by habitat can provide plausible hypotheses for the major pathways affecting each group. Ephemeridae (*Hexagenia spp*. and *Ephemera spp*.) densities decreased nearly 20-fold following the removal of rusty crayfish, and Heptageniidae (mainly *Stenonema spp.*) densities also declined. Ephemerids are large collector-gatherers that burrow into soft sediments (Hunt 1953), and Heptageniids are smaller scrapers live in the interstitial spaces of cobble/boulder habitats (Merritt & Cummins 1996). Rusty crayfish utilize cobble habitat to provide refuge from fish predation (Garvey *et al.* 2003), and they excavate sediment underneath cobbles to obtain this shelter. Both Ephemerids and Heptageniids are likely beneficiaries of reduced interstitial sediments and increased aeration in the presence of crayfish (Pringle *et al.* 1993; Flecker 1996; Usio & Townsend 2004; Bo *et al.* 2007; Johnson *et al.* 2010). Furthermore, Heptageniids compete with Gastropods for periphyton on cobbles, and could respond positively to the suppression of Gastropods by rusty crayfish (Nyström *et al.* 1999; Hertonsson *et al.* 2007). Finally, Heptageniids crawl quickly to avoid predation (Peckarsky 1980, 1996) making them likely targets for visual predators such as smallmouth bass and rock bass. In contrast to the negative response of the other dominant Ephemeroptera taxa, Caenidae (*Caenis spp*.) densities increased following the crayfish removal. Caenids are small, cryptic, and slow moving, and are often covered in sediment (Needham *et al.* 1969; Edmunds *et al.* 1976), making them relatively invulnerable to fish predation but potentially increasing their vulnerability to invertebrate predators such as crayfish (Matthews *et al.* 1993). All Ephemeroptera declined slightly but insignificantly in macrophyte habitat, although initial densities were much lower, indicating that the hypothesized positive effects of rusty crayfish are likely not as important in macrophyte as in cobble.

The responses of most other invertebrate taxa were positive in cobble and negative in macrophytes, although the majority were statistically insignificant. Invertebrate densities are notoriously variable across space and time, and our data are no exception, resulting in lack of statistical significance of many responses. Still, the overall responses of many invertebrate groups are consistent with the hypothesis that the direct negative effects of crayfish predation on invertebrates were strongest in cobble and were reduced as crayfish were removed. The decline of many invertebrate groups in macrophytes in spite of the documented positive effects of increased macrophyte cover and habitat heterogeneity on invertebrate density (Crowder & Cooper 1982; Gregg & Rose 1982, 1985; Beckett *et al.* 1992; Palmer *et al.* 2000) could be explained by increased fish consumption of invertebrates.

Fish predation: cause and consequence of changes in invertebrate densities

Restrictive fishing regulations implemented in the beginning of the study protected native predators to increase the efficacy of control measures (Tobin *et al.* 2011). Although the regulations did not result in a smallmouth bass population increase, the biomass of crayfish removed by fish consumption far exceeded that removed by trapping from 2001-2003 (Hein *et al.* 2006). As rusty crayfish densities were reduced, fish predation on benthic invertebrates increased via two primary mechanisms. *Lepomis* populations increased, resulting in increased predation on some invertebrates simply as a function of more predators. Additionally, as rusty crayfish densities declined the profitability of searching for and consuming them declined for generalist predators such as smallmouth bass and rock bass (Werner & Hall 1974). When invasive species provide an important prey item for generalist predators, removing the invasive prey item can have unexpected effects on alternative prey (Rodriguez 2006; Collins *et al.* 2009) as predators “switch” their diets based on encounter frequency (Murdoch *et al.* 1975). In this study, bass switched from consuming crayfish to other prey items which were more prevalent , with implications for the benthic invertebrate community.

Our data allow comparison of changes in energetic importance of prey to predators (the change in fish consumption of invertebrates) with changes in the dynamic importance of predators to prey (the change in invertebrate density) (Figure 12). Energetic importance of prey to predators (i.e., high representation in diets) is often not indicative of dynamic importance of predators to prey (i.e., predator control of prey abundance), and comparing the two types of trophic interactions can provide insight into the ways in which food web interactions relate to population and community dynamics (Pimm *et al.* 1991; Polis 1994; Closs *et al.* 1999; Solomon *et al.* 2010). If predators influence the abundance of their prey via top-down control, an inverse relationship between adjacent trophic levels is expected (Hairston *et al.* 1960; McQueen *et al.* 1989; Carpenter & Kitchell 1993). If, however, prey availability is the main factor determining predator consumption and predators exert little control over prey densities (i.e., the system is donor controlled), either a positive relationship or no relationship would be expected between predator consumption and prey availability (Arditi & Ginzburg 1989; McQueen *et al.* 1989; Closs *et al.* 1999; Worm & Myers 2003). Conceptually, the correlation between changes in prey density and predator consumption of that prey fall into four categories, two of which are consistent with top-down control and two of which are consistent with donor control (Figure 12A).

Total fish consumption of most invertebrate taxa increased as rusty crayfish were removed, with the exception of crayfish and Ephemeroptera. The concomitant response of invertebrates to this increase in consumption varied among taxa and among habitats (Figure 12B, Figure 12C). In cobble, increases in consumption corresponded with increases in invertebrate density for most groups, a pattern consistent with donor-controlled dynamics in this habitat. The direct effects of crayfish are likely most important in cobble, and following the release of predation pressure by crayfish, invertebrate densities generally increased in this substrate despite increased predation pressure by fishes. In macrophyte/soft substrates, invertebrate responses were more varied, likely as a result of multiple conflicting effects of increased habitat heterogeneity, decreased crayfish predation, increased fish predation, and changes in interactions among invertebrate groups. Some taxa (e.g., Odonata, Diptera, Amphipoda) exhibited responses consistent with top-down control, where increases in fish predation are correlated with decreases in density. Other taxa either did not change or increased in density as a function of the crayfish removal in spite of increases in fish predation, consistent with donor control dynamics where prey populations are not affected by predators, and generalist predator diets are determined mainly by abundance of their prey (Murdoch *et al.* 1975).

We recognize that correlations such as those presented here, while consistent with top-down or donor-controlled system dynamics, do not identify causality. Our data are insufficient to identify which mechanisms among many are responsible for the increase or decrease in the various invertebrate taxa. For example, strong top-down control can reduce prey numbers, causing prey to appear energetically unimportant to predators despite strong dynamic importance of predators on prey (Paine 1988; Polis 1994; Closs *et al.* 1999). Additionally, intensive predation on vulnerable life stages over a short duration may result in strong dynamic control of prey by predators, but these prey may be of little energetic importance to predators when diet information is integrated across the entire growing season (Polis 1994; Solomon *et al.* 2010). In this study, if predation by fishes in intermediate (unsampled) years was sufficient to drive prey densities to low levels or if predation occurred during short time windows such as periods of emergence, this prey item would subsequently appear infrequently in diets and we would erroneously conclude that the relationship between predators and this prey taxa was donor controlled . In spite of these limitations, the variability in the response of benthic macroinvertebrate taxa to release from crayfish predation and increases in fish predation provides insight into the relative importance of the multitude of direct and indirect effects of this littoral food web, and provides a fruitful area of future research.

Conclusion

Overall, the whole-lake manipulation removing invasive rusty crayfish from Sparkling Lake was successful in reducing the rusty crayfish population to a small fraction of its former abundance and in restoring many components of the native ecosystem. Fish predation was critical to the success of the rusty crayfish removal (Hein *et al.* 2006), but also contributed to the unexpected decline in some benthic invertebrates. The variability in the responses of benthic invertebrates is a reflection of multiple positive and negative indirect effects arising from the crayfish removal. Similar to other invasive species, the full extent of the ecosystem-level effects of rusty crayfish were only apparent following their removal (Hulme 2006), and the use of a whole-system manipulation illuminated the complexity of interactions that result from rusty crayfish invasions. However, the disadvantage of a whole-system approach is the difficulty in disentangling the effects of multiple drivers changing simultaneously, and future research should focus on isolating the various indirect effects identified by this study as potential drivers of littoral community structure.

Our results demonstrate that alleviation of the negative effects of strongly interacting invasive species is possible even in the absence of complete eradication. The rusty crayfish population remained low for three years after the cessation of removal trapping, and the native community continued to recover in this post-trapping period. While prevention should remain the cornerstone of any invasive species management strategy, it is heartening to know that efforts to alleviate the negative impacts of invasive species can be successful. While the trapping effort employed in this study likely exceeds the resources available for most management agencies, the population dynamics at low densities and the maintenance of the ecosystem response after trapping had ceased indicates that a pulse of trapping effort could sustain positive effects for many years. The results provided by this study in terms of the population dynamics of rusty crayfish and the reversibility of their impacts can be used to inform future models of optimal control for this nuisance species (Simberloff 2003; Epanchin-Niell & Hastings 2010), and provide a unique example of successful control of an established aquatic invasive species leading to sustained recovery of the native community in an inland lake.

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Literature Cited

Abrams P.A. (1987) Indirect interactions between species that share a predator: varieties of indirect effects. In: *Predation: direct and indirect impacts on aquatic communities* (eds. Kerfoot WC & Sih A), pp. 38-54. University Press of New England, Dartmouth College

Abrams P.A. (1991) Strengths of Indirect Effects Generated by Optimal Foraging. *Oikos*, 62, 167-176

Akaike H. (1973) Information theory as an extension of the maximum likelihood principle. In: *2nd International Symposium on Information Theory* (eds. Petrov BN & Csaksi F), pp. 267-281, Akademiai Kiado, Budapest, Hungary

Allendorf F.W., England P.R., Luikart G., Ritchie P.A. & Ryman N. (2008) Genetic effects of harvest on wild animal populations. *Trends Ecol. Evol.*, 23, 327

Arditi R. & Ginzburg L.R. (1989) Coupling in predator-prey dynamics: Ratio-Dependence. *J. Theor. Biol.*, 139, 311

Baayen R.H., Davidson D.J. & Bates D.M. (2008) Mixed-effects modeling with crossed random effects for subjects and items. *JMemL*, 59, 390

Bates D.M. & Sarkar D. (2007) lme4: Linear mixed-effects models using S4 classes. In:

Becker G.C. (1983) *Fishes of Wisconsin.* University of Wisconsin Press, Madison, WI.

Beckett D.C., Aartila T.P. & Miller A.C. (1992) Contrasts in Density of Benthic Invertebrates Between Macrophyte Beds and Open Littoral Patches in Eau Galle Lake, Wisconsin. *American Midland Naturalist*, 127, 77

Berger J.J. (1993) Ecological Restoration and NonIndigenous Plant Species: A Review. *Restoration Ecology*, 1, 74

Bergstrom D.M., Lucieer A., Kiefer K., Wasley J., Belbin L., Pedersen T.K. & Chown S.L. (2009) Indirect effects of invasive species removal devastate World Heritage Island. *J. Appl. Ecol.*, 46, 73

Blois-Heulin C., Crowley P.H., Arrington M. & Johnson D.M. (1990) Direct and Indirect Effects of Predators on the Dominant Invertebrates of Two Freshwater Littoral Communities. *Oecologia*, 84, 295

Bo T., Fenoglio S., Malacarne G., Pessino M. & Sgariboldi F. (2007) Effects of clogging on stream macroinvertebrates: An experimental approach. *Limnologica - Ecology and Management of Inland Waters*, 37, 186

Bohanan R.E. & Johnson D.M. (1983) Response of Littoral Invertebrate Populations to a Spring Fish Exclusion Experiment. *Freshwater Invertebrate Biology*, 2, 28-40

Bolker B.M., Brooks M.E., Clark C.J., Geange S.W., Poulsen J.R., Stevens M.H.H. & White J.-S.S. (2009) Generalized linear mixed models: a practical guide for ecology and evolution. *Trends Ecol. Evol.*, 24, 127

Brown G.P., Phillips B.L. & Shine R. (2011) The ecological impact of invasive cane toads on tropical snakes: Field data do not support laboratory-based predictions. *Ecology*, 92, 422-431

Brown K.M. (1998) The role of shell strength in selective foraging by crayfish for gastropod prey. *Freshwater Biol.*, 40, 255

Brown K.M. & Lodge D.M. (1993) Gastropod Abundance in Vegetated Habitats: The Importance of Specifying Null Models. *Limnol. Oceanogr.*, 38, 217

Burnham K.P. & Anderson D.R. (2002) *Model selection and multimodel inference: A practical information-theoretic approach.* Springer, New York.

Butkas K., Vadeboncoeur Y. & Vander Zanden M.J. (2010) Estimating benthic invertebrate production in lakes: a comparison of methods and scaling from individual taxa to the whole-lake level. *Aquatic Sciences*, 73, 153

Capelli G.M. (1980) Seasonal Variation in the Food Habits of the Crayfish Orconectes Propinquus (Girard) in Trout Lake, Vilas County, Wisconsin, U.S.a. (Decapoda, Astacidea, Cambaridae). *Crustaceana*, 38, 82-86

Capelli G.M. (1982) Displacement of Northern Wisconsin Crayfish by *Orconectes rusticus* (Girard). *Limnol. Oceanogr.*, 27, 741-745

Capelli G.M. & Magnuson J.J. (1983) Morphoedaphic and Biogeographic Analysis of Crayfish Distribution in Northern Wisconsin. *J. Crustacean Biol.*, 3, 548-564

Capelli G.M. & Munjal B.L. (1982) Aggressive interactions and resource competition in relation to species displacement among crayfish of the genus Orconectes. *J. Crustacean Biol.*, 2, 486-492

Carpenter S.R. (1998) The need for large-scale experiments to assess and predict the response of ecosystems to perturbation. *Successes, limitations, and frontiers in ecosystem science. Springer-Verlag, New York, New York, USA*, 287

Carpenter S.R., Chisholm S.W., Krebs C.J., Schindler D.W. & Wright R.F. (1995) Ecosystem experiments. *Science(Washington)*, 26, 324

Carpenter S.R. & Kitchell J.F. (1988) Consumer control of lake productivity. *Bioscience*, 38, 764-769

Carpenter S.R. & Kitchell J.F. (1993) *The Trophic Cascade in Lakes*. Cambridge University Press, Cambridge, UK.

Closs G.P., Balcombe S.R., Shirley M.J. & Raffaelli A.H.F.a.D. (1999) Generalist Predators, Interaction Strength and Food-web Stability. In: *Advances in Ecological Research*, p. 93. Academic Press

Collins P.W., Latta B.C. & Roemer G.W. (2009) Does the Order of Invasive Species Removal Matter? The Case of the Eagle and the Pig. *PLoS ONE*, 4, e7005

Cooper S.D., Smith D.W. & Bence J.R. (1985) Prey selection by freshwater predators with different foraging strategies. *Canadian Journal of Fisheries & Aquatic Sciences*, 42, 1720-1732

Correia A. & Anastácio P. (2008) Shifts in aquatic macroinvertebrate biodiversity associated with the presence and size of an alien crayfish. *Ecological Research*, 23, 729

Covich A.P., Crowl T.A., Alexander J.E. & Vaughn C.C. (1994) Predator-Avoidance Responses in Freshwater Decapod-Gastropod Interactions Mediated by Chemical Stimuli. *J. N. Am. Benthol. Soc.*, 13, 283

Crooks J.A. (2002) Characterizing ecosystem-level consequences of biological invasions: the role of ecosystem engineers. *Oikos*, 97, 153-166

Crowder L.B. & Cooper W.E. (1982) Habitat Structural Complexity and the Interaction Between Bluegills and Their Prey. *Ecology*, 63, 1802-1813

Crowl T.A. & Covich A.P. (1990) Predator-Induced Life-History Shifts in a Freshwater Snail. *Science*, 247, 949

Cummins K.W. & Wuycheck J.C. (1971) *Caloric equivalents for investigations in ecological energetics*. E. Schweizerbart.

Dahlsten D.L., Garcia R. & Lorraine H. (1989) Eradication as a pest management tool: concepts and contexts. In: *Eradication of exotic pests: Analysis with case histories* (eds. Dahlsten DL & Garcia R), pp. 3-15. Yale University Press, New Haven, Connecticut, USA.

DeWitt T.J., Robinson B.W. & Wilson D.S. (2000) Functional diversity among predators of a freshwater snail imposes an adaptive trade-off for shell morphology. *Evolutionary Ecology Research*, 2, 129

Didham R.K., Tylianakis J.M., Gemmell N.J., Rand T.A. & Ewers R.M. (2007) Interactive effects of habitat modification and species invasion on native species decline. *Trends Ecol. Evol.*, 22, 489-496

Diehl S. (1995) Direct and Indirect Effects of Omnivory in a Littoral Lake Community. *Ecology*, 76, 1727-1740

Donlan C.J., Tershy B.R. & Croll D.A. (2002) Islands and introduced herbivores: conservation action as ecosystem experimentation. *J. Appl. Ecol.*, 39, 235

Dorn N.J. & Wojdak J.M. (2004) The role of omnivorous crayfish in littoral communities. *Oecologia*, 140, 150

Edmunds G.F., Jensen S.L. & Berner L. (1976) *The Mayflies of North and Central America*. U of Minnesota Press.

Epanchin-Niell R.S. & Hastings A. (2010) Controlling established invaders: integrating economics and spread dynamics to determine optimal management. *Ecol. Lett.*, 13, 528-541

Fenberg P.B. & Roy K. (2008) Ecological and evolutionary consequences of sizeâ€ selective harvesting: how much do we know? *Mol. Ecol.*, 17, 209

Flecker A.S. (1996) Ecosystem Engineering by a Dominant Detritivore in a Diverse Tropical Stream. *Ecology*, 77, 1845

Garvey J.E., Rettig J.E., Stein R.A., Lodge D.M. & Klosiewski S.P. (2003) Scale-dependent associations among fish predation, littoral habitat, and distributions of crayfish species. *Ecology*, 84, 3339-3348

Gelman A. & Hill J. (2006) *Data Analysis Using Regression and Multilevel/Hierarchical Models*. Cambridge University Press.

Gilinsky E. (1984) The Role of Fish Predation and Spatial Heterogeneity in Determining Benthic Community Structure. *Ecology*, 65, 455

Goni R., Quetglas A. & Renones O. (2003) Size at maturity, fecundity and reproductive potential of a protected population of the spiny lobster <i>Palinurus elephas</i> (Fabricius, 1787) from the western Mediterranean. *Marine Biology*, 143, 583-592

Gregg W.W. & Rose F.L. (1982) The effects of aquatic macrophytes on the stream microenvironment. *Aquatic Botany*, 14, 309

Gregg W.W. & Rose F.L. (1985) Influences of aquatic macrophytes on invertebrate community structure, guild structure, and microdistribution in streams. *Hydrobiologia*, 128, 45

Guy C.S., Brown M.L. & Society A.F. (2007) *Analysis and interpretation of freshwater fisheries data*. American Fisheries Society.

Hairston N.G., Smith F.E. & Slobodkin L.B. (1960) Community Structure, Population Control, and Competition. *American Naturalist*, 94, 421-425

Hanson J.M., Chambers P.A. & Prepas E.E. (1990) Selective foraging by the crayfish Orconectes virilis and its impact on macroinvertebrates. *Freshwater Biol.*, 24, 69

Hanson P.C., Johnson T.B., Schindler D.E. & Kitchell J.F. (1997) Fish Bioenergetics 3.0. *Madison, WI: University of Wisconsin Sea Grant Institute*

Hart D.R. (2002) Intraguild predation, invertebrate predators, and trophic cascades in lake food webs. *J. Theor. Biol.*, 218, 111

Hayes N.M., Butkas K.J., Olden J.D. & Vander Zanden M.J. (2009) Behavioural and growth differences between experienced and naive populations of a native crayfish in the presence of invasive rusty crayfish. *Freshwater Biol.*, 54, 1876-1887

Hein C.L., Roth B.M., Ives A.R. & Vander Zanden M.J. (2006) Fish predation and trapping for rusty crayfish (Orconectes rusticus) control: a whole-lake experiment. *Can. J. Fish. Aquat. Sci.*, 63, 383–393

Hein C.L., Vander Zanden M.J. & Magnuson J.J. (2007) Intensive trapping and increased fish predation cause massive population decline of an invasive crayfish. *Freshwater Biol.*, 52, 1134-1146

Helms B.S. & Creed R.P. (2005) The effects of 2 coexisting crayfish on an Appalachian river community. *J. N. Am. Benthol. Soc.*, 24, 113

Hertonsson P., Ã…bjÃ¶rnsson K. & BrÃ¶nmark C. (2007) Competition and facilitation within and between a snail and a mayfly larva and the effect on the grazing process. *Aquatic Ecology*, 42, 669

Hilborn R. & Walters C.J. (1992) *Quantitative Fisheries Stock Assessment: Choice, Dynamics, and Uncertainty.* Kluwer Academic Publishers, Norwell, MA.

Hobbs H.H., Jass J.P. & Huner J.V. (1989) A Review of Global Crayfish Introductions With Particular Emphasis On Two North American Species (Decapoda, Cambaridae). *Crustaceana*, 56, 299

Holt R.D. & Lawton J.H. (1994) The Ecological Consequences of Shared Natural Enemies. *Annual Review of Ecology and Systematics*, 25, 495

Hulme P.E. (2006) Beyond control: wider implications for the management of biological invasions. *J. Appl. Ecol.*, 43, 835

Hunt B.P. (1953) *The Life History and Economic Importance of a Burrowing Mayfly, Hexagenia Limbata, in Southern Michigan Lakes*. Franklin DeKleine Company, Lansing, MI.

Hutchings J.A. (2000) Collapse and recovery of marine fishes. *Nature*, 406, 882

Hutchings J.A. & Reynolds J.D. (2004) Marine Fish Population Collapses: Consequences for Recovery and Extinction Risk. *Bioscience*, 54, 297

Isermann D.A. & Knight C., T. (2005) A Computer Program for Age–Length Keys Incorporating Age Assignment to Individual Fish. *North American Journal of Fisheries Management*, 25, 1153-1160

Johnson M.F., Rice S.P. & Reid I. (2010) Topographic disturbance of subaqueous gravel substrates by signal crayfish (Pacifastacus leniusculus). *Geomorphology*, 123, 269

Kramer M. (2005) R2 statistics for mixed models. In, p. 148. Kansas University Press, Manhattan, Kansas

Krebs C.J. (1999) *Ecological Methodology*. Second edn. Addison-Welsey Educational Publishing, Menlo Park, CA.

Kuparinen A. & Merila J. (2007) Detecting and managing fisheries-induced evolution. *Trends Ecol. Evol.*, 22, 652-659

Liebhold A. & Bascompte J. (2003) The Allee effect, stochastic dynamics and the eradication of alien species. *Ecol. Lett.*, 6, 133

Liermann & Hilborn (2001) Depensation: evidence, models and implications. *Fish and Fisheries*, 2, 33

Lodge D.M., Kershner M.W., Aloi J.E. & Covich A.P. (1994) Effects of an omnivorous crayfish (Orconectes rusticus) on a freshwater littoral food web. *Ecology*, 75, 1265–1281

Lodge D.M. & Lorman J.G. (1987) Reductions in submersed macrophyte biomass and species richness by the crayfish Orconectes rusticus. *Can. J. Fish. Aquat. Sci.*, 44, 591

Lodge D.M., Taylor C.A., Holdich D.M. & Skurdal J. (2000) Nonindigenous Crayfishes Threaten North American Freshwater Biodiversity: Lessons from Europe. *Fisheries*, 25, 7

Longhurst A. (2006) The sustainability myth. *Fisheries Research*, 81, 107

Magee L. (1990) R2 measures based on Wald and likelihood ratio joint significance tests. *American Statistician*, 250

Magnuson J.J., Capelli G.M., Lorman J.G. & Stein R.A. (1975) Consideration of crayfish for macrophyte control. In: *The Proceedings of a Symposium on Water Quality Management through Biological Control. Edited by PL Brezonik and JC Fox. University of Florida, Gainesville, Florida. Rep. No. ENV*, pp. 66-74

Matthews M.A., Reynolds J.D. & Keatinge M.J. (1993) Macrophyte reduction and benthic community alteration by the crayfish Austropotamobius pallipes (Leraboullet). *Freshwater Crayfish*, 9, 289

McCarthy J.M., Hein C.L., Olden J.D. & Jake Vander Zanden M. (2006) Coupling long-term studies with meta-analysis to investigate impacts of non-native crayfish on zoobenthic communities. *Freshwater Biol.*, 51, 224–235

McQueen D.J., Johannes M.R.S., Post J.R., Stewart T.J. & Lean D.R.S. (1989) Bottom-up and top-down impacts on freshwater pelagic community structure. *Ecol. Monogr.*, 59, 289

Merritt R.W. & Cummins K.W. (1996) *An Introduction to the Aquatic Insects of North America*. Third edn. Kendall/Hunt Publishing Company, Dubuque, IA.

Mittelbach G.G. (1984) Predation and Resource Partitioning in Two Sunfishes (Centrarchidae). *Ecology*, 65, 499

Momot W.T. (1991) Potential for Exploitation of Freshwater Crayfish in Coolwater Systems: Management Guidelines and Issues. *Fisheries*, 16, 14-21

Momot W.T. (1998) An example of how exploitation can increase production and yield in a northern crayfish (*Orconectes virilis*) population. In: *Proceedings of the North Pacific Symposium on Invertebrate Stock Assessment and Management* (eds. Jamieson GS & Campbell A), pp. 225-233. Canadian Special Publications in Fisheries and Aquatic Sciences

Momot W.T., Gowing H. & Jones P.D. (1978) The Dynamics of Crayfish and Their Role in Ecosystems. *American Midland Naturalist*, 99, 10

Murdoch W.W., Avery S. & Smyth M.E.B. (1975) Switching in Predatory Fish. *Ecology*, 56, 1094

Myers J.H., Simberloff D., Kuris A.M. & Carey J.R. (2000) Eradication revisited: dealing with exotic species. *Trends Ecol. Evol.*, 15, 316

Myers R.A., Barrowman N.J., Hutchings J.A. & Rosenberg A.A. (1995) Population Dynamics of Exploited Fish Stocks at Low Population Levels. *Science*, 269, 1106

Myers R.A., Bowen K.G. & Barrowman N.J. (1999) Maximum reproductive rate of fish at low population sizes. *Can. J. Fish. Aquat. Sci.*, 56, 2404

Needham J.G., Traver J.R. & Hsu Y.-c. (1969) *The biology of mayflies: with a systematic account of North American species*. E. W. Classey.

Nilsson E., Solomon C.T., Wilson K.A., Willis T.V., Larget B. & Vander Zanden M.J. (2012) Effects of an invasive crayfish on trophic relationships in north temperate lake food webs. *Freshwater Biol.*, 57, 10

Nogaro G., Mermillodâ€ blondin F., FranÃ§oisâ€ Carcaillet F., Gaudet J.p., Lafont M. & Gibert J. (2006) Invertebrate bioturbation can reduce the clogging of sediment: an experimental study using infiltration sediment columns. *Freshwater Biol.*, 51, 1458

Norton D.A. (2009) Species Invasions and the Limits to Restoration: Learning from the New Zealand Experience. *Science*, 325, 569

Nyström P., Brönmark C. & Graneli W. (1999) Influence of an exotic and a native crayfish species on a littoral benthic community. *Oikos*, 85, 545-553

Nystrom P., Stenroth P., Holmqvist N., Berglund O., Larsson P. & Graneli W. (2006) Crayfish in lakes and streams: individual and population responses to predation, productivity, and substratum availibility. *Freshwater Biol.*, 51, 2096-2113

Nyström P., Svensson O., Lardner B., Brönmark C. & Granéli W. (2001) The Influence of Multiple Introduced Predators on a Littoral Pond Community. *Ecology*, 82, 1023

Olsen T.M., Lodge D.M., Capelli G.M. & Houlihan R.J. (1991) Mechanisms of impact of an introduced crayfish (*Orconectes rusticus*) on littoral congeners, snails, and macrophytes. *Can. J. Fish. Aquat. Sci.*, 48, 1853-1861

Osenberg C.W. & Mittelbach G.G. (1989) Effects of Body Size on the Predator-Prey Interaction Between Pumpkinseed Sunfish and Gastropods. *Ecol. Monogr.*, 59, 405

Osenberg C.W., Mittelbach G.G. & Wainwright P.C. (1992) Two-stage life histories in fish: the interaction between juvenile competition and adult performance. *Ecology*, 255

Paine R.T. (1988) Road Maps of Interactions or Grist for Theoretical Development? *Ecology*, 69, 1648

Palmer M.A., Covich A.P., Lake S.A.M., Biro P., Brooks J.J., Cole J., Dahm C., Gibert J., Goedkoop W., Martens K., Verhoeven J.O.S. & Bund W.J.V.D. (2000) Linkages between Aquatic

Sediment Biota and Life Above Sediments as Potential Drivers of Biodiversity and Ecological Processes. *Bioscience*, 50, 1062

Parkyn S.M., Rabeni C.F. & Collier K.J. (1997) Effects of crayfish (Paranephrops planifrons: Parastacidae) on inâ€ stream processes and benthic faunas: A density manipulation experiment. *New Zealand Journal of Marine and Freshwater Research*, 31, 685

Peckarsky B.L. (1980) Predator-Prey Interactions between Stoneflies and Mayflies: Behavioral Observations. *Ecology*, 61, 932

Peckarsky B.L. (1985) Do predaceous stoneflies and siltation affect the structure of stream insect communities colonizing enclosures. *Can. J. Zool.*, 63, 1519

Peckarsky B.L. (1996) Alternative Predator Avoidance Syndromes of Stream-Dwelling Mayfly Larvae. *Ecology*, 77, 1888

Perry W.L., Lodge D.M. & Lamberti G.A. (1997) Impact of crayfish predation on exotic zebra mussels and native invertebrates in a lake-outlet stream. *Canadian Journal of Fisheries & Aquatic Sciences*, 54, 120-125

Pimm S.L. (1980) Food web design and the effect of species deletion. *Oikos*, 35, 139-149

Pimm S.L., Lawton J.H. & Cohen J.E. (1991) Food web patterns and their consequences. *Nature*, 350, 669-674

Pinheiro J.C. & Bates D.M. (2000) *Mixed-effects models in S and S-PLUS*. Springer, New York.

Polis G.A. (1994) Food webs, trophic cascades and community structure. *Aust. J. Ecol.*, 19, 121

Pringle C.M., Blake G.A., Covich A.P., Buzby K.M. & Finley A. (1993) Effects of omnivorous shrimp in a montane tropical stream: sediment removal, disturbance of sessile invertebrates and enhancement of understory algal biomass. *Oecologia*, 93, 1

Qian S.S. & Shen Z. (2007) Ecological applications of multilevel analysis of variance. *Ecology*, 88, 2489

Revsbech N.P., JÃ¸rgensen B.B. & Blackburn T.H. (1980) Oxygen in the Sea Bottom Measured with a Microelectrode. *Science*, 207, 1355

Ricciardi A. & Rasmussen J.B. (1999) Extinction Rates of North American Freshwater Fauna. *Conserv. Biol.*, 13, 1220-1222

Ricker W.E. (1975) Computation and Interpretation of Biological Statistics of Fish Populations. In. Bulletin of the Fisheries Research Board of Canada

Robinson J.V. & Wellborn G.A. (1987) Mutual Predation in Assembled Communities of Odonate Species. *Ecology*, 68, 921

Rodriguez L.F. (2006) Can invasive species facilitate native species? Evidence of how, when, and why these impacts occur. *Biol. Invasions*, 8, 927-939

Roell M.J. & Orth D.J. (1992) Production of three crayfish populations in the New River of West Virginia, USA. *Hydrobiologia*, 228, 185

Rosenthal S.K., Stevens S.S. & Lodge D.M. (2006) Whole-lake effects of invasive crayfish (*Orconectes* spp.) and the potential for restoration. *Canadian Journal of Fisheries & Aquatic Sciences*, 63, 1276-1285

Roth B.M., Hein C.L. & Vander Zanden M.J. (2006) Using bioenergetics and stable isotopes to assess the trophic role of rusty crayfish (Orconectes rusticus) in lake littoral zones. *Can. J. Fish. Aquat. Sci.*, 63, 335–344

Roth B.M., Tetzlaff J.C., Alexander M.L. & Kitchell J.F. (2007) Reciprocal relationships between exotic rusty crayfish, macrophytes, and Lepomis species in northern Wisconsin lakes. *Ecosystems*, 10, 75–86

Sala O.E., Chapin Iii F.S., Armesto J.J., Berlow E., Bloomfield J., Dirzo R., Huber-Sanwald E., Huenneke L.F., Jackson R.B., Kinzig A. & others (2000) Global biodiversity scenarios for the year 2100. *Science*, 287, 1770-1774

Schindler D.W. (1998) Whole-Ecosystem Experiments: Replication Versus Realism: The Need for Ecosystem-Scale Experiments. *Ecosystems*, 1, 323

Seaburg K.G. (1957) A Stomach Sampler for Live Fish. *The Progressive Fish-Culturist*, 19, 137

Sih A., Crowley P., McPeek M., Petranka J. & Strohmeier K. (1985) Predation, competition, and prey communities: a review of field experiments. *Annual Review of Ecology and Systematics*, 16, 269-311

Simberloff D. (2003) How much information on population biology is needed to manage introduced species? *Conserv. Biol.*, 17, 83-92

Skurdal J. & Taugbol T. (1994) Do we need harvest regulations for European crayfish? *Reviews in Fish Biology and Fisheries*, 4, 461-485

Smith E.P. & Zaret T.M. (1982) Bias in Estimating Niche Overlap. *Ecology*, 63, 1248

Solomon C.T., Roth B.M., Hrabik T.R. & Vander Zanden M.J. (2010) Comparing energetic and dynamic descriptions of a single food web linkage. *Oikos*, 120, 194

Statzner B., vet E.F.v., Champagne J.-Y., Morel R. & Herouin E. (2000) Crayfish as geomorphic agents and ecosystem engineers: Biological behavior affects sand and gravel erosion in experimental streams. *Limnol. Oceanogr.*, 45, 1030

Stein R.A., Goodman C.G. & Marschall E.A. (1984) Using Time and Energetic Measures of Cost in Estimating Prey Value for Fish Predators. *Ecology*, 65, 702

Team R.D.C. (2011) R: A language and environment for statistical computing. In. R Foundation for Statistical Computing, Vienna, Austria

Tobin P.C., Berec L.k. & Liebhold A.M. (2011) Exploiting Allee effects for managing biological invasions. *Ecol. Lett.*, 615-624

Usio N., Kamiyama R., Saji A. & Takamura N. (2009) Size-dependent impacts of invasive alien crayfish on a littoral marsh community. *Biol. Conserv.*, 142, 1480

Usio N. & Townsend C.R. (2004) ROLES OF CRAYFISH: CONSEQUENCES OF PREDATION AND BIOTURBATION FOR STREAM INVERTEBRATES. *Ecology*, 85, 807

Vander Zanden M.J., Olden J.D. & Gratton C. (2006) Food-Web Approaches in Restoration Ecology. In: *Foundations of Restoration Ecology* (eds. Falk DA, Palmer MA & Zedler JB). Island Press, Washington, D.C.

Vitousek P.M., D'Antonio C.M., Loope L.L., Rejmanek M. & Westbrooks R. (1997) Introduced species: a significant component of human-caused global change. *New Zealand Journal of Ecology*, 21, 1

Wahle R.A. & Steneck R.S. (1991) Recruitment habits and nursery grounds of the American lobster *Homarus americanus*: A demographic bottleneck? *Marine Ecology Progress Series*, 69, 231-243

Walters C. & Kitchell J.F. (2001) Cultivation/depensation effects on juvenile survival and recruitment: implications for the theory of fishing. *Can. J. Fish. Aquat. Sci.*, 58, 39

Weaver M.J., Magnuson J.J. & Clayton M.K. (1993) Analyses for Differentiating Littoral Fish Assemblages with Catch Data from Multiple Sampling Gears. *Transactions of the American Fisheries Society*, 122, 1111

Werner E.E. & Hall D.J. (1974) Optimal Foraging and the Size Selection of Prey by the Bluegill Sunfish (Lepomis Macrochirus). *Ecology*, 55, 1042

White E.M., Wilson J.C. & Clarke A.R. (2006) Biotic indirect effects: a neglected concept in invasion biology. *Diversity& Distributions*, 12, 443-455

Whitledge G.W., Hayward R.S., Zweifel R.D. & Rabeni C.F. (2003) Development and laboratory evaluation of a bioenergetics model for subadult and adult smallmouth bass. *Transactions of the American Fisheries Society*, 132, 316

Whitledge G.W. & Rabeni C.F. (1997) Energy sources and ecological role of crayfishes in an Ozark stream: insights from stable isotopes and gut analysis. *Can. J. Fish. Aquat. Sci.*, 54, 2555-2563

Wilson K.A., Magnuson J.J., Lodge D.M., Hill A.M., Kratz T.K., Perry W.L. & Willis T.V. (2004) A long-term rusty crayfish (Orconectes rusticus) invasion: dispersal patterns and community change in a north temperate lake. *Can. J. Fish. Aquat. Sci.*, 61, 2255–2266

Wootton J.T. (1994a) The nature and consequences of indirect effects in ecological communities. *Annual Review of Ecology and Systematics*, 25, 443

Wootton J.T. (1994b) Predicting Direct and Indirect Effects: An Integrated Approach Using Experiments and Path Analysis. *Ecology*, 75, 151

Worm B. & Myers R.A. (2003) META-ANALYSIS OF CODâ€“SHRIMP INTERACTIONS REVEALS TOP-DOWN CONTROL IN OCEANIC FOOD WEBS. *Ecology*, 84, 162

Wright J.P. & Jones C.G. (2006) The Concept of Organisms as Ecosystem Engineers Ten Years On: Progress, Limitations, and Challenges. *Bioscience*, 56, 203

Yodzis P. (1988) The Indeterminacy of Ecological Interactions as Perceived Through Perturbation Experiments. *Ecology*, 69, 508

Zavaleta E.S., Hobbs R.J. & Mooney H.A. (2001) Viewing invasive species removal in a whole-ecosystem context. *Trends Ecol. Evol.*, 16, 454-459

Zipkin E.F., Kraft C.E., Cooch E.G. & Sullivan P.J. (2009) When can efforts to control nuisance and invasive species backfire? *Ecol. App.*, 19, 1585-1595

Zipkin E.F., Sullivan P.J., Cooch E.G., Kraft C.E., Shuter B.J. & Weidel B.C. (2008) Overcompensatory response of a smallmouth bass (Micropterus dolomieu) population to harvest: release from competition? *Can. J. Fish. Aquat. Sci.*, 65, 2279

FIGURE CAPTIONS

Figure 1. Conceptual model of interactions between rusty crayfish, the littoral food web, and management actions implemented as a part of the whole-lake manipulation (shaded boxes). Filled circles indicate negative effects, arrows indicate positive effects. Macroinvertebrates include non-crayfish benthic invertebrates, both positive and negative interactions could potentially exist within this group. See text for additional information regarding interactions.

Figure 2. A. Log of catch per unit effort (CPUE, number per trap day) of rusty crayfish (filled circles) and virile crayfish (open triangles) in Sparkling Lake. Removal trapping took place from 2001-2008 (shaded area); from 2009-2011 all trapped crayfish were released. B. Log of densities (# per m^2) of age-0 (open circles) and older (filled circles) rusty crayfish from Sparkling Lake. Densities are from cobble (preferred) habitat only. Error bars are standard error for all series.

Figure 3. Juvenile (age-0) density as a function of adult female density of rusty crayfish (both in $\# \cdot m^{-2}$). Solid grey points are from Sparkling Lake, open points are from cross-lakes surveys. Including a separate model for Sparkling Lake did not improve model fit based on AIC values. The dashed line represents the best-fit linear stock recruitment relationship fit to all data combined ($y=7.99+15.98*x$, Adjusted $R^2=0.616$, $p<0.001$).

Figure 4. A&B. Probability densities of carapace length (mm) of gravid females in years of low crayfish density (<1 CPUE; black polygon) and years of high crayfish density ($\geq$1 CPUE; grey polygon) from (A) Cross-lakes surveys, and (B) Sparkling Lake. Mean (SD) of CL in low and high

crayfish density systems are 21.7(4.6) and 25.5(3.8), respectively, for cross-lakes (A) and 25.4(5.6) and 28.9(6.4), respectively, in Sparkling Lake (B). C&D. The relationship between the number of eggs and carapace length of gravid females from (C) cross-lakes surveys and (D) Sparkling Lake. Lines indicate best fit model for high crayfish densities (>1 CPUE; solid line and filled points) and low crayfish densities (<1 CPUE; dashed line and open points). Lines in (C) were fit to all data combined using multi-level models with random effects for year and lake; Lines in (D) are the overall model fit plus the best linear unbiased predictor (BLUP) for Sparkling Lake.

Figure 5. Total percent cover of all macrophyte species (estimated effect +/- 95% confidence intervals) in various depth ranges; A. 0-1 m; B. 1-2 m; C. 2-3 m; D. 3-4 m (Adjusted R^2=0.39). Estimated effect is the restricted maximum likelihood (REML) estimate of the effect of crayfish relative abundance (high vs. low) and depth; non-overlapping confidence intervals indicate statistically significant differences (see text for further details).

Figure 6. Effect size of changes in invertebrate density as a function of relative crayfish abundance in the two habitat types. Positive values represent increases from 2002-2003 to 2008-2010 (as crayfish abundance declined). Filled bars are statistically significant (based on non-overlapping 95% confidence intervals; see text for analysis details). Black fill indicates significant response of entire invertebrate orders; grey fill indicates family-specific responses. Only families which appeared in $\geq$10% of samples were included in family-specific analysis. All individuals from a given order/class were included for analyses of higher taxonomic groups.

Figure 7. A. Catch per unit effort (summed for beach seines, electrofishing, fyke nets, and trammel nets) of *Lepomis* spp. in Sparkling Lake from 1981-2011. The rusty crayfish removal took place from 2001-2008 (shaded area). B-D. Population estimates (+/- 95% confidence intervals) estimated using the modified Schnabel mark-recapture method for B. *Lepomis* spp. (estimates not available from 2001-2004 due to low sample sizes); C. Rock bass; D. Smallmouth bass.

Figure 8. Diet composition (percent by number) over time for A. Rock bass, and B. Smallmouth bass. Abbreviations are as described in Table 1, although "OTH" also includes Bivalvia, Isopoda, Hydracarina, and Megaloptera for ease of display. See Appendix 7 for sample sizes in each year.

Figure 9. Morisita's similarity index of diets for A. rock bass and B. smallmouth bass between all pairs of years. Lower values (lighter colors) indicate more dissimilar diets. Asterisks indicate statistically significant (α=0.05) differences based on bootstrapped data.

Figure 10. Diet percent by number over time for A. Bluegill sunfish; and B. Pumpkinseed sunfish. A total of 23 pumpkinseed and no bluegill were collected from 2001-2004, thus diets were not analyzed for these species in these years. Abbreviations are as described in Table 1, although "OTH" also includes Bivalvia, Coleoptera, Crayfish, Fish, Isopoda, Hydracarina, and Megaloptera for ease of display. See Appendix 7 for sample sizes in each year.

Figure 11. Total annual consumption of prey groups estimated from Bioenergetics simulations. Abbreviations of prey groups are listed in Table 1. Colors correspond to fish species:

White=Bluegill, light grey=pumpkinseed sunfish, medium grey=rock bass, dark grey=smallmouth bass.

Figure 12. Change in consumption (total for all fish species from Bioenergetics) and density of invertebrates from years of high crayfish abundance to years of low crayfish abundance. Positive values indicate an increase and negative values indicate a decrease in later (low crayfish abundance) years. Changes are differences on natural log scale (ratio on the raw data scale). A. Conceptual diagram of quadrats consistent with hypotheses of top-down control (predator consumption controlling prey abundance) and donor control (prey abundance not influenced by predator consumption). B&C. Calculated values for cobble (B) and macrophyte/soft (C) habitats. Consumption changes were calculated on whole-lake basis and therefore values are identical in both habitats. Crayfish (Cray) density change was calculated from density surveys in cobble only (Figure 2). Other abbreviations for invertebrate taxa are described in table 1. The units in Figure 9 are differences on a natural log scale, meaning that an increase of 2 corresponds with a ratio of consumption after removal to consumption before removal of 2 natural log units (e^2), or an approximately 7-fold increase in consumption.

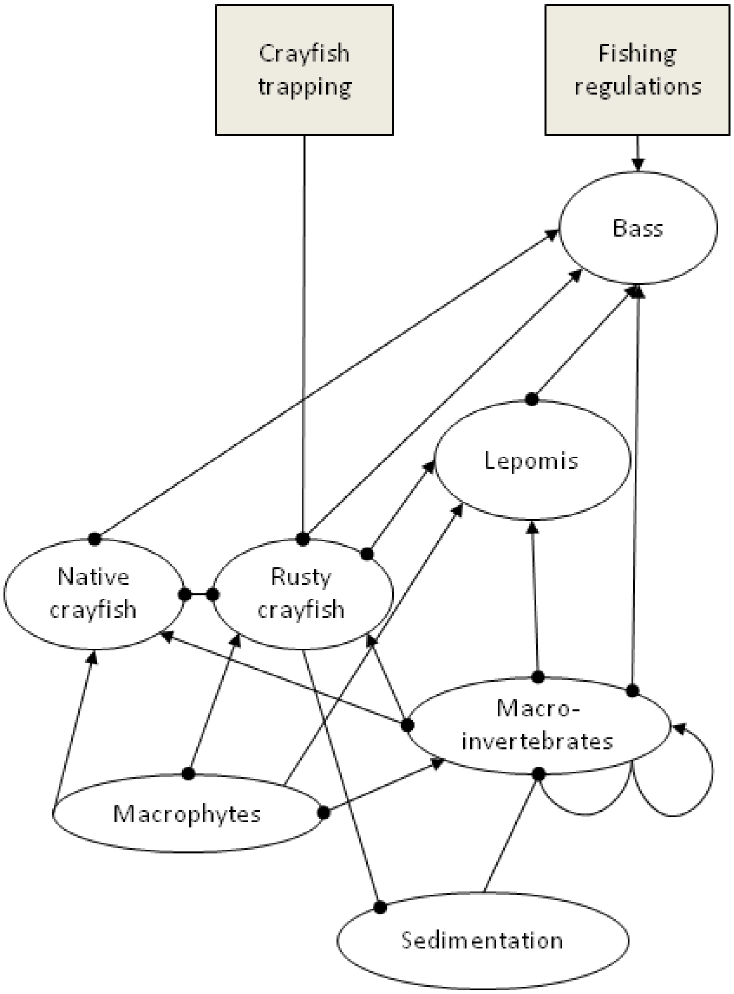
Crayfish trapping
Fishing regulations
Bass
Lepomis
Native crayfish
Rusty crayfish
Macro-invertebrates
Macrophytes
Sedimentation

Figure 1.

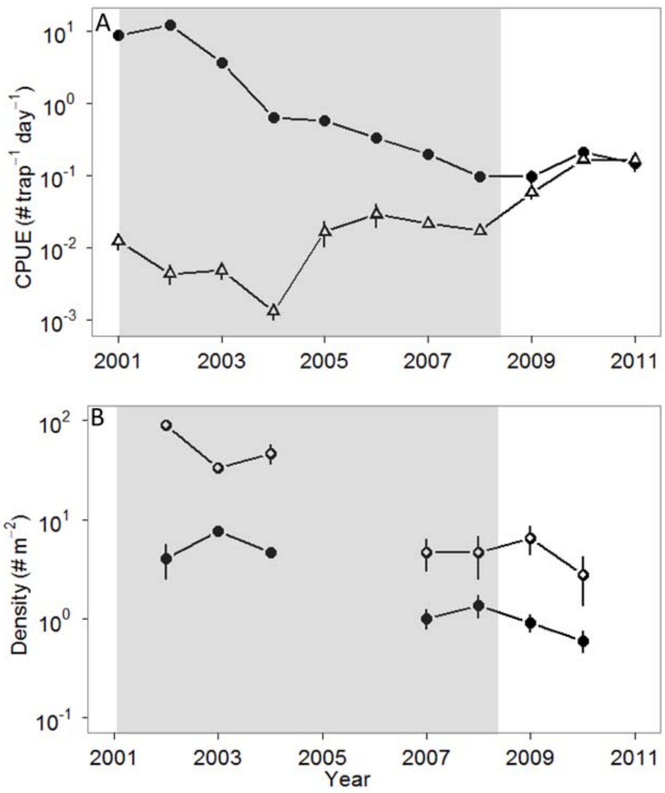
A
CPUE (# trap^{-1} day^{-1})
10^1
10^0
10^{-1}
10^{-2}
10^{-3}
2001
2003
2005
2007
2009
2011
B
Density (# m^{-2})
10^2
10^1
10^0
10^{-1}
2001
2003
2005
2007
2009
2011
Year

Figure 2.

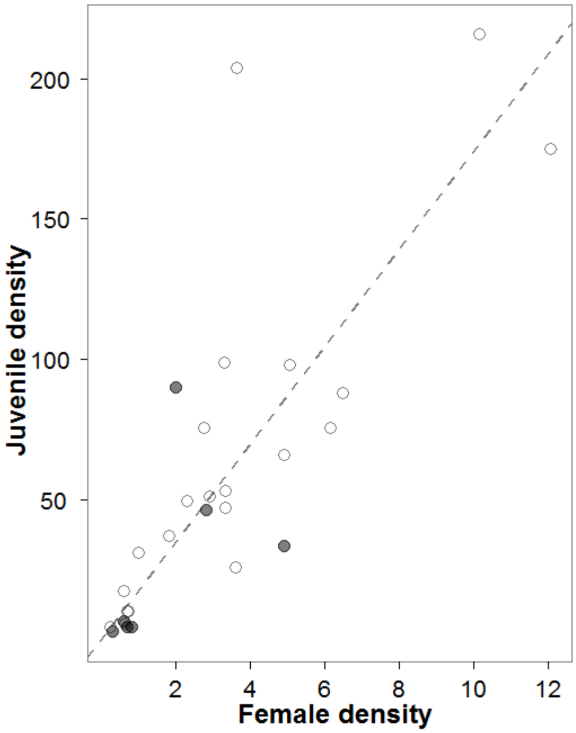

Figure 3.

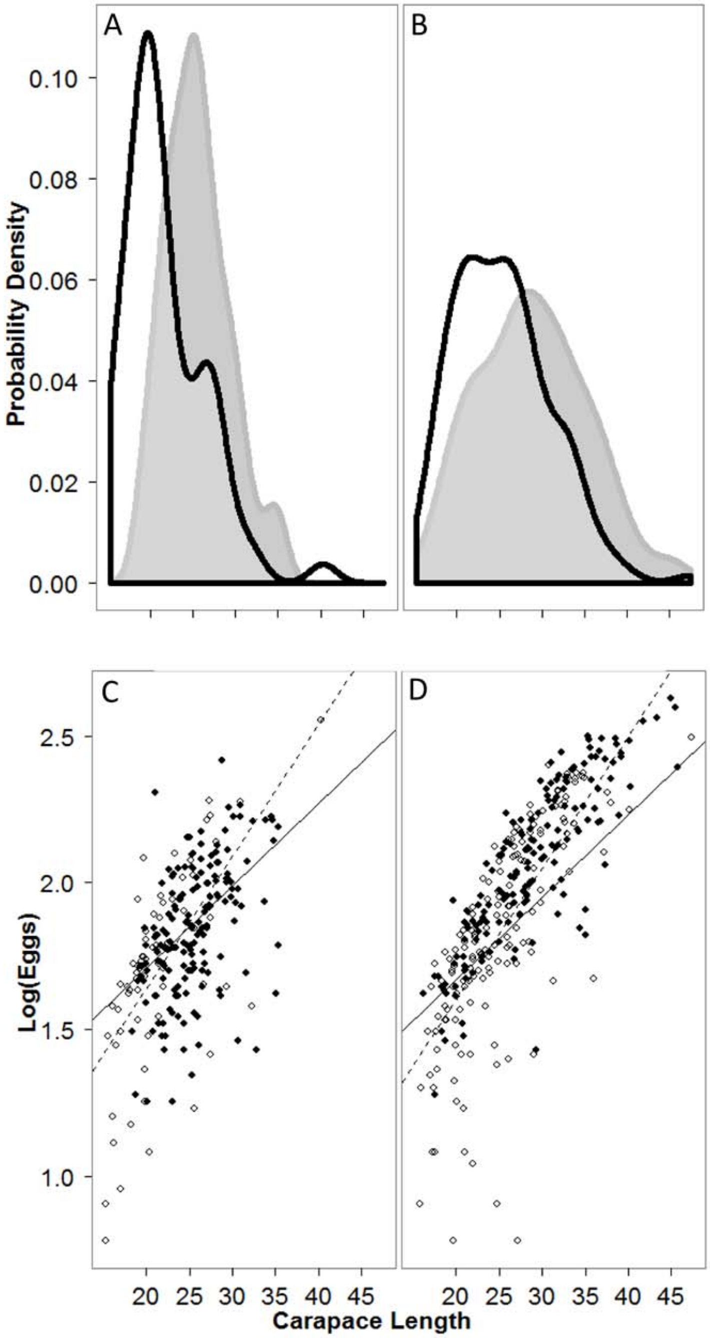
A
B
C
D
Probability Density
0.00
0.02
0.04
0.06
0.08
0.10
Log(Eggs)
1.0
1.5
2.0
2.5
20
25
30
35
40
45
Carapace Length

Figure 4.

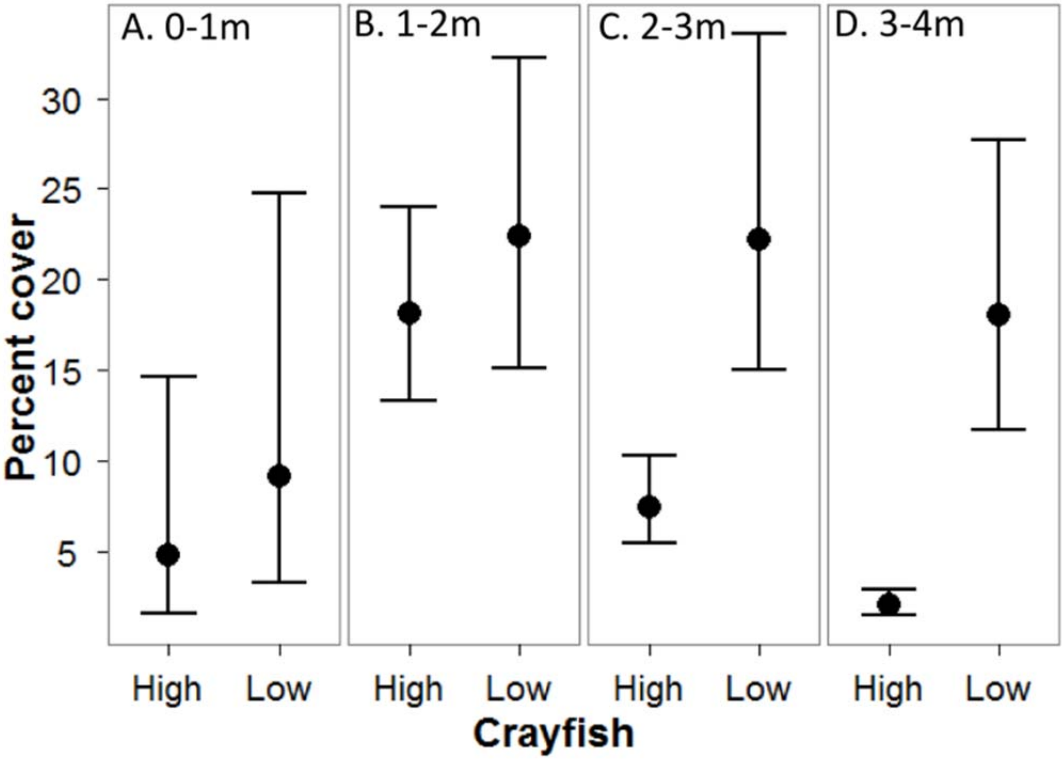
A. 0-1m
B. 1-2m
C. 2-3m
D. 3-4m
Percent cover
30
25
20
15
10
5
High
Low
High
Low
High
Low
High
Low
Crayfish

Figure 5.

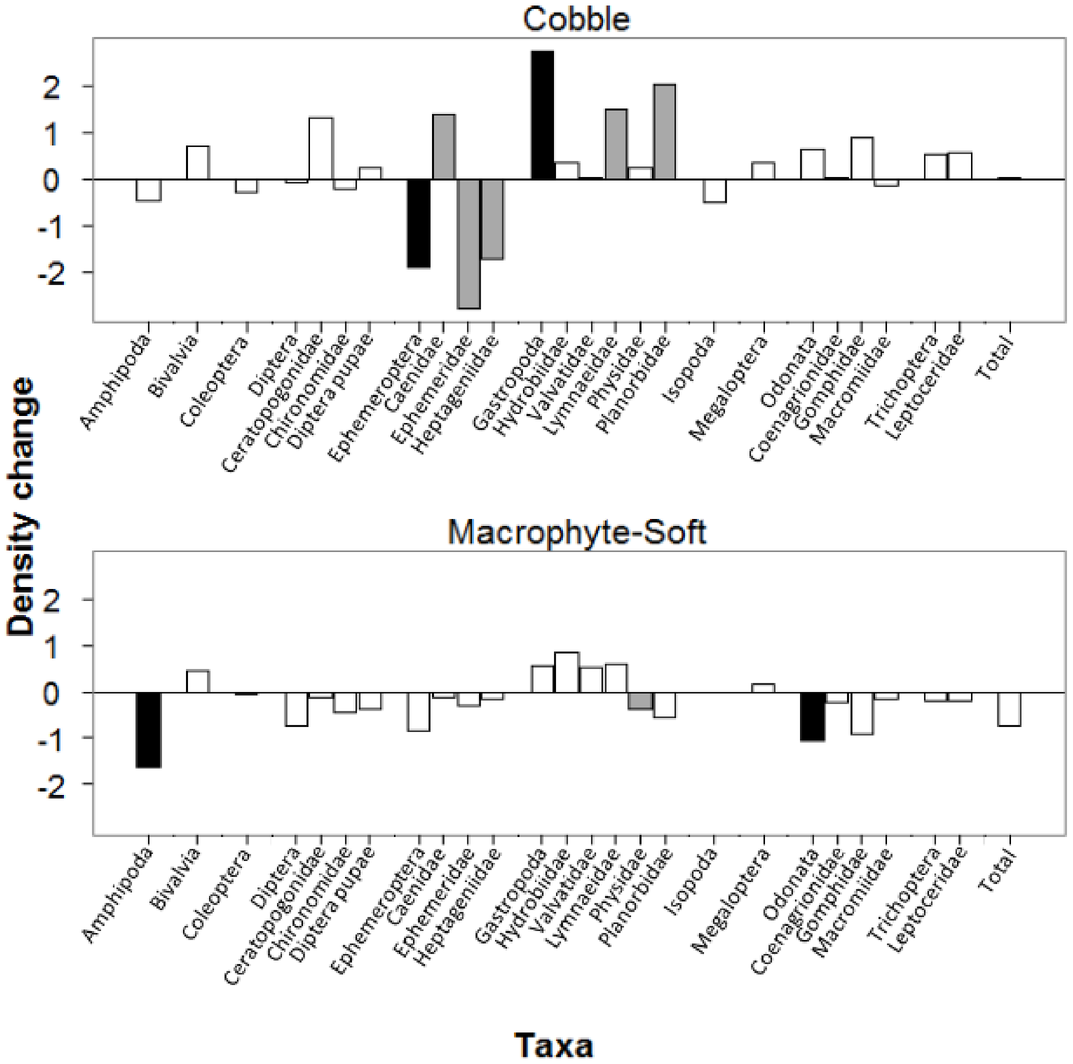
Cobble
Macrophyte-Soft
Density change
Taxa
2
1
0
-1
-2
Amphipoda
Bivalvia
Coleoptera
Diptera
Ceratopogonidae
Chironomidae
Diptera pupae
Ephemeroptera
Caenidae
Ephemeridae
Heptageniidae
Gastropoda
Hydrobiidae
Valvatidae
Lymnaeidae
Physidae
Planorbidae
Isopoda
Megaloptera
Odonata
Coenagrionidae
Gomphidae
Macromiidae
Trichoptera
Leptoceridae
Total

Figure 6.

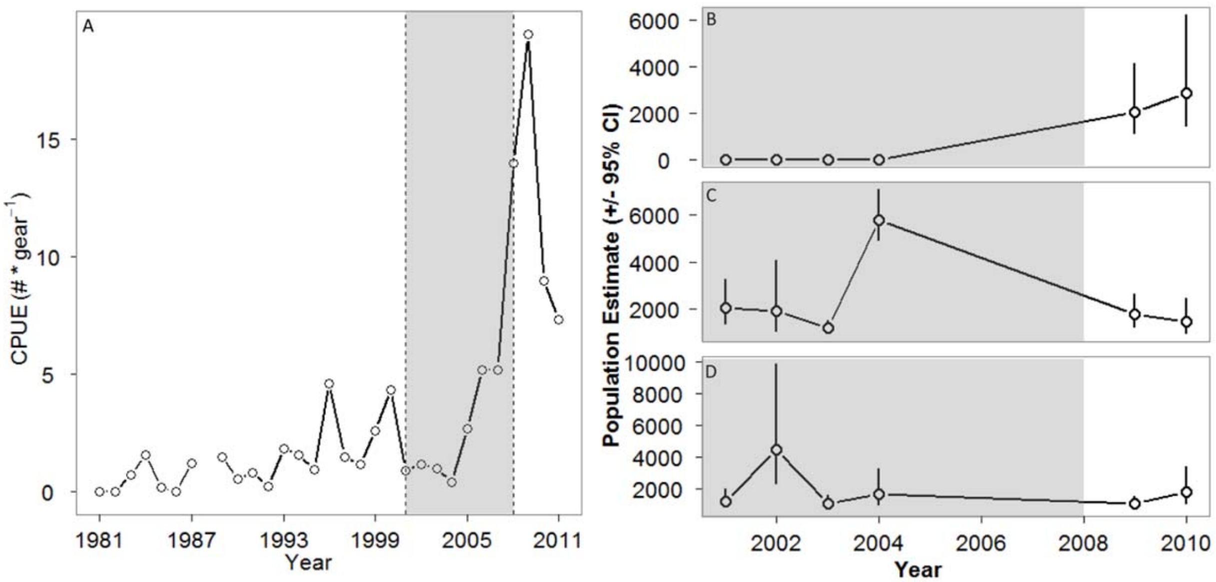
A
CPUE (# * gear^{-1})
0
5
10
15
1981
1987
1993
1999
2005
2011
Year
B
C
D
Population Estimate (+/- 95% CI)
6000
4000
2000
0
6000
4000
2000
10000
8000
6000
4000
2000
2002
2004
2006
2008
2010
Year

Figure 7.

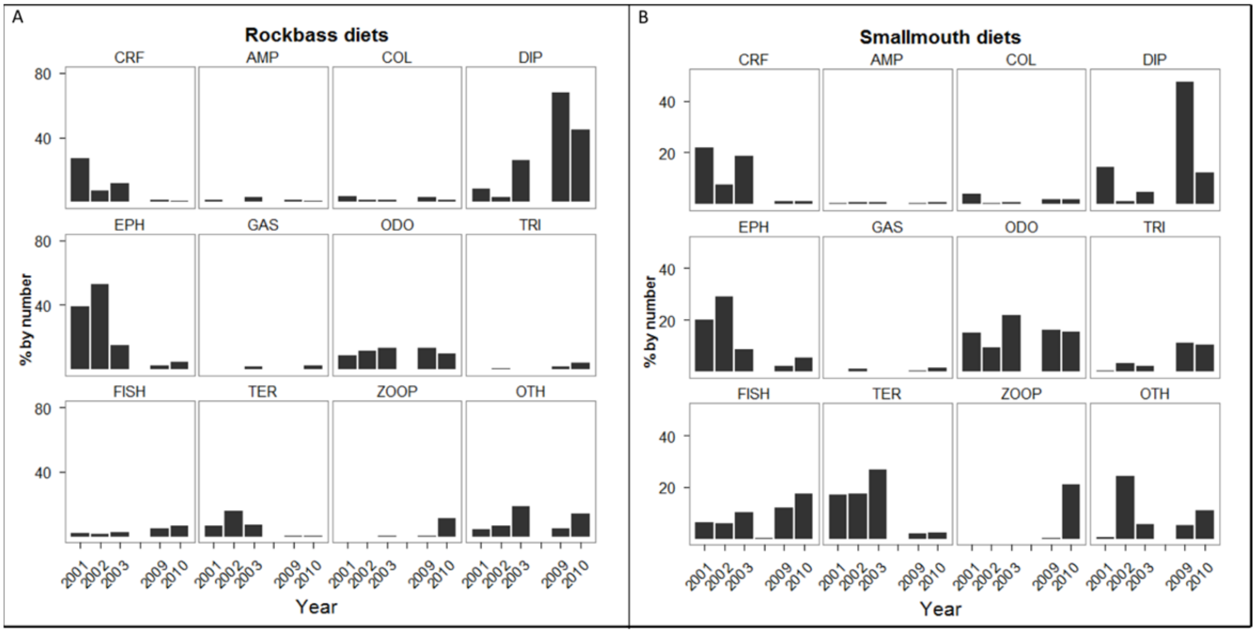
A
Rockbass diets
B
Smallmouth diets
CRF
AMP
COL
DIP
EPH
GAS
ODO
TRI
FISH
TER
ZOOP
OTH
% by number
80
40
20
2001
2002
2003
2009
2010
Year

Figure 8.

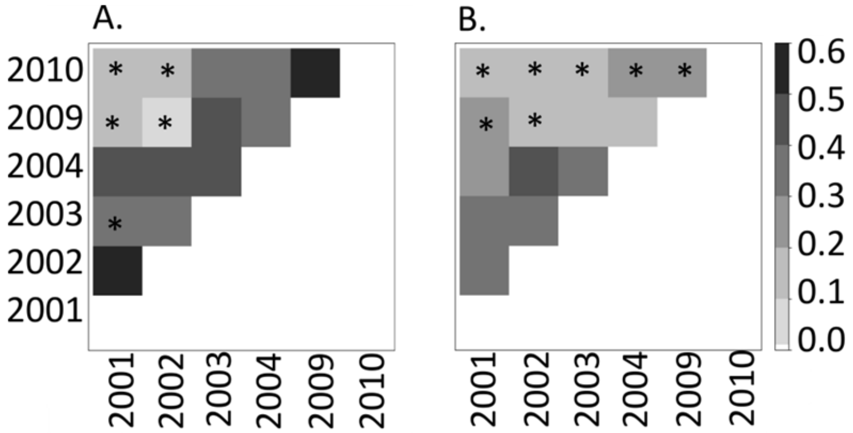

Figure 9.

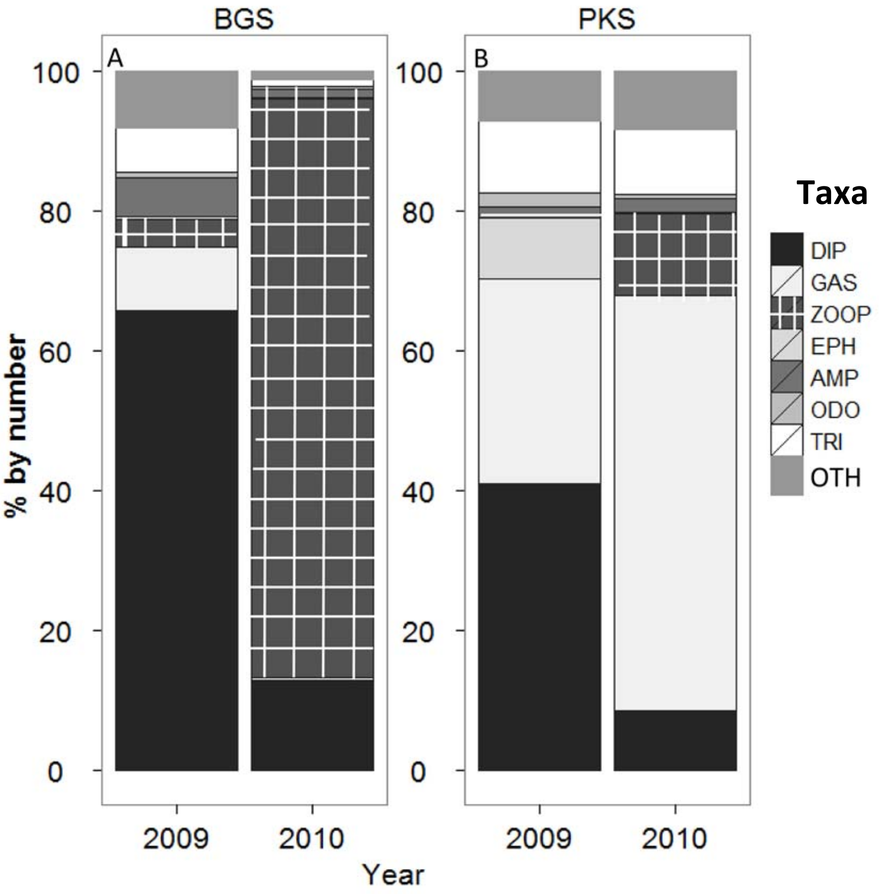
BGS
PKS
A
B
100
80
60
40
20
0
% by number
2009
2010
Year
Taxa
DIP
GAS
ZOOP
EPH
AMP
ODO
TRI
OTH

Figure 10.

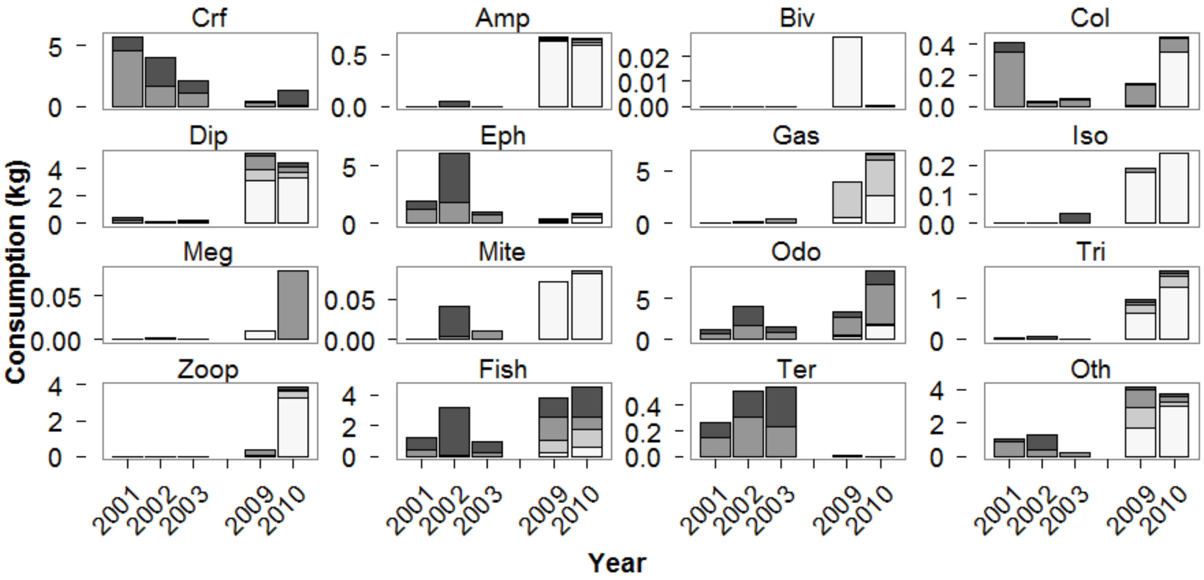
Crf
Amp
Biv
Col
Dip
Eph
Gas
Iso
Meg
Mite
Odo
Tri
Zoop
Fish
Ter
Oth
Consumption (kg)
Year
2001
2002
2003
2009
2010
5
0
0.5
0.0
0.02
0.01
0.00
0.4
0.2
4
2
0.1
0.05
1
0.4

Figure 11.

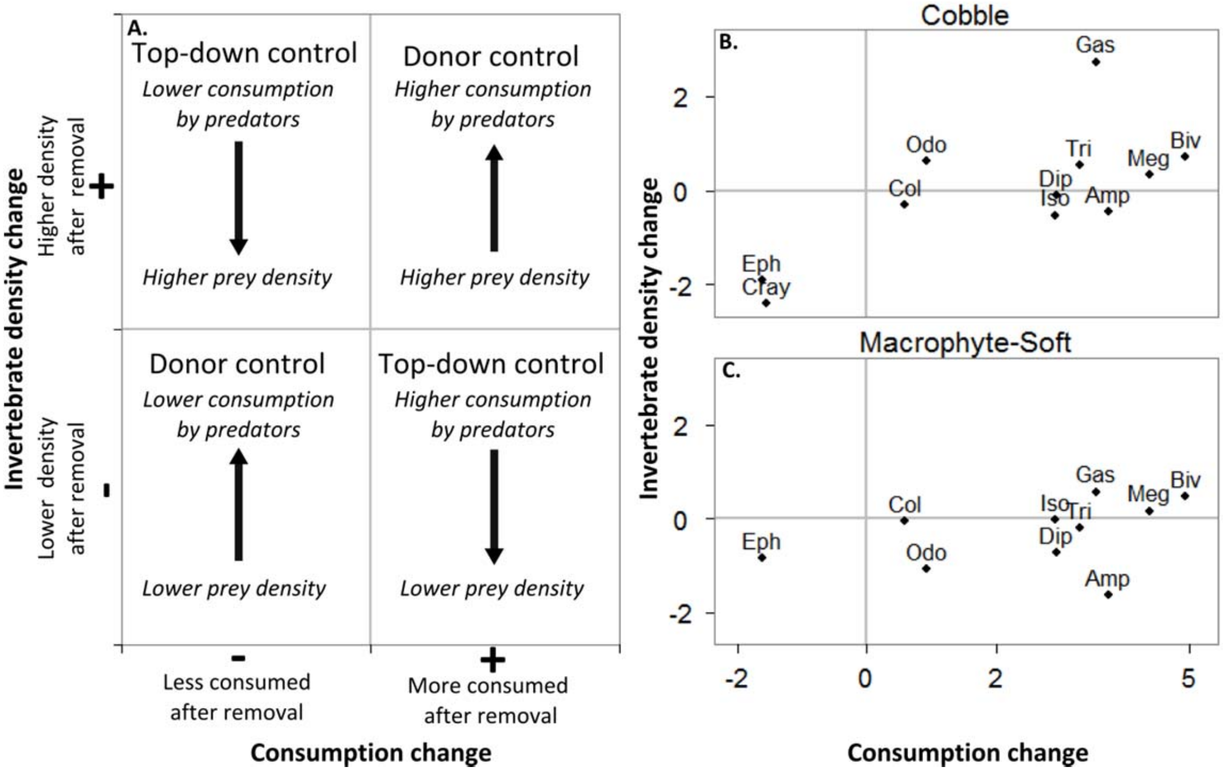
A.
Top-down control
Lower consumption by predators
Higher prey density
Donor control
Higher consumption by predators
Higher prey density
Donor control
Lower consumption by predators
Lower prey density
Top-down control
Higher consumption by predators
Lower prey density
Invertebrate density change
+
Higher density after removal
-
Lower density after removal
-
Less consumed after removal
+
More consumed after removal
Consumption change
Cobble
B.
Gas
Odo
Tri
Biv
Meg
Col
Dip
Iso
Amp
Eph
Cray
Macrophyte-Soft
C.
Gas
Biv
Meg
Col
Iso
Tri
Dip
Eph
Odo
Amp
Invertebrate density change
2
0
-2
2
0
-2
-2
0
2
5
Consumption change

Figure 12.

Table 1. Prey items found in fish diets, groupings/abbreviations used in figures, energy density values, and sources. If multiple energy densities were available for a prey group (e.g., multiple species within an order), the mean value of all taxa was used (exceptions noted). When energy densities were presented on a per dry mass basis, they were converted to wet mass using percent water values for similar taxa from Cummins and Wuycheck (1971).

Prey item description	**Abbreviation**	**Energy density ($J \cdot g^{-1}$ wet mass)**	**Source**
Amphipoda	Amp	4429	Hanson 1997
Annelida	Oth	2699	Cummins & Wuycheck 1971
Arachnid	Oth	5320	Gray 2005
Bivalva	Biv	2008	Cummins & Wuycheck 1971
Coleoptera	Col	7970	Gray 2005
Crayfish	Crf	3766	Roell & Orth 1993
Zooplankton	Zoop	2653	Hanson 1997
Diptera adult	Dip	6317	Gray 2005
Diptera larvae	Dip	1763	Hanson 1997
Ephemeroptera adult	Eph	9686[a]	Cummins & Wuycheck 1971
Ephemeroptera larvae	Eph	4703[b]	Cummins & Wuycheck 1971
Gastropoda	Gas	1799	Cummins & Wuycheck 1971
Hemiptera	Oth	9686[a]	Cummins & Wuycheck 1971
Hydracarina	Oth	4099	Cummins & Wuycheck 1971
Hymenoptera	Oth	5710[c]	Cummins & Wuycheck 1971
Isopoda	Iso	3142	Cummins & Wuycheck 1971
Megaloptera	Meg	4360	Cummins & Wuycheck 1971
Odonata adult	Odo	9686[a]	Cummins & Wuycheck 1971
Odonata larvae	Odo	3139[d]	Cummins & Wuycheck 1971
Oligochaeta	Oth	2699[e]	Cummins & Wuycheck 1971
Plant matter	Not displayed	1331[f]	Cummins & Wuycheck 1971
Terrestrial items	Ter	9686[a]	Cummins & Wuycheck 1971
Trichoptera adult	Tria	7760	Gray 2005
Trichoptera larvae	Tril	3848	Cummins & Wuycheck 1971
Unidentified	Oth	4903[g]	Cummins & Wuycheck 1971
Unidentified invertebrate	Oth	3314[h]	Cummins & Wuycheck 1971

Fish	Fish	5328[i]	Cummins & Wuycheck 1971

[a] All terrestrial insects

[b] Baetidae larvae

[c] Honey bee (*Apis mellifera*) excluded

[d] Gomphidae and Libellulidae larvae

[e] Aquatic annilids

[f] *Najas spp*. and *Chara spp*.

[g] All other prey groups

[h] Aquatic arthropods

[e] Cyprinidae

Appendix 1: Lakes included in stock-recruitment and fecundity analyses. All lakes are in Vilas County, Wisconsin, USA.

Lake	**S-R survey years**	**Latitude**	**Longitude**	**Max depth (m)**	**Perimeter (km)**	**Area (ha)**
Arrowhead Lake	2002-2004	45.90634	-89.69024	13.11	3.50	40.05
Big Lake	2002,2004	46.15474	-89.76970	18.59	15.17	343.64
Birch Lake	2002-2004	46.21767	-89.83838	13.72	10.50	212.03
Big Portage Lake	2002	46.12560	-89.28492	12.19	10.84	240.47
Little Star Lake	2002	46.11529	-89.86147	20.42	6.36	107.12
Round Lake	2002-2004	46.17186	-89.71024	7.62	3.66	71.52
Sparkling Lake	2002-2004, 2007-2010	46.00865	-89.69971	19.51	3.75	65.50
White Sand Lake	2002	46.08872	-89.59413	21.64	9.32	304.57
Plum Lake	2002	46.00328	-89.51930	17.37	23.33	427.75
Trout Lake	2002-2004	46.02900	-89.66500	35.70	25.90	1607.90
Wild Rice Lake	2002-2004	46.06481	-89.79323	7.90	5.90	153.00
Big Crooked Lake	NA	46.12913	-89.68154	26.52	12.87	276.00
Boulder Lake	NA	46.12556	-89.65855	7.01	12.07	131.00
Stormy Lake	NA	46.05280	-89.32308	19.20	8.26	211.25

Appendix 2. Lakes included in fecundity analysis, rusty crayfish catch·trap day^{-1} in the survey year, category of crayfish density, number of gravid females collected, mean carapace length of gravid females, and mean number of eggs per female. Rusty crayfish CPUE is from a single survey of 30 traps set around the perimeter of the lake for 24 hours with the exception of Sparkling Lake, which is the annual mean of CPUE from the removal experiment. Gravid females were collected via snorkel surveys; no rusty crayfish were collected in traps from Arrowhead or Stomy Lakes.

Lake	Rusty crayfish CPUE	Rusty crayfish category	# gravid females	Mean carapace length (mm)	Mean eggs/female
Arrowhead	0.00	Low	11	21.34	80.64
Big Crooked	9.83	High	29	25.14	69.72
Big Lake	17.80	High	50	23.92	51.24
Boulder	5.46	High	42	27.50	109.60
Sparkling 2002	11.41	High	77	27.32	102.86
Sparkling 2003	2.82	High	89	30.20	170.33
Sparkling 2004	0.65	Low	56	27.04	123.46
Sparkling 2008	0.10	Low	29	23.71	57.48
Sparkling 2009	0.10	Low	36	23.17	65.94
Stormy	0.00	Low	27	18.49	39.78
Trout	28.60	High	50	26.11	79.96
Wild Rice	0.05	Low	31	24.58	85.32

Appendix 3.

Growth rates of smallmouth and rock bass

Rock bass and smallmouth bass growth rates were determined by back-calculating length at age from scales. Fish were sampled via electrofishing on each of four nights mid-summer of 2000, biweekly from late May to mid-August from 2001- 2004 and 2009 -2010. A few smaller sampling efforts by the Wisconsin Department of Natural Resources and researchers from the University of Wisconsin-Madison added to the sample size for 2005 and 2006. Additional rock bass data were collected by LTER from 1981 to 2010 using Trammel and Fyke nets. Total length (TL; mm), weight (g), and scales were collected during all fish sampling efforts. This allowed for a good representation of fish densities during both high and low rusty crayfish density years (2001 and 2002 = high crayfish density years and 2003, 2004, 2009, and 2010 = low crayfish density years). Scale annuli were used to determine annual growth increments for rock bass and smallmouth bass (see below). Otoliths were collected from a small subsample ($n_r = 16$, $n_s = 24$) at the end of 2010.

Scales were aged by two independent readers. A double-blind comparison of ages determined from scale reading and ages determined from otolith reading were used to validate our ability to read scales accurately. Fish scales were then used to produce back-calculated lengths-at-ages using the Fraser-Lee back-calculation model (Fraser 1916, Lee 1920):

$$L_i = \frac{S_i}{S_c}(L_c - c) + c$$

Where S_c is the fish TL at time i, S_i is the scale length at time i, S_c is the scale length at time of capture, L_c is the fish TL at time of capture and c represents the length of fish when scale growth begins. For this analysis published estimates of c of 25 mm and 35 mm where used for rock bass and smallmouth bass respectively (Carlander 1982).

After back-calculated fish lengths were determined, a high or low crayfish density growth-year was assigned to each back-calculated fish length based on the year in which growth occurred. A Von Bertalanffy growth model (Von Bertalanffy 1957) modified to allow different parameter estimates for high and low crayfish growth years (groups) was then fit to the back-calculated lengths-at-ages:

$$L_t = L_\infty[group]\left(1 - e^{-K[group](t-t_o[group])}\right) + \varepsilon$$

Where L_t is the back-calculated length in year t, L_∞ is the asymptote of a model of average length at age (Francis 1988), *k* is the Brody growth coefficient which measures the rate of approach to the asymptotic size, t_0 is the theoretical age at which a fish would be of length 0 (Schnute and Fournier 1980), and ε is the residual error and is normally distributed with a mean of 0 and variance σ^2. We first fit the above model, allowing separate estimates of all three Von Bertalanffy growth parameters for high and low crayfish years. We then fit subsequent models allowing one parameter in common for the two groups, two parameters in common for the two groups, and all three parameters in common for the two groups. We used AIC to assess which parameterization best fit our data and to test for differences in growth among high and low crayfish density years.

Adding random effects to our growth model allowed us to account for the nested structure of our back-calculated data and non-independence of length measurements obtained from the same individual fish (Wagner 2006). The inclusion of random effects allowed us to account for variation at the individual fish level (Gaeta 2011). Following determination of the best fixed effects model, random effects for individual fish were applied to the Von Bertalanffy growth model:

$$L_t = L_\infty\left(1 - e^{-K + [\varepsilon_{ji}](t - t_o[group]))}\right) + \varepsilon$$

Where ε_{ji} is an additional error term accounting for variation among individual fish and is normally distributed with a mean of 0 and a variance estimated by the model. Due to the structure of our data including random effects for multiple parameters of the Von Bertalanffy growth model simultaneously resulted in non-converging models. Therefore, we chose to include random effects for *K* only, for both smallmouth bass and rock bass, as we felt that it was the most likely parameter to vary based on individual life history traits. All analyses were performed using R v2.12.0 (R Core Development Team 2010).

Results

Rock bass

Double-blind results for comparing ages estimated from scales and otoliths demonstrated 69% agreement with 94% of scale readings falling within 1 year of the otolith determined ages

(Figure 4.1, n = 16). A total of 344 rock bass ranging from 1 to 9 years old produced 1,536 growth observations for the Von Bertalanffy growth model (Figure 4.2). The two parameters in common model which contained separate t_0 values for each group was the best fit model based on AIC (Table 4.1), indicating slower growth rates in years of low crayfish density (Figure 4.2).

Smallmouth Bass

Double-blind results for comparing ages estimated from scales and otoliths demonstrated 54% agreement with 87.5% of scale readings falling within 1 year of the otolith determined ages (Figure 4.3, n = 24). A total of 333 smallmouth bass ranging from 1 to 14 years old produced 1,161 growth observations for the Von Bertalanffy growth model (Figure 4.4). The two parameters in common model with different values for t_0 was the best fit model based on AIC (Table 1) indicating slower growth rates in years of low crayfish density (Figure 4.4).

Appendix 4 Literature Cited

Carlander, K.D. 1982. Standard intercepts for calculating lengths from scale measurements for some centrarchid and percid fishes. *Transactions of the American Fisheries Society*. 111: 332-336.

Francis, R.I.C.C. 1988. Are growth parameters estimated from tagging and age-length data comparable? *Canadian Journal of Fisheries and Aquatic Sciences*. 45: 936-942.

Fraser, C.M. 1916. Growth of spring salmon. *Transactions of the Pacific Fisheries Society*. 1915: 29-39.

Gaeta, J.W., M.J. Guarascio, G.G. Sass, and S.R. Carpenter. 2011. Lakeshore residential development and growth of largemouth bass (*Micropterus salmoides*): a cross-lake comparison. *Ecology of Freshwater Fish*. 20: 92-101.

Lee, R.M. 1920. A review of the methods of age and growth determination in fishes by means of scales. *Fisheries Investigations, London Series*. 2: 1-32.

R Core Development Team. 2010. R: a language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing.

Schnute, J. and D. Fournier. 1980. *A new approach to length-frequency analysis: Growth structure. Canadian Journal of Fisheries and Aquatic Sciences.* 37: 1337-1351.

Von Bertalanffy, L. 1957. Quantitative laws in metabolism and growth. *The Quarterly Review of Biology*. 32: 217-231.

Wagner, T., D.B. Hayes, and M.T. Bremigan. 2006. Accounting for multilevel data structures in fisheries data using mixed models. *Fisheries*. 31: 180-187.

Table 4.1. Summary of fixed-effects model parameterizations for the Von Bertalanffy growth model with degrees of freedom and AIC values. Model names indicate which of the three model parameters varied between groups.

Smallmouth bass			Rock bass		
Model	df	AIC	Model	df	AIC
Gen[1]	7	11723.09	T	5	13059.68
LT	6	11723.54	LT	6	13061.41
T	5	11724.45	KT	6	13061.49
KT	6	11724.58	Gen[1]	7	13063.00
K	5	11730.39	LK	6	13070.67
LK	6	11732.09	K	5	13077.50
L	5	11732.96	L	5	13084.02
Com[2]	4	11783.12	Com[2]	4	13165.65

[1] Refers to the model wherein all parameters varied between groups. [2] Refers to the model wherein all parameters were the same for both groups.

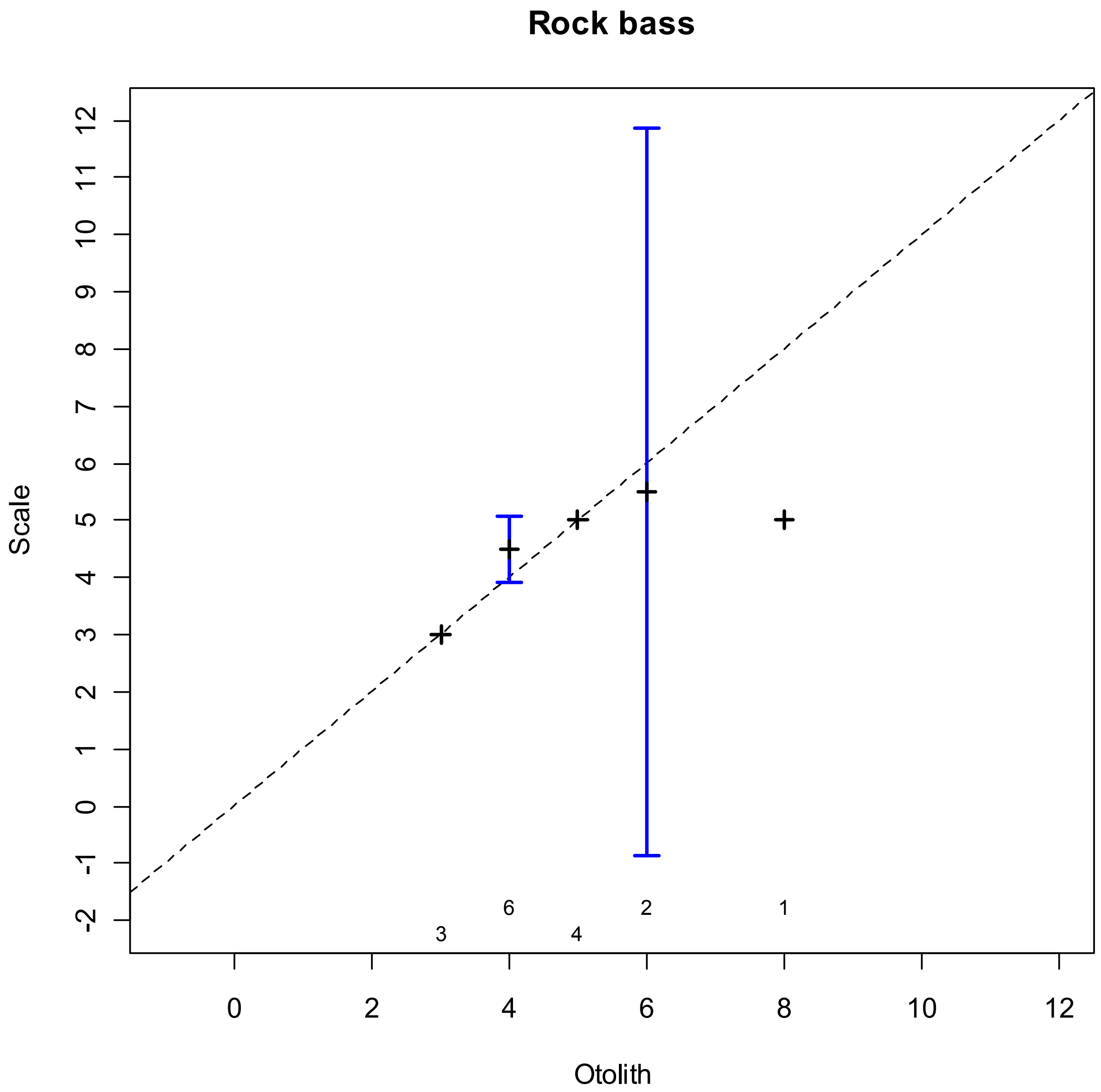

Figure 4.1. Double-blind age estimation results comparing rock bass otoliths and scales. Scales and otoliths were collected from Sparkling Lake, Vilas County, Wisconsin, USA, in August 2010. Precision = 68.75%, precision +/- 1 yr = 93.75%. Blue error bars indicate 95% C.I.

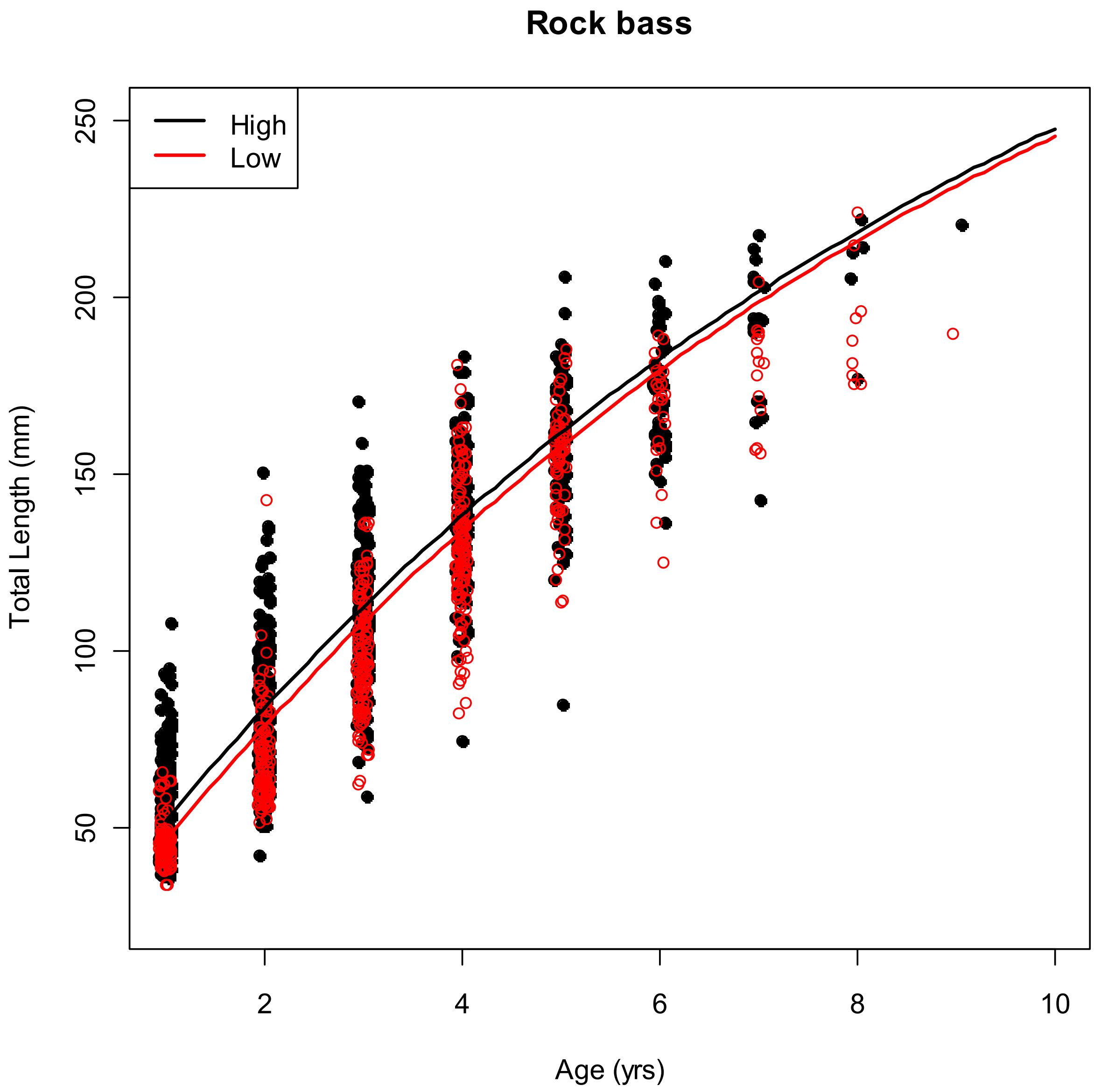

Figure 4.2. Back-calculated length-at-age data fitted to the Von Bertalanffy growth model with separate curves for high (black) and low (red) crayfish density. Data were collected from rock bass scales from Sparkling Lake, Vilas County, Wisconsin, USA, from 1981 through 2005, 2009, and 2010. 1,536 length-at-age observations (high = 1009, low = 527) were calculated from 344

fish. The fitted model has different parameter values for t_0 only and random effects were applied to individual fish for the *K* parameter.

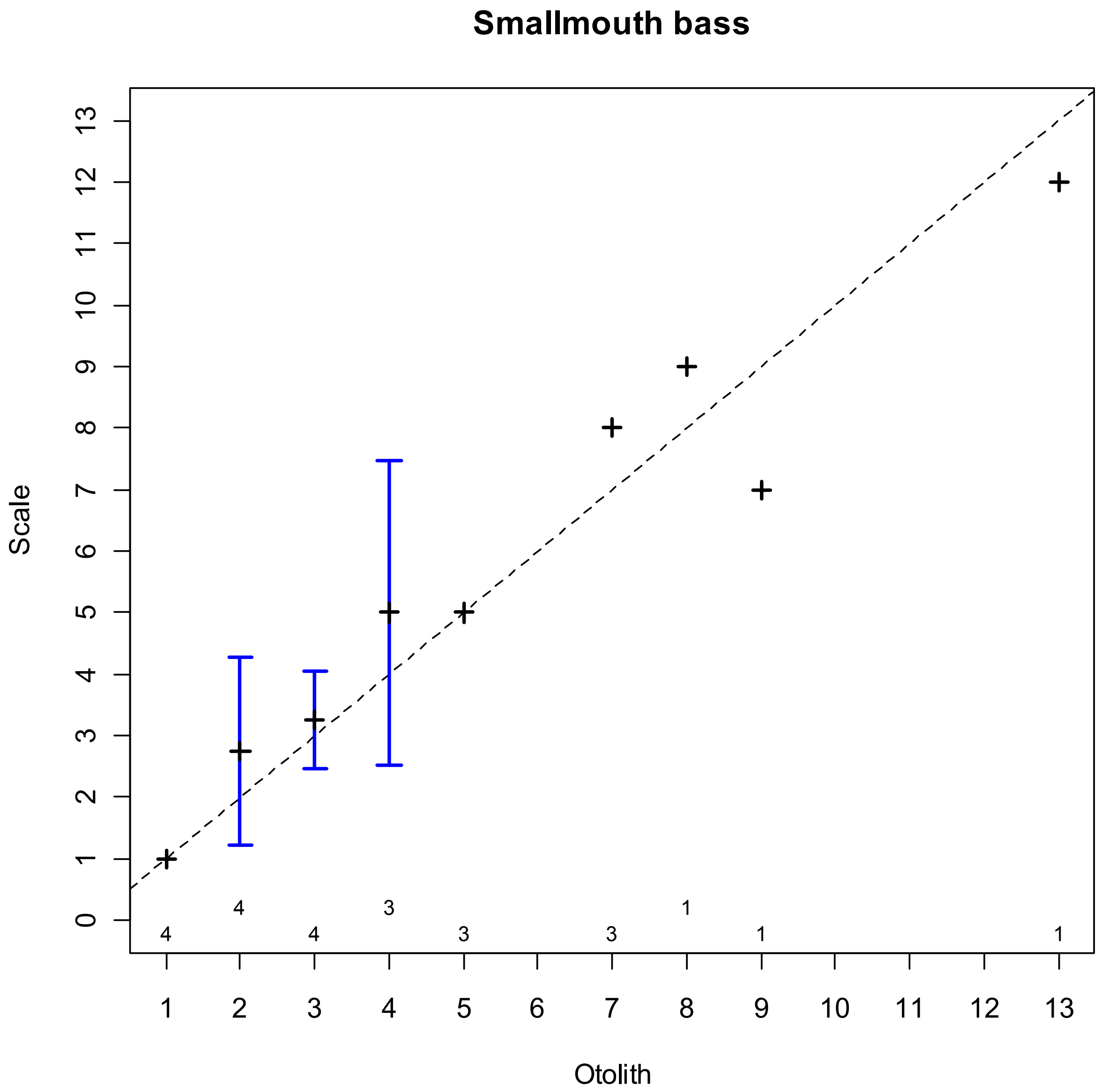

Figure 4.3. Double-blind age estimation results comparing smallmouth bass otoliths and scales. Scales and otoliths were collected from Sparkling Lake, Vilas County, Wisconsin, USA, in August 2010. Precision = 54.12%, precision +/- 1 yr = 87.45%. Blue error bars indicate 95% C.I.

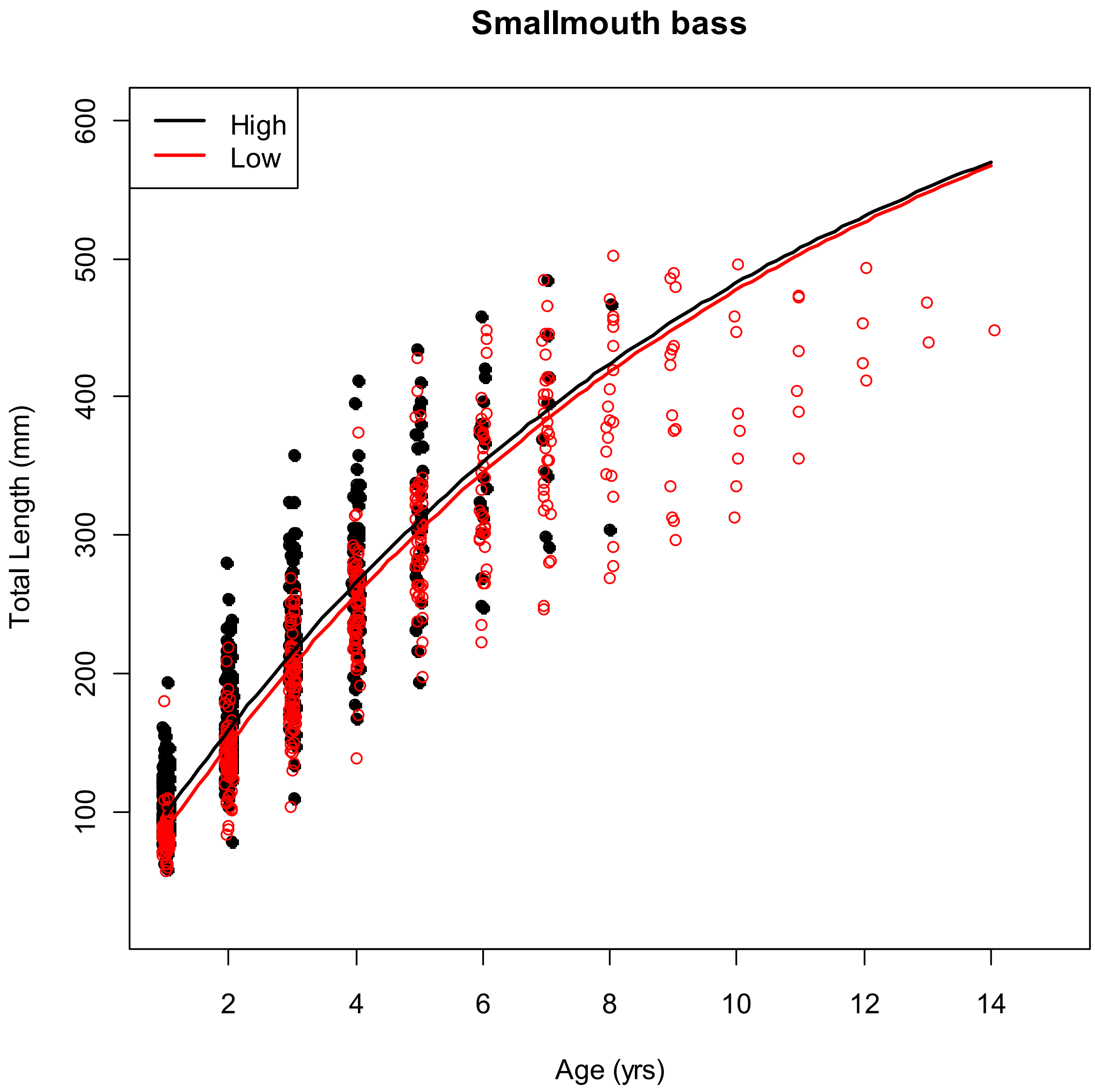

Figure 4.4. Back-calculated length-at-age data fitted to the Von Bertalanffy growth model with separate curves for high (black) and low (red) crayfish density.. Data were collected from smallmouth bass scales from Sparkling Lake, Vilas County, Wisconsin, USA, from 2001 through 2005, 2009, and 2010. 1,161 length-at-age observations (high=693, low=468) were calculated from 333 fish. The fitted model has different parameter values for t_0 only and random effects were applied to individual fish for the *K* parameter.

Appendix 4. Model fit for different combinations of fixed effects for analysis of rusty crayfish stock-recruitment and fecundity. The best fit models were selected based on AIC – extra parameters were included only if they decreased AIC by >2 units. Random effects structure for the Fecundity models was held constant to account for non-independence of samples from the same lake and year, and AIC values were generated based on maximum likelihood (ML) parameter estimates.

Analysis	**Response variable**	**Fixed effects**	**Random effects**	**AIC**	**ΔAIC**
Stock-recruitment	Juvenile (age-0) density	Female density	NA	284.4	NA
		Female density + Sparkling[a]		287.2	2.8
		Female density + Sparkling +Female density*Sparkling		285.7	1.3
Fecundity	LN(eggs)	CL[b]+Density[c]+CL*Density	CL*Year, CL*Lake	-184.2	NA
		CL+Density		-179.6	4.6
		CL		-170.2	14
		Density		-174.4	9.8
		(Intercept only)		-166.1	18.1

[a] Binary (dummy) variable indicating whether data were from Sparkling Lake

[b] Carapace Length; centered on mean value for model selection

[c] Categorical variable representing high (≥1 CPUE) or low (<1 CPUE) rusty crayfish density

Appendix 5.

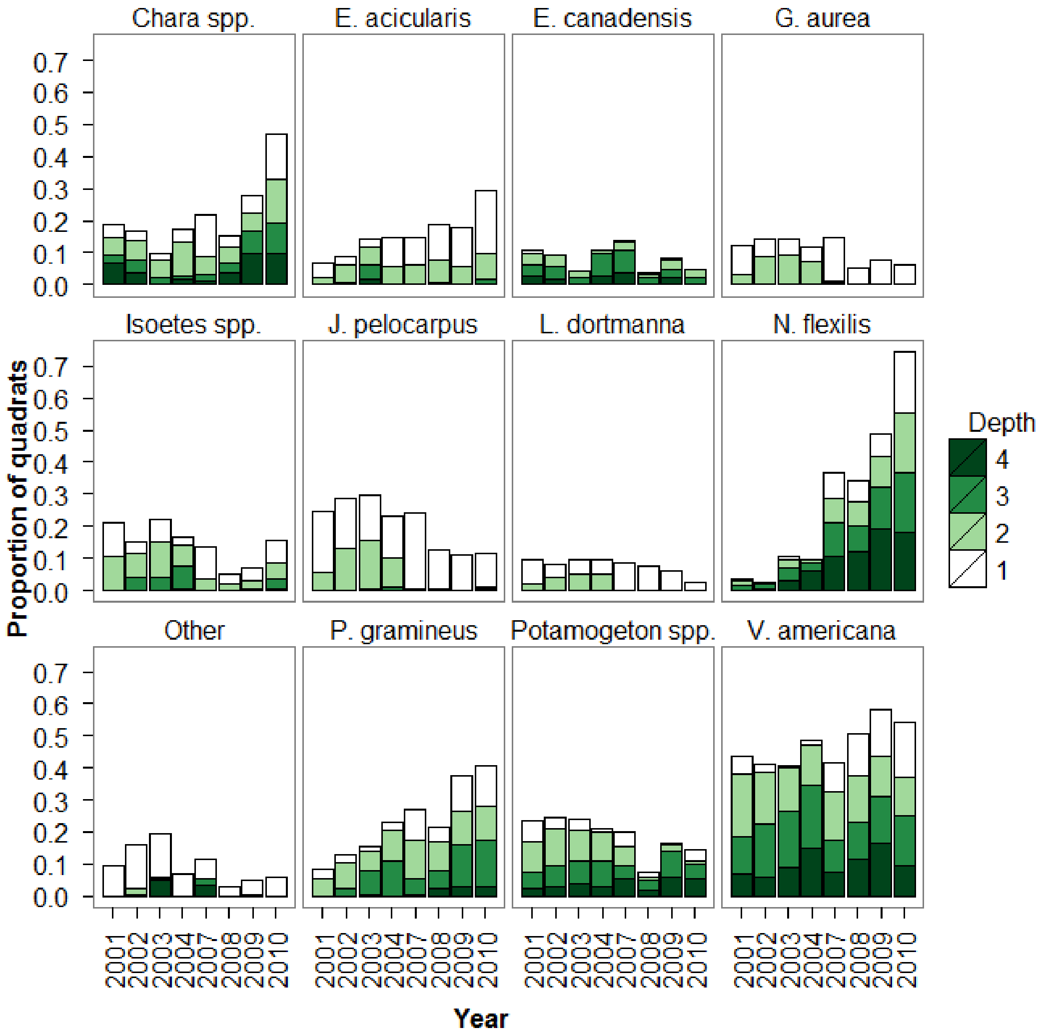

Figure 5.1. Proportion of quadrats containing at least one stem of each macrophyte species as a function of depth, where 1=0-1m, 2=1-2m, 3=2-3m, and 4=3-4m. Species are *Eleocharis acicularis*, *Elodea canadensis, Gratiola aurea, Isoetes spp., Juncus pelocarpus, Lobelia dortmanna, Najas flexilis, Potamogeton gramineus*, and *Vallisneria americana*. *Potamogeton spp*. includes *P. ampifolius, P. diversifolius, P. epihydrus, P. praelongus, P. pusilis*, and *P. spirillus*.

“Other”= includes *Elatine minima*, *emergent Eleocharis spp., Ericocaulon aquaticum, Nitella spp., Ranunculus flammula, Sagittaria spp.*, and *Scirpus spp*.

Appendix 6. Results of hierarchical models fit to each invertebrate taxa. “Total” includes all taxa except Oligochaetes which were not well sampled. Insect orders and Mollusk classes were analyzed as a whole and percentages represent percent by number of total. Families (italics) were analyzed separately if they appeared in 10% or more of samples, and percentages represent percent by number of order (or class).

	Fixed effects				**Random effects**		
Taxa (%[a])	**Crayfish density[b]**	**Habitat**	**Est.[c]**	**95% CI[d]**	**Term**	**σ[2]**	**Adj R[2e]**
Total	High	Macrophyte-Soft	7.22	6.77-7.70	Year:Site[f]	0.72	0.39
	Low	Macrophyte-Soft	6.48	6.09-6.86	Site	0.11	
	High	Cobble	6.89	6.16-7.55	Residual	0.39	
	Low	Cobble	6.91	6.05-7.82			
Amphipoda (15%) *(100% Hyalella azteca)*	High	Macrophyte-Soft	5.40	4.59-6.15	Year:Site	1.23	0.50
	Low	Macrophyte-Soft	3.76	3.11-4.46	Site	0.84	
	High	Cobble	4.64	3.61-5.74	Residual	0.90	
	Low	Cobble	4.18	2.83-5.45			
Bivalvia (5.1%) *(100% Sphaeriidae)*	High	Macrophyte-Soft	3.01	2.30-3.61	Year:Site	0.99	0.38
	Low	Macrophyte-Soft	3.47	2.92-4.01	Site	0.27	
	High	Cobble	2.01	1.13-3.10	Residual	0.84	
	Low	Cobble	2.73	1.60-3.92			
Diptera (62.1%)	High	Macrophyte-Soft	6.21	5.60-6.87	Year:Site	1.62	0.39
	Low	Macrophyte-Soft	5.48	4.95-5.94	Site	0.00	
	High	Cobble	5.59	4.49-6.45	Residual	0.75	
	Low	Cobble	5.50	4.29-6.92			
Ceratopogonidae (53.8%)	High	Macrophyte-Soft	3.59	2.72-4.52	Year:Site	2.72	0.55
	Low	Macrophyte-Soft	3.46	2.66-4.16	Site	0.75	
	High	Cobble	2.33	1.03-3.68	Residual	0.86	
	Low	Cobble	3.65	2.21-5.45			
Chironomidae (45.8%)	High	Macrophyte-Soft	5.64	5.13-6.22	Year:Site	0.98	0.27

	Low	Macrophyte-Soft	5.18	4.73-5.58	Site	0.02	
	High	Cobble	5.51	4.64-6.28	Residual	0.71	
	Low	Cobble	5.29	4.30-6.53			
Diptera pupae (0.4%)	High	Macrophyte-Soft	2.07	1.88-2.29	Year:Site	0.13	0.18
	Low	Macrophyte-Soft	1.71	1.55-1.87	Site	0.00	
	High	Cobble	1.66	1.34-1.96	Residual	0.15	
	Low	Cobble	1.89	1.46-2.31			
Coleoptera (0.2%)	High	Macrophyte-Soft	1.83	1.55-2.06	Year:Site	0.14	0.33
	Low	Macrophyte-Soft	1.76	1.55-1.98	Site	0.09	
	High	Cobble	1.89	1.55-2.26	Residual	0.10	
	Low	Cobble	1.59	1.14-1.99			
Ephemeroptera (4.9%)	High	Macrophyte-Soft	2.96	2.39-3.54	Year:Site	0.74	0.67
	Low	Macrophyte-Soft	2.13	1.66-2.63	Site	0.37	
	High	Cobble	5.10	4.19-5.89	Residual	0.47	
	Low	Cobble	3.19	2.13-4.09			
Caenidae (23.1%)	High	Macrophyte-Soft	2.05	1.65-2.41	Year:Site	0.21	0.19
	Low	Macrophyte-Soft	1.92	1.61-2.22	Site	0.05	
	High	Cobble	1.77	1.24-2.36	Residual	0.60	
	Low	Cobble	3.16	2.41-3.89			
Ephemeridae (52.4%)	High	Macrophyte-Soft	2.08	1.74-2.44	Year:Site	0.16	0.77
	Low	Macrophyte-Soft	1.76	1.49-2.10	Site	0.13	
	High	Cobble	4.85	4.26-5.30	Residual	0.29	
	Low	Cobble	2.05	1.40-2.63			
Heptageniidae (16.3%)	High	Macrophyte-Soft	1.85	1.48-2.18	Year:Site	0.23	0.57
	Low	Macrophyte-Soft	1.69	1.43-2.03	Site	0.11	
	High	Cobble	3.49	2.98-3.99	Residual	0.26	
	Low	Cobble	1.78	1.08-2.29			
Gastropoda (6.4%)	High	Macrophyte-Soft	3.48	2.96-4.17	Year:Site	0.78	0.49

	Low	Macrophyte-Soft	4.05	3.54-4.56	Site	0.34	
	High	Cobble	1.66	0.67-2.46	Residual	0.75	
	Low	Cobble	4.40	3.34-5.53			
Hydrobiidae (31.7%)	High	Macrophyte-Soft	2.52	2.03-3.04	Year:Site	0.44	0.46
	Low	Macrophyte-Soft	3.36	2.94-3.80	Site	0.24	
	High	Cobble	1.46	0.65-2.11	Residual	0.55	
	Low	Cobble	1.79	0.93-2.67			
Valvatidae (13.1%)	High	Macrophyte-Soft	1.82	1.43-2.21	Year:Site	0.31	0.46
	Low	Macrophyte-Soft	2.33	2.00-2.66	Site	0.21	
	High	Cobble	1.52	0.94-2.04	Residual	0.23	
	Low	Cobble	1.56	0.93-2.24			
Lymnaeidae (16.6%)	High	Macrophyte-Soft	1.68	1.30-2.08	Year:Site	0.25	0.25
	Low	Macrophyte-Soft	2.28	1.97-2.60	Site	0.05	
	High	Cobble	1.57	0.93-2.11	Residual	0.59	
	Low	Cobble	3.04	2.26-3.78			
Physidae (2.3%)	High	Macrophyte-Soft	2.07	1.90-2.26	Year:Site	0.07	0.10
	Low	Macrophyte-Soft	1.72	1.58-1.85	Site	0.00	
	High	Cobble	1.61	1.32-1.88	Residual	0.17	
	Low	Cobble	1.84	1.47-2.24			
Planorbidae (36.4%)	High	Macrophyte-Soft	3.00	2.48-3.51	Year:Site	1.06	0.50
	Low	Macrophyte-Soft	2.44	2.00-2.82	Site	0.04	
	High	Cobble	1.76	1.03-2.59	Residual	0.45	
	Low	Cobble	3.80	2.81-4.83			
Isopoda (1.5%)	High	Macrophyte-Soft	2.09	1.58-2.52	Year:Site	0.40	0.25
(100% Caecidotea)	Low	Macrophyte-Soft	2.07	1.68-2.46	Site	0.19	
	High	Cobble	2.13	1.52-2.85	Residual	0.46	
	Low	Cobble	1.60	0.78-2.41			
Megaloptera (0.6%)	High	Macrophyte-Soft	1.75	1.41-2.12	Year:Site	0.07	0.36

100% Sialis spp.	Low	Macrophyte-Soft	1.88	1.57-2.18	Site	0.16	
	High	Cobble	2.51	2.07-3.00	Residual	0.34	
	Low	Cobble	2.86	2.26-3.40			
Odonata (3.1%)	High	Macrophyte-Soft	4.07	3.55-4.59	Year:Site	0.44	0.49
	Low	Macrophyte-Soft	3.00	2.51-3.44	Site	0.48	
	High	Cobble	3.02	2.32-3.74	Residual	0.45	
	Low	Cobble	3.66	2.82-4.50			
Coenagrionidae (10.7%)	High	Macrophyte-Soft	2.14	1.80-2.41	Year:Site	0.11	0.14
	Low	Macrophyte-Soft	1.91	1.65-2.17	Site	0.09	
	High	Cobble	1.75	1.35-2.22	Residual	0.28	
	Low	Cobble	1.79	1.24-2.28			
Gomphidae (80.4%)	High	Macrophyte-Soft	3.76	3.22-4.30	Year:Site	0.50	0.46
	Low	Macrophyte-Soft	2.85	2.38-3.31	Site	0.42	
	High	Cobble	2.66	1.92-3.38	Residual	0.48	
	Low	Cobble	3.54	2.62-4.39			
Macromiidae (3.4%)	High	Macrophyte-Soft	1.84	1.70-1.99	Year:Site	0.00	-0.03
	Low	Macrophyte-Soft	1.66	1.56-1.78	Site	0.00	
	High	Cobble	1.94	1.70-2.16	Residual	0.16	
	Low	Cobble	1.80	1.49-2.11			
Trichoptera (1.2%)	High	Macrophyte-Soft	2.67	2.34-3.04	Year:Site	0.14	0.01
	Low	Macrophyte-Soft	2.47	2.20-2.73	Site	0.00	
	High	Cobble	2.46	1.90-3.00	Residual	0.80	
	Low	Cobble	3.00	2.27-3.78			
Leptoceridae (84%)	High	Macrophyte-Soft	2.49	2.13-2.88	Year:Site	0.19	0.05
	Low	Macrophyte-Soft	2.28	1.99-2.58	Site	0.02	
	High	Cobble	2.40	1.82-2.95	Residual	0.68	
	Low	Cobble	2.95	2.25-3.72			

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[a]For orders, indicates percent (by number) of total invertebrates collected across all years. For

families, indicates the percent of the order collected across all years.

[b] Categorical variable indicating whether rusty crayfish relative abundance was high (>1 CPUE) or low (<1 CPUE).

[c] Restricted maximum likelihood (REML) estimate; data were modeled on natural log scale

[d] Generated from Markov Chain Monte Carlo resampling

[e] Calculated using the likelihood ratio method (Magee 1990; Kramer 2005)

[f] Random effects (i.e., varience compenents) were estimated for year nested within site (transect/depth combination), site, and residual (unexplained) error.

Appendix 7. Diet sample sizes (number of fish) for each species and year used in this analysis. BGS=bluegill sunfish, PKS=pumpkinseed sunfish, RKB=rock bass, SMB=smallmouth bass. One pumpkinseed diet was collected in 2001 but not used in this analysis.

	2001	**2002**	**2003**	**2004**	**2009**	**2010**	**Total**
BGS	0	0	0	0	28	44	72
PKS	0	0	0	0	22	33	56
RKB	101	98	59	80	90	75	517
SMB	121	107	84	87	132	101	661
Total	222	205	143	167	272	253	1306

CHAPTER 4

Variability in community interaction networks in two littoral habitats revealed by the experimental removal of an invasive crayfish

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To be submitted for publication with coauthors Luke Winslow and M. Jake Vander Zanden

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Abstract

Food web structure is critical in determining ecosystem responses to anthropogenic disturbances. Spatial variation in species interaction strengths can influence how communities respond to perturbation, but is seldom quantified due to the rigorous data requirements associated with quantitative food web models. We used experimental results of a whole-lake removal of invasive rusty crayfish (*Orconectes rusticus*) from a north temperate lake to inform qualitative models of species interactions. We simulated all possible qualitative community interaction networks from a base model including 32 trophic and non-trophic interactions. For each community matrix, we predicted the directional response of each species to the removal of rusty crayfish, and compared predictions to the observed response in two littoral habitat types. Of the 4.3 billion potential community structures, 0.07% and 0.003% were consistent with experimental results in cobble and macrophyte habitat, respectively. Direct interactions between rusty crayfish were more important in cobble than in macrophyte habitat. *Lepomis* spp. interacted strongly with multiple invertebrate prey in macrophyte habitat, and the indirect effects of rusty crayfish mediated through their effects on macrophytes were also important. The interactions most important for explaining changes in the littoral community varied among cobble and macrophyte habitats, highlighting the need to understand and quantify variability in

food web structure. This variability could be particularly important for understanding and managing species invasions, and should be a research priority.

Introduction

Predicting ecosystem responses to perturbation is among the central goals of ecology, particularly in the face of increasing anthropogenic disturbances (Tylianakis et al. 2008). Ecosystem responses to such disturbance in terms of changes in abundance of single species have been well-documented (Sala et al. 2000). However, species are embedded in communities and linked via networks of positive and negative interactions (i.e., food webs, or more generally, interaction webs; Lawton & Warren 1988; Paine 1988; Pimm *et al.* 1991; Polis 1991; Cohen *et al.* 1993). Food webs are remarkably complex, consisting of multiple direct and indirect pathways through which changes in one species may affect others (Polis 1994). This interaction structure is critical in determining how a system will respond to anthropogenic disturbance (Ives 1995; Wootton *et al.* 1996; Suttle *et al.* 2007; Harmon *et al.* 2009; O'Gorman *et al.* 2012). Indirect effects, whereby a species influences another via intermediary species or by changing the strength of interactions between two species (Wootton 1994) can lead to unexpected responses to perturbation (Yodzis 1988; Menge 1995; Abrams *et al.* 1996; Paine *et al.* 1998; White *et al.* 2006). Additionally, differential responses of species in a network to disturbance may lead to re-arrangement of community structure and alteration of interaction strengths (van der Putten *et al.* 2004; Tylianakis *et al.* 2008), further complicating efforts to predict responses to perturbations

Food webs vary in space and time (Holt 1996; Winemiller 1996; Holt 2002), even when composed of similar or identical species (Lane 1986; Montano-Moctezuma *et al.* 2007; Tylianakis *et al.* 2007; Montano-Moctezuma *et al.* 2008). Abiotic conditions such as habitat can influence trophic interactions (Menge & Sutherland 1987; Grabowski 2004; Winder & Schindler 2004; Snyder & Evans 2006; Warfe & Barmuta 2006), and habitat heterogeneity may allow coexistence between competitors or stabilize predator-prey interactions (Crowder & Cooper 1982; Holt 1984; Danielson 1991; Oksanen *et al.* 1992; McCann *et al.* 2005; Rooney *et al.* 2008). Because food web structure influences how ecosystems respond to perturbation, understanding this variation may shed insight into the differential responses of communities to anthropogenic disturbances (Winemiller & Polis 1996; Tylianakis *et al.* 2008). Yet spatial heterogeneity in food web structure and how it affects ecosystem responses to change has been given relatively little attention (Holt 1996; Winemiller 1996; van der Putten *et al.* 2004; McCann *et al.* 2005).

Species additions (via biotic invasions) and deletions (via extinction) represent major disturbances to ecosystems, and food web structure determines how these disturbances are propagated throughout the community (Pimm 1980; Pimm *et al.* 1991; Lodge 1993; Vander Zanden *et al.* 1999a; Schoener *et al.* 2002). Once established, invasive species can alter food web interactions and community structure through a variety of mechanisms (e.g., Beisner *et al.* 2003; Baxter *et al.* 2004; Byrnes *et al.* 2007). However, the impacts of invasive species impacts can be highly spatially variable (Williamson & Fitter 1996; Parker *et al.* 1999; Williamson 1999;

Kulhanek *et al.* 2011), and depend on the food web context into which they invade (Shea & Chesson 2002; Tylianakis *et al.* 2008).

In this study, we use a whole-lake experimental removal of an established invasive species to assess the relative importance of direct and indirect interactions between native and invasive species, and how they vary in different habitat types. The full extent of the impacts of invasive species, particularly in terms of their indirect effects, are sometimes only apparent following the removal of established invaders (Zavaleta *et al.* 2001; Bergstrom *et al.* 2009; Ramsey & Norbury 2009). We removed invasive rusty crayfish (*Orconectes rusticus*) from a north temperate lake where they had been established for over two decades. Rusty crayfish are invasive omnivores known to impact macrophytes (Lodge & Lorman 1987; Olsen *et al.* 1991; Rosenthal *et al.* 2006), benthic macroinvertebrates (Lodge *et al.* 1994; Wilson *et al.* 2004; McCarthy *et al.* 2006; Nilsson *et al.* 2012), and fishes (Wilson *et al.* 2004; Roth *et al.* 2007). Over the course of an eight year removal program, rusty crayfish densities declined by two orders of magnitude. The littoral community exhibited a strong response to this removal, and some responses were counterintuitive based simply on the direct effects of crayfish, the direction of response differed among habitat types for some species. Differences in food web structure among habitats could explain these differential responses, despite the same species being present in both habitats.

We use a qualitative modeling or “loop analysis” approach (Levins 1974; Puccia & Levins 1985; Dambacher *et al.* 2002, 2003) to assess the relative importance of community interactions, and how these interactions vary among littoral habitat types. We simulated all biologically plausible models for comparison with empirical data from the experimental rusty crayfish removal. The frequency of occurrence of interactions in models that could accurately predict the system response to perturbation was used as an indicator of the relative strength of that interaction in each habitat (Lane 1986; Montano-Moctezuma *et al.* 2007, 2008). Our objectives were to (1) identify important community interactions in littoral systems invaded by rusty crayfish; and (2) assess how food web structure varies across littoral habitat types. We first provide an overview of the qualitative modeling method and briefly describe the experimental removal, then describe the details of the current study. A full description of the experimental crayfish removal can be found in (Chapter 3).

Methods

Qualitative modeling overview

A community of *n* interacting species can be represented by a Lotka-Volterra system of differential equations. The population growth rate of each species is influenced by other species following the form:

$$\frac{1}{N_t}\frac{dN_t}{dt} = f_i(N_1, N_2, \dots, N_n),$$

where N_i is the population density of species *i*, and f_i is a function describing its per capita growth rate (Levins 1974; Yodzis 1988). The effect of a change in density of species *j* on the per capita growth rate of a population of species *i* is represented by a_{ij}, defined as the partial derivative of f_i with respect to N_j ($a_{ij} = \delta f_i / \delta N_j$) (Levins 1974; Berlow *et al.* 2004). Thus, an interaction web of *n* species in an ecological community can be represented as an *n* by *n* square matrix (**A**) where a_{ij} is the element in the i^{th} row and j^{th} column representing the effect of species *j* on the per capita growth rate of species *i* (Puccia & Levins 1985; Dambacher *et al.* 2002).

Often it is difficult to populate the A matrix with quantitative estimates of species interaction strengths, particularly for realistic interaction webs containing multiple species (Levins 1974). Even the basic structure of food webs in terms of who interacts with whom is sometimes unknown (Polis 1994). When interaction strengths can be measured they are subject to a high level of uncertainty, which can have major effects on the predictions generated from such a matrix even in such coarse terms as the sign of the response (Yodzis 1988). The difficulties associated with measuring interaction strengths is compounded when a research objective is to compare web structures across space and/or time (Lane 1986; Winemiller & Polis 1996).

One solution to these difficulties is to use a qualitative **A** matrix. Qualitative modeling of community interactions does not require detailed information regarding the strength of interactions between community members; rather, it relies on a matrix of community interactions (**A**) consisting of positive (1), negative (-1), and zero (0) interactions (Levins 1974; Puccia & Levins 1985). Qualitative interaction matrices can be visually represented by signed digraphs composed of positive interactions (→) and negative interactions (—●) between groups (Figure 1). This qualitative approach allows inclusion of variables and interactions hypothesized to be important in a community, even when precise measurements of interaction strength are not possible. While an oversimplification of an interaction web, qualitative models aim to gain insights into food web structure despite extremely high levels of uncertainty about interaction strength and model form (Levins 1974; Hulot *et al.* 2000).

Qualitative models can be used to predict the outcome of perturbations given a specified community matrix (Ramsey & Veltman 2005; Raymond *et al.* 2011). Sustained changes in the density of one community member, known as press perturbations (Bender et al. 1984), will affect other community members via both direct and indirect pathways. Depending on the net effect of these multiple pathways, each species will respond to a perturbation either positively, negatively, or not at all. In qualitative modeling, the effects at equilibrium of a press perturbation is represented by the negative inverse of the community matrix ($-\mathbf{A}^{-1}$) also known as the prediction matrix (Levins 1974; Bender *et al.* 1984; Puccia & Levins 1985; Dambacher *et al.* 2002). The prediction matrix represents the response of each species (rows) to changes in the abundance of each other species (columns).

Study system and experimental data

Rusty crayfish were experimentally removed from Sparkling Lake, Vilas County, WI, USA (46.008°, -89.701°). Sparkling lake is a 64 ha mesotrophic seepage lake with a maximum depth of 20 m, and is a study lake of the North Temperate Lakes Long Term Ecological Research (NTL-LTER) program, which has monitored physical, chemical, and biological variables since 1981 (http://lter.limnology.wisc.edu). Rusty crayfish invaded Sparkling Lake in the 1970's. A whole-lake manipulation was initiated in Sparkling Lake in 2001 (Hein *et al.* 2007); rusty crayfish were manually removed via trapping from 2001-2008, and monitoring trapping continued from 2008-

2011. Fishing regulations were also changed in 2001 with the intention of reducing angler harvest and increasing fish predation on juvenile crayfish (Hein *et al.* 2006). Macrophyte percent cover, benthic macroinvertebrate densities, fish populations, and fish diets were also monitored during the experimental removal. Responses of these groups were separated in two major littoral habitat types: cobble, and sandy/muck substrate which became dominated by macrophytes as the removal progressed (hereafter referred to as macrophyte habitat). Macrophytes were also present in cobble habitats, although at much lower abundance.

We grouped the littoral community into 10 groups of fishes, invertebrates, and plants, or "trophic species" (sensu Menge 1976), representing aggregate groups sharing common predators and prey (Table 1). The benthic macroinvertebrate orders (non-crayfish) included in this analysis compose 91% of sampled benthic invertebrates by number (the remaining 9% was composed of Bivalva, Coleoptera, Isopoda, and Megaloptera). We use as a metric of change in each trophic species the overall response of each group from years of high rusty crayfish abundance (2002-2003; catch rates $\geq$1 crayfish per trap per day) to years of low crayfish abundance (2008-2010; catch rates $<$ 1 crayfish per trap per day; Table2). Fish were not sampled in 2008 so the "low crayfish" years are 2009-2010 for both bass and *Lepomis* population estimates. The abundance of each trophic species was modeled on the natural log scale as a function of categorical rusty crayfish density (high or low), habitat (when applicable) and their interaction, and for some groups included random effects to account for non-independence among samples (See Table 2). The change in each group's abundance was quantified as the difference between the maximum-likelihood estimate of abundance in years of low and high crayfish abundance. For benthic macroinvertebrates, differences of less than 0.1 natural log units (less than 1 animal per m^2) were interpreted as no change. The qualitative responses in each habitat type (increase, decrease, or remain the same) were used as validation criteria to evaluate the plausibility of different food web structures using a qualitative modeling approach (described below).

Diets of littoral fishes were collected via gastric lavage bimonthly in the summers of 2001-2004 and 2009-2010. Diet composition of bass and *Lepomis* was characterized as the overall percent by number of each prey species used in this analysis, calculated across all diets in all years for rock bass and smallmouth bass, and bluegill and pumpkinseed sunfish, respectively.

Qualitative simulations

Analysis of community interaction webs can be complicated by structural uncertainty – that is, in some cases there may be interactions between species that could be potentially included or excluded from the model, and including or excluding interactions may fundamentally change model predictions (Lane 1986; Polis 1994; Montano-Moctezuma *et al.* 2007; Raymond *et al.* 2011). Qualitative simulations can be used to assess the relative importance of each interaction and are useful for making inferences about food web interactions when changes in species abundance resulting from a perturbation are known, but interactions between species are not (Montano-Moctezuma *et al.* 2007; Raymond *et al.* 2011). Qualitative simulations generate community matrices encompassing all possible combinations of a set of unknown interactions. The predicted responses to a press perturbation can then be calculated from the negative inverse of the community matrix (described above), and compared to known responses to experimental perturbations. Community matrices matching known outcomes are considered valid representations of the modeled community.

We used qualitative simulations to assess the relative importance of interactions between invasive rusty crayfish and invaded littoral communities in two habitat types. We constructed a base model (Figure 1) composed of 32 biologically plausible interactions between trophic species (see below), as well as negative self-dampening effects for each group (self-effects are not shown in Figure 1 for clarity). Self-dampening effects represent density-dependent population growth as a result of intra-group competition, as well as dependence on elements not included in the model, and were included in every simulated food web (Raymond *et al.* 2011). Linkages included in the base model were directional, that is, we specified whether a given interaction was positive or negative *a priori*. Interactions can be either unidirectional or bidirectional; that is, a_{ij} need not necessarily equal a_{ji} (Levins 1974). Due to the vast number of potential model structures in this study, if a predatory interaction was included, predators negatively affected prey and prey positively affected predators (a_{ij}=-a_{ji}), and if a competitive interaction was included, both species negatively influenced the other (a_{ij}=a_{ji}=-1).

We used the same base model for both littoral habitat types. The base model includes both trophic (predator-prey) and non-trophic (competitive, habitat, destructive) interactions (Figure 1), and represents an “interaction web”: a model of intermediate complexity representing interactions between groups suspected to be of importance in determining community structure (Polis 1991; Menge 1995). Although community matrix models are most commonly applied to networks of trophic interactions they are equally applicable to other non-consumptive interactions (Tylianakis *et al.* 2007; Raymond *et al.* 2011). We constrained our analysis to those most likely to influence community structure based on empirical diet data and published literature. We included predator-prey interactions between *Lepomis* and all invertebrate species (including rusty crayfish). All predator-prey interactions between bass and other animals were included with the exception of Gastropoda, which appeared in bass diets an order of magnitude less frequently than any other invertebrate prey (Chapter 3). Predator-prey interactions between rusty crayfish and invertebrate prey were included with the exception of Amphipoda, as crayfish generally consume less active invertebrate prey (Momot *et al.* 1978; Whitledge & Rabeni 1997). A negative interaction between rusty crayfish and macrophytes is well documented (Lodge & Lorman 1987; Lodge 1991; Olsen *et al.* 1991). Macrophytes provide critical habitat for *Lepomis* (Mittelbach 1981a; Crowder & Cooper 1982; Mittelbach 1984) and benthic macroinvertebrates (Rabe & Gibson 1984; Gregg & Rose 1985; Brown & Lodge 1993; Rennie & Jackson 2005), and positive interactions between macrophytes and these groups were included with the exception of Diptera, which in this system are primarily sediment dwellers (Merritt & Cummins 1996). Predator-prey relationships between Odonata, Diptera, Ephemeroptera, and Trichoptera were also included (Merritt & Cummins 1996). We included very few potential competitive interactions between trophic species. The negative self-effects included for each trophic species encompass intraspecies and intraorder competition, which is more common than interspecies (or interorder) competition (Connell 1983). However, we did include potential competitive interactions between Gastropoda, Ephemeroptera, and

Trichoptera, the three orders containing some scraper taxa most likely to compete for periphyton resources (Table 1).

A total of 4,294,967,296 (2^{32}) interaction webs representing all possible combinations of the 32 unknown interactions were possible. To assess the relative importance of each interaction, we followed the procedure outlined in Figure 2, similar to that used by Montaño-Moctezuma and colleagues (2007). For each model configuration, we first assessed the Lyapunov stability of the community matrix following the methods of Puccia and Levins (1985) and Dambacher (2003), and unstable models were discarded. The negative inverse of the community matrix was then calculated for stable models, and model predictions were validated against experimental data from both macrophyte and cobble habitats. Models whose predictions did not match either validation set were discarded. Stable models for which the direction of the predicted response of each community member to a sustained removal of rusty crayfish matched the observed responses in a given habitat were considered plausible representations of community interaction structure (hereafter “valid models”) for that habitat.

The relative importance of each interaction was assessed based on the percentage of valid models containing that interaction for each habitat (Montano-Moctezuma *et al.* 2007). Because each interaction was included in 50% of the full set of models, the null expectation is that any given interaction will be present in 50% of valid models. We used this 50% cutoff as an indicator of importance of an interaction. Interactions that were present in more than 50% of valid models for both habitats were considered to be a part of the “core model” (sensu Lane 1986); that is, these interactions produce the strongest outcomes in both littoral habitats. The co-occurrence of various interactions (e.g., the presence of a positive feedback between *Lepomis* and rusty crayfish) was tabulated and compared to the frequency expected from the full set of models.

Results

Removal experiment results

The experimental crayfish removal resulted in substantial changes in most trophic species which varied among habitats (Figure 3). Rusty crayfish abundance declined by two orders of magnitude over the course of the experimental removal. *Lepomis*, macrophyte cover, and Gastropoda increased in abundance, while Amphipoda and Ephemeroptera declined over the course of the crayfish removal in both habitats. Odonata and Trichoptera both increased in cobble and decreased in macrophytes, and Diptera decreased in macrophyte habitat, and remained virtually unchanged in cobble habitat (decline of <0.1 natural log units, or less than 1 animal·m^{-2}).

Qualitative simulations

Out of 4,294,967,296 possible interaction webs, 308,833 (0.072%) were valid for cobble habitat, and 12,673 (0.0030%) were valid for macrophyte habitat. No models were valid for both habitats, indicating that different interaction webs best describe the community in the two habitats.

The importance of each interaction in valid models differed in the two habitats (Table 3). In cobble, 15 of 32 interactions occurred in more than 50% of valid models (Figure 4). Only 3 interactions occurred in 75% or more of valid models: rusty crayfish destruction of macrophytes, *Lepomis* predation on Amphipoda, and Odonata predation on Ephemeropera. Rusty crayfish also interacted strongly with Bass, Trichoptera, and Gastropoda in cobble habitat. Use of macrophytes as habitat was critical for explaining the response of Gastropoda, Odonata, and Trichoptera in cobble habitat.

In macrophyte habitat, 13 of 32 interactions occurred in 50% or more of valid models (Table 3), and almost two-thirds of these (8) were present in 75% or more of valid models (Figure 5). Of these 8 highly frequent interactions, 5 were predator-prey interactions involving *Lepomis* and their prey. *Lepomis* interactions with bass and macrophytes also occurred in greater than 50% of valid models in macrophyte habitat. Additionally, rusty crayfish interactions with Gastropoda and macrophytes occurred in >75% of valid models, and as did macrophyte provision of habitat to Gastropoda.

Of the 32 potential interactions, 8 were present in >50% of valid models for both habitats, and these interactions compose the “core model” of interactions for the Sparkling Lake littoral community (Figure 6). *Lepomis* are involved in four of these core interactions, and rusty crayfish are directly connected to Gastropoda and Macrophytes.

Of all potential interactions between rusty crayfish and other littoral community members, 61% were present in cobble and 47% were present in macrophyte habitat. Of all potential interactions between *Lepomis* and other littoral community members, 52% were present in cobble and 69% were present in macrophyte habitat. All valid models in both habitats contained rusty crayfish destruction of macrophytes and *Lepomis* predation on Amphipoda. *Lepomis* predation on Diptera was present in 100% of valid models in macrophyte habitat, but in only 15% of valid models in cobble habitat. Competitive interactions between invertebrate species were rarely included in valid models, but were present almost twice as often in macrophyte (19%) than in cobble (10%).

The frequency of occurrence of a predator-prey relationship between *Lepomis* and their prey in valid models in macrophyte habitat was strongly related to the consumption of that prey species by *Lepomis* observed empirically (Figure 7A). There was no relationship between occurrence in valid models and diet composition for *Lepomis* in cobble or bass in either habitat type (Figure 7B-D).

Discussion

We used the results of a whole-lake manipulation of an invasive species combined with a qualitative modeling approach to infer the relative importance of community interactions in explaining the response of littoral species in two habitat types. The littoral community in Sparkling Lake can be represented by only a small fraction of the possible community structures evaluated in this study.

Variation in community structure in two habitat types

Despite being composed of the same trophic species, the structure of littoral communities differs in cobble and macrophyte habitat. The direct effects of rusty crayfish were generally less important in macrophyte habitat than in cobble, while direct interactions between *Lepomis* and invertebrate prey were common in macrophytes. However, by affecting macrophytes, rusty crayfish interact with every other trophic species via indirect effects in both habitat types. The multiple indirect pathways through which rusty crayfish are connected to their invertebrate prey and how these pathways vary among habitats could explain the inconsistent response of benthic macroinvertebrates to rusty crayfish invasion. In three whole-lake studies evaluating the effects of rusty crayfish on benthic invertebrates, rusty crayfish negatively affected Diptera, Ephemeroptera, and Odonata in one study (McCarthy *et al.* 2006), Amphipoda, Trichoptera, and Odonata in another (Diptera and Ephemeroptera were not affected, Wilson *et al*. 2004), and Amphipoda and Trichoptera in a third (again, Ephemeroptera and Diptera were not affected; Nilsson *et al.* 2012). Perhaps differences in interactions among species observed in this study translate to differences on larger scales (i.e., cross- lakes), and can explain the differential responses of most invertebrate taxa to rusty crayfish invasion. Our study demonstrates that in certain contexts, the indirect effects of rusty crayfish may outweigh direct effects, similar to what has been observed for other invasive species (White *et al.* 2006; Brown *et al.* 2011) .

Habitat heterogeneity can influence species interactions with dramatic ecosystem-level consequences (Paine 1966, 1971; Menge 1976; Menge & Sutherland 1987; Power 1992). Predation effectiveness varies with habitat complexity and structural heterogeneity allows persistence of vulnerable prey (Savino & Stein 1982; Diehl 1992; Closs *et al.* 1999; Corkum & Cronin 2004; Grabowski 2004; Warfe & Barmuta 2004; Rennie & Jackson 2005; Warfe & Barmuta 2006). Both cobble and macrophyte habitats provide habitat complexity, but the species likely to benefit from each habitat type differ. Rusty crayfish utilize cobble habitat preferentially to avoid predation by bass (Capelli & Magnuson 1983; Garvey *et al.* 1994; Kershner & Lodge 1995), and other non-crayfish invertebrates can obtain shelter from fish predation in cobble as well (Peckarsky 1979; Mittelbach 1981b; Brown & Lodge 1993; Free *et al.* 2009). However, invertebrate predators such as crayfish are effective predators in cobble (Momot *et al.* 1978; Hanson *et al.* 1990), and the direct predatory effects of rusty crayfish on benthic macroinvertebrates are strongest in cobble habitat, perhaps in part as a result of the aggregation of rusty crayfish in this habitat in order to avoid their own predators. *Lepomis* utilize macrophyte habitat preferentially to avoid predation by piscivorous fish such as bass, and the foraging efficiency of *Lepomis* on invertebrates is maximized at intermediate macrophyte densities ((Mittelbach 1981a; Crowder & Cooper 1982; Mittelbach 1984, 1988). The strong predatory effects of *Lepomis* in macrophytes are thus consistent with their life history.

Consistently important interactions

Several interactions were present in more than 50% of valid models in both habitats. These core interactions are certainly not the only interactions occurring in nature, but are likely to be critical in determining the community response to perturbation and perhaps are the interactions consistently important in other locations (Lane 1986). The core model of the Sparkling Lake community indicates that *Lepomis* are important interactors, exerting predation pressure on Amphipoda, Ephemeroptera, and Gastropoda. Invasive rusty crayfish interact directly only with macrophytes and Gastropoda in the core model, and these are the trophic groups most consistently and dramatically affected by rusty crayfish invasions (Lodge 1991; Olsen *et al.* 1991; Lodge *et al.* 1994; Wilson *et al.* 2004). Interestingly, rusty crayfish negatively affect Gastropoda directly via predation and indirectly via macrophyte destruction, and Gastropoda are the only group in our model for which rusty crayfish would produce this double negative effect, which perhaps explains the consistent negative response of Gastropoda to rusty crayfish invasions.

Lepomis are strong interactors in the Sparkling Lake littoral community and can dampen the effects of rusty crayfish. It has been proposed that positive feedbacks between rusty crayfish, macrophytes, and *Lepomis* can result in alternative stable states following rusty crayfish establishment: one state where rusty crayfish achieve high densities, and another where *Lepomis* dominate and rusty crayfish densities remain low (Roth *et al.* 2007). Based on this analysis, rusty crayfish consistently negatively affect *Lepomis* indirectly via their destruction of macrophytes in both habitat types. However, the positive feedback between *Lepomis* and rusty crayfish was more variable, and present more often in cobble. While *Lepomis* are likely important in determining the impacts of rusty crayfish invasions, their effectiveness in influencing rusty crayfish abundance depends on the presence or absence of other community interactions.

The importance of *Lepomis* predatory interactions in structuring the Sparkling Lake littoral community is corroborated by the correlation between empirical diet data and the relative importance of predatory effects of *Lepomis* in valid models (Figure 7). Prey items that constitute a large portion of *Lepomis* diets are also affected directly by *Lepomis* in the majority of community models in macrophyte habitat. *Lepomis* exert little dynamic control over prey in cobble. Because we used whole-lake estimates of *Lepomis* population and diet composition, this discrepancy is likely a result of *Lepomis* foraging mainly in macrophytes (Mittelbach 1981a; Crowder & Cooper 1982; Mittelbach 1984; Osenberg & Mittelbach 1996). In contrast, prey items constituting a large proportion of bass diets do not experience strong dynamic interactions with bass based on our modeling approach. Energetic importance of prey to predators (i.e., high representation in diets) is often not indicative of dynamic importance of predators to prey (i.e., predator control of prey abundance), and comparing the two types of trophic interactions can provide insight into the ways in which food web interactions relate to population and community dynamics (Pimm *et al.* 1991; Polis 1994; Closs *et al.* 1999; Solomon *et al.* 2010) . This coupling of energetic and trophic importance for *Lepomis* but not bass could be due to the fact that prey are ill-adapted for dealing with *Lepomis* predation. The morphologies of prey can change due to phenotypic plasticity in response to predation risk; for example, the shell morphology of Physid snails ranges between relatively long, spired shells when crayfish predation risk is high, and shorter, fatter shells when *Lepomis* predation is high (DeWitt *et al.* 2000). When multiple potential predators are present, as is the case in the Sparkling Lake littoral community, prey phenotype adapts in response to the riskiest predator

(Relyea 2003). Prior to the rusty crayfish removal, *Lepomis* predation posed little risk due to extremely low (virtually undetectable) numbers (see Chapter 3). The strong dynamic control of *Lepomis* could be a transient result of prey adapted to predation pressures exerted by rusty crayfish and/or bass, but not *Lepomis* (Osenberg & Mittelbach 1996).

Although the model results provide a biologically plausible depiction of community structure, some results were surprising. Both bass and *Lepomis* are larger and more mobile than other trophic species included in this analysis. Because they can move between the two habitats more easily than the other species, they can serve as links between spatially heterogenous environments, and are predicted to be important in determining community composition (McCann *et al.* 2005; Rooney *et al.* 2008). Although our models revealed strong interactions between bass and some of their prey, these interactions were not consistent among the two habitat types. Of all trophic groups included in this analysis, bass are the longest lived and therefore the least likely to meet assumptions of equilibrium implicit in community models of press perturbations and required for the full influence of indirect effects to be apparent (Bender *et al.* 1984; Yodzis 1988; Menge 1997). The bass results should therefore be interpreted with caution.

Theory predicts that species with the greatest impacts on other species in the community will be most buffered from change in terms of their population density (Ives 1995). *Lepomis* were the strongest interactors based on qualitative modeling results, but *Lepomis* populations responded dramatically to the experimental removal of rusty crayfish in Sparkling Lake and can be dramatically affected by rusty crayfish invasions (Wilson *et al.* 2004; Roth *et al.* 2007).

Similar lack of correspondence between theoretical predictions and experimental results were observed for zooplankton responses to manipulations of planktivorous fishes , and could be a result of lack of ecological distinctiveness of strongly interacting species (Ives *et al.* 1999). Despite interacting strongly with many invertebrate prey, each of those prey are subject to predation by two to three other predators included in our model. Thus, similarity to other species in their community role may overwhelm the buffering effect provided by being a strongly interacting species (Ives *et al.* 1999).

The qualitative modeling approach: caveats and utility for applied problems

The qualitative approach used in this study allowed the identification of strong interactions among community members in an invaded community. However, interpreting the results requires several caveats. Even though we used a rigorous simulation approach to assess a vast number of alternative model configurations, our results were constrained by our definition of the system and potential interactions. So, for example, we found that rusty crayfish negatively affect macrophytes in 100% of valid models, but since models were constrained to predict an increase in macrophytes and rusty crayfish were the only possible negative influence (beyond self dampening effects), this is an inevitable result of our base model structure and experimental validation criteria. Even if we had included all possible combinations of uncoupled interactions in any direction for all species pairs and self-effects (resulting in $9^{n(n-1)/2} \cdot 3^n = 5x10^{47}$ possible interaction matrices in all; Lane 1986), our results would still be constrained by the species we chose to include and how we chose to aggregate them.

Consistency between predictions from community matrices and experimental results does not imply that we have accurately specified community structure (Bender *et al.* 1984). It is certain that all trophic species included in this analysis are affected by other forces not included here, and our model cannot rule out alternative interpretations of experimental results. However, complete and accurate specification of all relevant interactions for any food web is an arduous (perhaps impossible) task, particularly when examined on relevant (i.e., whole system) scales (Bender *et al.* 1984; Polis 1991, 1994; Berlow *et al.* 2004). In truth, all food web models are simplifications of reality and are aggregated at some level (e.g., individuals, genotypes, ages aggregated within a species; Polis 1994). As a result of the difficulties associated with quantification of food web interactions, much of our understanding of food web properties comes from model systems (e.g., May 1972; Pimm 1980; Pimm *et al.* 1991; Cohen *et al.* 1993; McCann *et al.* 1998), or very simple food chains/webs (e.g.,Hairston *et al.* 1960; Oksanen 1991; Abrams 1992; Hulot *et al.* 2000), neither of which are necessarily accurate portrayals of empirical realities (Polis 1991, 1994; Polis & Strong 1996; Vander Zanden *et al.* 1999b; Montoya & Sole 2003; Berlow *et al.* 2004) but both of which have contributed valuable insight to the ecological interactions governing real systems.

The strength of qualitative models is in their generality (Levins 1966), and the fact that alternative hypotheses regarding community structure can be rapidly generated and evaluated using experimental results (Dambacher *et al.* 2002). The value of the qualitative approach used here is particularly evident in the context of understanding the impacts of strong drivers of global change such as invasive species. Invasive species are a major driver of biodiversity loss and economic harm, particularly in aquatic systems (Ricciardi & Rasmussen 1999; Sala *et al.* 2000). Improved knowledge of food web structure could improve invasive species management efforts. (e.g., Bergstrom *et al.* 2009; Ramsey & Norbury 2009), as species interactions may determine the likelihood of establishment or impact of an invasive species (Vander Zanden *et al.* 1999a; Shea & Chesson 2002; Harvey & Kareiva 2005). However, incorporation of community interactions into management decisions can be burdensome due to high data demands (Hilborn 1992). Researchers are unlikely to identify all interactions between invasive species and invaded communities, much less quantify them, when species invade a novel ecosystem. Even less likely is quantification of the variability of these interactions across space and time, despite the knowledge that such variation is likely to be common and important (Winemiller 1996; Holt 2002) . Even coarse knowledge of species interaction webs across different locations could shed insight into the variable effects of invasive species, potentially improving efforts to predict the vulnerability of systems to the negative influence of invasive species and direct prevention efforts (e.g., Peterson & Vieglais 2001).

When the risks of inaction are high, it may be irresponsible to wait until all potential interactions have been quantified before making decisions (Hansen & Jones 2008). Qualitative approaches to specifying community interactions can shed insight into important community interactions in the absence of perfect information. Few studies have examined food web structure across gradients, despite the importance of understanding this variation for the conservation of biodiversity and understanding responses to perturbation (McCann 2007). Understanding variation in community interactions is one of the most critical challenges currently facing ecologists in order to better understand the consequences of this variation for provision of ecosystem services and maintenance of biodiversity under ever increasing levels of anthropogenic disturbance (van der Putten *et al.* 2004; Tylianakis *et al.* 2008).

Literature Cited

Abrams P.A. (1992). Predators that Benefit Prey and Prey that Harm Predators: Unusual Effects of Interacting Foraging Adaptation. *The American Naturalist*, 140, 573.

Abrams P.A., Menge B.A., Mittelbach G.G., Spiller D.A. & Yodzis P. (1996). The Role of Indirect Effects in Food Webs. In: *Food Webs: Integration of Patterns and Dynamics* (eds. Polis GA & Winemiller KO). Chapman and Hall New York, pp. 371-395.

Baxter C.V., Fausch K.D., Murakami M. & Chapman P.L. (2004). Fish invasion restructures stream and forest food webs by interrupting reciprocal prey subsidies. *Ecology*, 85, 2656.

Becker G.C. (1983). *Fishes of Wisconsin.* University of Wisconsin Press, Madison, WI.

Beisner B.E., Ives A.R. & Carpenter S.R. (2003). The effects of an exotic fish invasion on the prey communities of two lakes. *Journal of Animal Ecology*, 72, 331.

Bender E.A., Case T.J. & Gilpin M.E. (1984). Perturbation Experiments in Community Ecology: Theory and Practice. *Ecology*, 65, 1.

Bergstrom D.M., Lucieer A., Kiefer K., Wasley J., Belbin L., Pedersen T.K. & Chown S.L. (2009). Indirect effects of invasive species removal devastate World Heritage Island. *J. Appl. Ecol.*, 46, 73.

Berlow E.L., Neutel A.M., Cohen J.E., De Ruiter P.C., Ebenman B., Emmerson M., Fox J.W., Jansen V.A.A., Iwan Jones J., Kokkoris G.D., Logofet D.O., McKane A.J., Montoya J.M. & Petchey O. (2004). Interaction strengths in food webs: issues and opportunities. *Journal of Animal Ecology*, 73, 585.

Brown G.P., Phillips B.L. & Shine R. (2011). The ecological impact of invasive cane toads on tropical snakes: Field data do not support laboratory-based predictions. *Ecology*, 92, 422-431.

Brown K.M. & Lodge D.M. (1993). Gastropod Abundance in Vegetated Habitats: The Importance of Specifying Null Models. *Limnol. Oceanogr.*, 38, 217.

Byrnes J.E., Reynolds P.L. & Stachowicz J.J. (2007). Invasions and Extinctions Reshape Coastal Marine Food Webs. *PLoS ONE*, 2, e295.

Capelli G.M. (1980). Seasonal Variation in the Food Habits of the Crayfish Orconectes Propinquus (Girard) in Trout Lake, Vilas County, Wisconsin, U.S.a. (Decapoda, Astacidea, Cambaridae). *Crustaceana*, 38, 82-86.

Capelli G.M. & Magnuson J.J. (1983). Morphoedaphic and Biogeographic Analysis of Crayfish Distribution in Northern Wisconsin. *J. Crustacean Biol.*, 3, 548-564.

Closs G.P., Balcombe S.R., Shirley M.J. & Raffaelli A.H.F.a.D. (1999). Generalist Predators, Interaction Strength and Food-web Stability. In: *Advances in Ecological Research*. Academic Press, p. 93.

Cohen J.E., Beaver R.A., Cousins S.H., DeAngelis D.L., Goldwasser L., Heong K.L., Holt R.D., Kohn A.J., Lawton J.H., Martinez N., O'Malley R., Page L.M., Patten B.C., Pimm S.L., Polis G.A., RejmÃ¡nek M., Schoener T.W., Schoenly K., Sprules W.G., Teal J.M., Ulanowicz R.E., Warren P.H., Wilbur H.M. & Yodzis P. (1993). Improving Food Webs. *Ecology*, 74, 252.

Connell J.H. (1983). On the Prevalence and Relative Importance of Interspecific Competition: Evidence from Field Experiments. *The American Naturalist*, 122, 661.

Corkum L. & Cronin D. (2004). Habitat complexity reduces aggression and enhances consumption in crayfish. *Journal of Ethology*, 22, 23.

Crowder L.B. & Cooper W.E. (1982). Habitat Structural Complexity and the Interaction Between Bluegills and Their Prey. *Ecology*, 63, 1802-1813.

Dambacher J.M., Li H.W. & Rossignol P.A. (2002). Relevance of community structure in assessing indeterminacy of ecologcial predictions. *Ecology*, 83, 1372-1385.

Dambacher J.M., Li H.W. & Rossignol P.A. (2003). Qualitative predictions in model ecosystems. *Ecol. Model.*, 161, 79-93.

Danielson B.J. (1991). Communities in a Landscape: The Influence of Habitat Heterogeneity on the Interactions between Species. *The American Naturalist*, 138, 1105.

DeWitt T.J., Robinson B.W. & Wilson D.S. (2000). Functional diversity among predators of a freshwater snail imposes an adaptive trade-off for shell morphology. *Evolutionary Ecology Research*, 2, 129.

Diehl S. (1992). Fish Predation and Benthic Community Structure: The Role of Omnivory and Habitat Complexity. *Ecology*, 73, 1646-1661.

Free G., Solimini A., Rossaro B., Marziali L., Giacchini R., Paracchini B., Ghiani M., Vaccaro S., Gawlik B., Fresner R., Santner G., Schönhuber M. & Cardoso A. (2009). Modelling lake macroinvertebrate species in the shallow sublittoral: relative roles of habitat, lake morphology, aquatic chemistry and sediment composition. *Hydrobiologia*, 633, 123.

Garvey J.E., Stein R.A. & Thomas H.M. (1994). Assessing How Fish Predation and Interspecific Prey Competition Influence a Crayfish Assemblage. *Ecology*, 75, 532-547.

Grabowski J.H. (2004). Habitat complexity disrupts predator-prey interactions but not the trophic cascade on oyster reefs. *Ecology*, 85, 995.

Gregg W.W. & Rose F.L. (1985). Influences of aquatic macrophytes on invertebrate community structure, guild structure, and microdistribution in streams. *Hydrobiologia*, 128, 45.

Hairston N.G., Smith F.E. & Slobodkin L.B. (1960). Community Structure, Population Control, and Competition. *American Naturalist*, 94, 421-425.

Hansen G.J.A. & Jones M.L. (2008). The value of information in fishery management. *Fisheries*, 33.

Hanson J.M., Chambers P.A. & Prepas E.E. (1990). Selective foraging by the crayfish Orconectes virilis and its impact on macroinvertebrates. *Freshwater Biol.*, 24, 69.

Harmon J.P., Moran N.A. & Ives A.R. (2009). Species Response to Environmental Change: Impacts of Food Web Interactions and Evolution. *Science*, 323, 1347.

Harvey C.J. & Kareiva P.M. (2005). Community context and the influence of non-indigenous species on juvenile salmon survival in a Columbia River reservoir. *Biol. Invasions*, 7, 651.

Hein C.L., Roth B.M., Ives A.R. & Vander Zanden M.J. (2006). Fish predation and trapping for rusty crayfish (*Orconectes rusticus*) control: a whole-lake experiment. *Can. J. Fish. Aquat. Sci.*, 63, 383–393.

Hein C.L., Vander Zanden M.J. & Magnuson J.J. (2007). Intensive trapping and increased fish predation cause massive population decline of an invasive crayfish. *Freshwater Biol.*, 52, 1134-1146.

Hilborn R. (1992). Current and future trends in fisheries stock assessment and management. *South African Journal of Marine Science*, 12, 975-988.

Holt R.D. (1984). Spatial heterogeneity, indirect interactions, and the coexistence of prey species. *American Naturalist*, 377-406.

Holt R.D. (1996). Food Webs in Space: An Island Biogeographic Perspective. In: *Food Webs: Integration of Patterns and Dynamics*. Chapman & Hall Press New York, pp. 313-323.

Holt R.D. (2002). Food webs in space: on the interplay of dynamic instability and spatial processes. *Ecological Research*, 17, 261.

Hulot F.D., Lacroix G., Lescher-Moutoue F. & Loreau M. (2000). Functional diversity governs ecosystem response to nutrient enrichment. *Nature*, 405, 340.

Ives A.R. (1995). Predicting the Response of Populations to Environmental Change. *Ecology*, 76, 926.

Ives A.R., Carpenter S.R. & Dennis B. (1999). COMMUNITY INTERACTION WEBS AND ZOOPLANKTON RESPONSES TO PLANKTIVORY MANIPULATIONS. *Ecology*, 80, 1405.

Kershner M.W. & Lodge D.M. (1995). Effects of littoral habitat and fish predation on the distribution of an exotic crayfish, Orconectes rusticus. *J. N. Am. Benthol. Soc.*, 14, 414–422.

Kulhanek S.A., Leung B. & Ricciardi A. (2011). Using ecological niche models to predict the abundance and impact of invasive species: application to the common carp. *Ecol. App.*, 21, 203-213.

Lane P.A. (1986). Symmetry, Change, Perturbation, and Observation Mode in Natural Communities. *Ecology*, 67, 223.

Lawton J.H. & Warren P.H. (1988). Static and dynamic explanations for patterns in food webs. *Trends Ecol. Evol.*, 3, 242.

Levins R. (1966). The strategy of model building in population biology. *Am. Sci.*, 54, 421-431.

Levins R. (1974). The qualitative analysis of partially specified systems. *Ann. N. Y. Acad. Sci.*, 231, 123-138.

Lodge D.M. (1991). Herbivory on freshwater macrophytes. *Aquatic Botany*, 41, 195.

Lodge D.M. (1993). Species invasions and deletions: community effects and responses to climate and habitat change. In: *Biotic Interactions and Global Change* (eds. Kareiva PM, Kingsolver JG & Huey RB). Sinauer Associates Inc. Sunderland, MA, pp. 367-387.

Lodge D.M., Kershner M.W., Aloi J.E. & Covich A.P. (1994). Effects of an omnivorous crayfish (*Orconectes rusticus*) on a freshwater littoral food web. *Ecology*, 75, 1265–1281.

Lodge D.M. & Lorman J.G. (1987). Reductions in submersed macrophyte biomass and species richness by the crayfish *Orconectes rusticus*. *Can. J. Fish. Aquat. Sci.*, 44, 591-597.

May R.M. (1972). Will a Large Complex System be Stable? *Nature*, 238, 413.

McCann K. (2007). Protecting biostructure. *Nature*, 446, 29.

McCann K., Hastings A. & Huxel G.R. (1998). Weak trophic interactions and the balance of nature. *Nature*, 395, 794.

McCann K.S., Rasmussen J.B. & Umbanhowar J. (2005). The dynamics of spatially coupled food webs. *Ecol. Lett.*, 8, 513-523.

McCarthy J.M., Hein C.L., Olden J.D. & Jake Vander Zanden M. (2006). Coupling long-term studies with meta-analysis to investigate impacts of non-native crayfish on zoobenthic communities. *Freshwater Biol.*, 51, 224–235.

Menge B.A. (1976). Organization of the New England Rocky Intertidal Community: Role of Predation, Competition, and Environmental Heterogeneity. *Ecol. Monogr.*, 46, 355-393.

Menge B.A. (1995). Indirect Effects in Marine Rocky Intertidal Interaction Webs: Patterns and Importance. *Ecol. Monogr.*, 65, 21.

Menge B.A. (1997). Dection of Direct Versus Indirect Effects: Were Experiments Long Enough? *The American Naturalist*, 149, 801.

Menge B.A. & Sutherland J.P. (1987). Community Regulation: Variation in Disturbance, Competition, and Predation in Relation to Environmental Stress and Recruitment. *The American Naturalist*, 130, 730-757.

Merritt R.W. & Cummins K.W. (1996). *An Introduction to the Aquatic Insects of North America*. Third edn. Kendall/Hunt Publishing Company, Dubuque, IA.

Mittelbach G.G. (1981a). Foraging Efficiency and Body Size: A Study of Optimal Diet and Habitat Use by Bluegills. *Ecology*, 62, 1370.

Mittelbach G.G. (1981b). Patterns of invertebrate size and abundance in aquatic habitats. *Can. J. Fish. Aquat. Sci.*, 38, 896.

Mittelbach G.G. (1984). Predation and Resource Partitioning in Two Sunfishes (Centrarchidae). *Ecology*, 65, 499.

Mittelbach G.G. (1988). Competition Among Refuging Sunfishes and Effects of Fish Density on Littoral Zone Invertebrates. *Ecology*, 69, 614.

Momot W.T., Gowing H. & Jones P.D. (1978). The Dynamics of Crayfish and Their Role in Ecosystems. *American Midland Naturalist*, 99, 10.

Montano-Moctezuma G., Li H.W. & Rossignol P.A. (2007). Alternative community structures in a kelp-urchin community: A qualitative modeling approach. *Ecol. Model.*, 205, 343-354.

Montano-Moctezuma G., Li H.W. & Rossignol P.A. (2008). Variability of community interaction networks in marine reserves and adjacent exploited areas. *Fisheries Research*, 94, 99-108.

Montoya J.M. & Sole R.V. (2003). Topological properties of food webs: from real data to community assembly models. *Oikos*, 102, 614.

Nilsson E., Solomon C.T., Wilson K.A., Willis T.V., Larget B. & Vander Zanden M.J. (2012). Effects of an invasive crayfish on trophic relationships in north temperate lake food webs. *Freshwater Biol.*, 57, 10.

O'Gorman E.J., Fitch J.E. & Crowe T.P. (2012). Multiple anthropogenic stressors and the structural properties of food webs. *Ecology*, 93, 441.

Oksanen L. (1991). Trophic levels and trophic dynamics: A consensus emerging? *Trends Ecol. Evol.*, 6, 58.

Oksanen T., Oksanen L. & Gyllenberg M. (1992). Exploitation ecosystems in heterogeneous habitat complexes II: impact of small-scale heterogeneity on predator-prey dynamics. *Evolutionary Ecology*, 6, 383.

Olsen T.M., Lodge D.M., Capelli G.M. & Houlihan R.J. (1991). Mechanisms of impact of an introduced crayfish (*Orconectes rusticus*) on littoral congeners, snails, and macrophytes. *Can. J. Fish. Aquat. Sci.*, 48, 1853-1861.

Osenberg C.W. & Mittelbach G.G. (1996). The relative importance of resource limitation and predator limitation in food chains. *Food webs: integration of patterns and dynamics. Chapman and Hall, New York, New York, USA*, 134.

Paine R.T. (1966). Food web complexity and species diversity. *American Naturalist*, 100, 65-75.

Paine R.T. (1971). A short-term experimental investigation of resource partitioning in a New Zealand rocky intertidal habitat. *Ecology*, 52, 1096.

Paine R.T. (1988). Road Maps of Interactions or Grist for Theoretical Development? *Ecology*, 69, 1648.

Paine R.T., Tegner M.J. & Johnson E.A. (1998). Compounded Perturbations Yield Ecological Surprises. *Ecosystems*, 1, 535.

Parker I.M., Simberloff D., Lonsdale W.M., Goodell K., Wonham M., Kareiva P.M., Williamson M.H., Von Holle B., Moyle P.B., Byers J.E. & others (1999). Impact: toward a framework for understanding the ecological effects of invaders. *Biol. Invasions*, 1, 3-19.

Peckarsky B.L. (1979). Biological Interactions as Determinants of Distributions of Benthic Invertebrates Within the Substrate of Stony Streams. *Limnol. Oceanogr.*, 24, 59.

Peterson A.T. & Vieglais D.A. (2001). Predicting Species Invasions Using Ecological Niche Modeling: New Approaches from Bioinformatics Attack a Pressing Problem. *Bioscience*, 51, 363-371.

Pimm S.L. (1980). Food web design and the effect of species deletion. *Oikos*, 35, 139-149.

Pimm S.L., Lawton J.H. & Cohen J.E. (1991). Food web patterns and their consequences. *Nature*, 350, 669-674.

Polis G.A. (1991). Complex Trophic Interactions in Deserts: An Empirical Critique of Food-Web Theory. *The American Naturalist*, 138, 123.

Polis G.A. (1994). Food webs, trophic cascades and community structure. *Aust. J. Ecol.*, 19, 121.

Polis G.A. & Strong D.R. (1996). Food web complexity and community dynamics. *American Naturalist*, 147, 813-846.

Power M.E. (1992). Habitat Heterogeneity and The Functional Signifiance of Fish in River Food Webs. *Ecology*, 1675-1688.

Puccia C.J. & Levins R. (1985). *Qualitative Modeling of Complex Systems*. Harvard University Press, Cambridge, MA.

Rabe F.W. & Gibson F. (1984). The Effect of Macrophyte Removal on the Distribution of Selected invertebrates in a Littoral Environment. *Journal of Freshwater Ecology*, 2, 359.

Ramsey D. & Veltman C. (2005). Predicting the effects of perturbations on ecological communities: what can qualitative models offer? *Journal of Animal Ecology*, 74, 905.

Ramsey D.S.L. & Norbury G.L. (2009). Predicting the unexpected: using a qualitative model of a New Zealand dryland ecosystem to anticipate pest management outcomes, Predicting the unexpected: using a qualitative model of a New Zealand dryland ecosystem to anticipate pest management outcomes. *Austral Ecology*, 34, 409-421.

Raymond B., McInnes J., Dambacher J.M., Way S. & Bergstrom D.M. (2011). Qualitative modelling of invasive species eradication on subantarctic Macquarie Island. *J. Appl. Ecol.*, 48, 181-191.

Relyea R.A. (2003). HOW PREY RESPOND TO COMBINED PREDATORS: A REVIEW AND AN EMPIRICAL TEST. *Ecology*, 84, 1827.

Rennie M.D. & Jackson L.J. (2005). The influence of habitat complexity on littoral invertebrate distributions: patterns differ in shallow prairie lakes with and without fish. *Canadian Journal of Fisheries & Aquatic Sciences*, 62, 2088.

Ricciardi A. & Rasmussen J.B. (1999). Extinction Rates of North American Freshwater Fauna. *Conserv. Biol.*, 13, 1220-1222.

Rooney N., McCann K.S. & Moore J.C. (2008). A landscape theory for food web architecture. *Ecol. Lett.*, 11, 867-881.

Rosenthal S.K., Stevens S.S. & Lodge D.M. (2006). Whole-lake effects of invasive crayfish (*Orconectes* spp.) and the potential for restoration. *Canadian Journal of Fisheries & Aquatic Sciences*, 63, 1276-1285.

Roth B.M., Hein C.L. & Vander Zanden M.J. (2006). Using bioenergetics and stable isotopes to assess the trophic role of rusty crayfish (Orconectes rusticus) in lake littoral zones. *Can. J. Fish. Aquat. Sci.*, 63, 335–344.

Roth B.M., Tetzlaff J.C., Alexander M.L. & Kitchell J.F. (2007). Reciprocal relationships between exotic rusty crayfish, macrophytes, and Lepomis species in northern Wisconsin lakes. *Ecosystems*, 10, 75–86.

Sala O.E., Chapin Iii F.S., Armesto J.J., Berlow E., Bloomfield J., Dirzo R., Huber-Sanwald E., Huenneke L.F., Jackson R.B., Kinzig A. & others (2000). Global biodiversity scenarios for the year 2100. *Science*, 287, 1770-1774.

Savino J.F. & Stein R.A. (1982). Predator-Prey Interaction between Largemouth Bass and Bluegills as Influenced by Simulated, Submersed Vegetation. *Transactions of the American Fisheries Society*, 111, 255-266.

Schoener T.W., Spiller D.A. & Losos J.B. (2002). Predation on a common Anolis lizard: can the food-web effects of a devastating predator be reversed? *Ecol. Monogr.*, 72, 383.

Shea K. & Chesson P. (2002). Community ecology theory as a framework for biological invasions. *Trends Ecol. Evol.*, 17, 170-176.

Snyder W.E. & Evans E.W. (2006). Ecological Effects of Invasive Arthropod Generalist Predators. *Annual Review of Ecology, Evolution, and Systematics*, 37, 95-122.

Solomon C.T., Roth B.M., Hrabik T.R. & Vander Zanden M.J. (2010). Comparing energetic and dynamic descriptions of a single food web linkage. *Oikos*, 120, 194.

Strong D.R. (1972). Life History Variation Among Populations of an Amphipod (Hyalella Azteca). *Ecology*, 53, 1103.

Suttle K.B., Thomsen M.A. & Power M.E. (2007). Species interactions reverse grassland responses to changing climate. *Science*, 315, 640-642.

Thorp J.H. & Covich A.P. (2010). *Ecology and Classification of North American Freshwater Invertebrates*. Third edn. Elsevier, Boston, MA.

Tylianakis J.M., Didham R.K., Bascompte J. & Wardle D.A. (2008). Global change and species interactions in terrestrial ecosystems. *Ecol. Lett.*, 11, 1351-1363.

Tylianakis J.M., Tscharntke T. & Lewis O.T. (2007). Habitat modification alters the structure of tropical host-parasitoid food webs. *Nature*, 445, 202.

van der Putten W.H., de Ruiter P.C., Martijn Bezemer T., Harvey J.A., Wassen M. & Wolters V. (2004). Trophic interactions in a changing world. *Basic and Applied Ecology*, 5, 487.

Vander Zanden M.J., Casselman J.M. & Rasmussen J.B. (1999a). Stable isotope evidence for the food web consequences of species invasions in lakes. *Nature*, 401, 464-467.

Vander Zanden M.J., Shuter B.J., Lester N. & Rasmussen J.B. (1999b). Patterns of Food Chain Length in Lakes: A Stable Isotope Study. *The American Naturalist*, 154, 406.

Warfe D. & Barmuta L. (2006). Habitat structural complexity mediates food web dynamics in a freshwater macrophyte community. *Oecologia*, 150, 141-154.

Warfe D.M. & Barmuta L.A. (2004). Habitat structural complexity mediates the foraging success of multiple predator species. *Oecologia*, 141, 171.

White E.M., Wilson J.C. & Clarke A.R. (2006). Biotic indirect effects: a neglected concept in invasion biology. *Diversity& Distributions*, 12, 443-455.

Whitledge G.W. & Rabeni C.F. (1997). Energy sources and ecological role of crayfishes in an Ozark stream: insights from stable isotopes and gut analysis. *Can. J. Fish. Aquat. Sci.*, 54, 2555-2563.

Williamson M. (1999). Invasions. *Ecography*, 22, 5.

Williamson M. & Fitter A. (1996). The varying success of invaders. *Ecology*, 77, 1661-1666.

Wilson K.A., Magnuson J.J., Lodge D.M., Hill A.M., Kratz T.K., Perry W.L. & Willis T.V. (2004). A long-term rusty crayfish (Orconectes rusticus) invasion: dispersal patterns and community change in a north temperate lake. *Can. J. Fish. Aquat. Sci.*, 61, 2255–2266.

Winder M. & Schindler D.E. (2004). Climate change uncouples trophic interactions in an aquatic ecosystem. *Ecology*, 85, 2100-2106.

Winemiller K.O. (1996). Factors driving temporal and spatial variation in aquatic floodplain food webs. In: *Food Webs: Integration of Patterns and Dynamics* (eds. Polis GA & Winemiller KO). Chapman & Hall Press New York, pp. 298-312.

Winemiller K.O. & Polis G.A. (1996). Food Webs: What Can They Tell Us About the World? In: *Food Webs: Integration of Patterns and Dynamics* (eds. Polis GA & Winemiller KO). Chapman and Hall New York, pp. 1-22.

Wootton J.T. (1994). Predicting Direct and Indirect Effects: An Integrated Approach Using Experiments and Path Analysis. *Ecology*, 75, 151.

Wootton J.T., Parker M.S. & Power M.E. (1996). Effects of Disturbance on River Food Webs. *Science*, 273, 1558.

Yodzis P. (1988). The Indeterminacy of Ecological Interactions as Perceived Through Perturbation Experiments. *Ecology*, 69, 508.

Zavaleta E.S., Hobbs R.J. & Mooney H.A. (2001). Viewing invasive species removal in a whole-ecosystem context. *Trends Ecol. Evol.*, 16, 454-459.

Table 1. Trophic species included in the interaction web of the Sparkling Lake littoral community.

Group	**Description (functional group)**	**Taxa**
Bass	Littoral non-sunfish fishes (generalist predators)[1,2]	Smallmouth bass (*Micropterus dolomieu*), rock bass (*Amboploites rupestris*)
Lepomis	Sunfishes (mainly invertivores)[1,2]	Bluegill sunfish (*L. macrochirus*), pumpkinseed sunfish (*L. gibbosus*)
Rusty crayfish	Invasive rusty crayfish (omnivores)[3]	Rusty crayfish (*Orconectes rusticus*)
Odonata	Dragonfly larvae (mainly predators)[4]	Aeshnidae, Coenagrionidae, Corduliiadae, Gomphidae, Libellulidae, Macromiidae
Ephemeroptera	Mayfly larvae (scrapers, collector-gatherers)[4]	Baetidae, Caenidae, Ephemerellidae, Ephemeridae, Heptageniidae, Leptophlebiidae, Polymitarcyidae
Trichoptera	Caddisfly larvae (collector-gatherers, scrapers, shredders, herbivores)[4]	Hydroptilidae, Leptoceridae, Lymnephilidae, Phryganeidae, Polycentropodidae
Gastropoda	Snails (scrapers)[5]	Hydrobiidae, Lymnaeidae, Physidae, Planorbidae, Valvatidae
Diptera	Midge larvae (collector-gatherers, predators)[4]	Ceratopogonidae, Chironomidae, Chaoboridae
Amphipoda	Amphipods (grazer, collector-gatherer)[6]	*Hyalella azteca*
Macrophyte	Aquatic plants (primary producers)	All littoral vegetation. Dominated by *Chara spp., Eleocharis acicularis, Isoetes spp., Juncus pelocarpus, Najas flexilis, Potamogeton gramineus,* and *Vallisneria americana*

[1] Emperical diet data

[2] (Becker 1983)

[3] (Capelli 1980; Whitledge & Rabeni 1997; Roth *et al.* 2006);

[4] (Merritt & Cummins 1996)

[5] (Thorp & Covich 2010)

[6] (Strong 1972)

Table 2. Methods of quantifying the response of each trophic species to rusty crayfish removal from Sparkling Lake.

Taxa	**Response variable (lowest unit of observation)**	**Units[a]**	**Fixed effects**	**Random effects**
Rusty crayfish	CPUE (site)	#·trap^{-1}·day^{-1}	Yeargroup[b], Habitat, Yeargroup*Habitat	Transect[c], Year
Bass	Mark-recapture population estimate (whole lake)	Number	Yeargroup	NA
Lepomis	Mark-recapture population estimate (whole lake)	Number	Yeargroup	NA
Macrophytes	Percent cover of all species (quadrat)	% cover (all spp.)	Yeargroup, Habitat, Yeargroup*Habitat	Transect, Year, Depth[d]
Amphipoda	Density (quadrat)	#·m^{-2}	Yeargroup, Habitat, Yeargroup*Habitat	Site[e], Year
Diptera	Density (quadrat)	#·m^{-2}	Yeargroup, Habitat, Yeargroup*Habitat	Site[e], Year
Ephemeroptera	Density (quadrat)	#·m^{-2}	Yeargroup, Habitat, Yeargroup*Habitat	Site[e], Year
Gastropoda	Density (quadrat)	#·m^{-2}	Yeargroup, Habitat, Yeargroup*Habitat	Site[e], Year
Odonata	Density (quadrat)	#·m^{-2}	Yeargroup, Habitat, Yeargroup*Habitat	Site[e], Year
Trichoptera	Density (quadrat)	#·m^{-2}	Yeargroup, Habitat, Yeargroup*Habitat	Site[e], Year

[a] all modeled on natural log scale

[b] High (2002-2003) or low (2008-2010) crayfish density

[c] one of 43 standardized trapping and monitoring locations

[d] Categorical classification: 0-1m, 1-2m, 2-3m, 3-4m

[e] Depth-specific transect location (either 1,3, or 5 m depth)

Table 3. Interactions evaluated using qualitative model simulations, the percent of valid models (those matching field observations) in cobble and macrophyte habitats, difference in frequency of occurrence in the two habitats (cobble-macrophyte; positive values = more frequent in cobble; negative values=more frequent in macrophyte) and whether an interaction was included in the core model of critical interactions (present in >50% of valid models from both habitats).

			Frequency in valid models (%)			
From	**To**	**Type**	**Cobble**	**Macrophyte**	**Difference**	**Core model?**
Bass	*Lepomis*	Predator-prey	44	**65.8**	-21.8	No
Bass	Crayfish	Predator-prey	**69.7**	40.7	29	No
Bass	Odonate	Predator-prey	40	49	-9	No
Bass	Ephemeroptera	Predator-prey	**62.9**	41.9	21	No
Bass	Trichoptera	Predator-prey	43.5	42.3	1.2	No
Bass	Diptera	Predator-prey	20.8	45.3	-24.5	No
Bass	Amphipoda	Predator-prey	47.5	**51**	-3.5	No
Lepomis	Crayfish	Predator-prey	41.5	22.4	19.1	No
Lepomis	Gastropod	Predator-prey	**56.5**	**89.8**	-33.3	Yes
Lepomis	Ephemeroptera	Predator-prey	**65.7**	**78.6**	-12.9	Yes
Lepomis	Diptera	Predator-prey	14.9	**100**	-85.1	No
Lepomis	Trichoptera	Predator-prey	50	**85.9**	-35.9	No
Lepomis	Odonate	Predator-prey	**52.1**	47.9	4.2	No
Lepomis	Amphipoda	Predator-prey	**100**	**100**	0	Yes
Odonate	Ephemeroptera	Predator-prey	**78.7**	**66.1**	12.6	Yes
Odonate	Diptera	Predator-prey	27.8	41.5	-13.7	No
Odonate	Trichoptera	Predator-prey	46.8	**53.9**	-7.1	No
Crayfish	Gastropod	Predator-prey	**66.3**	**86.8**	-20.5	Yes
Crayfish	Ephemeroptera	Predator-prey	26.8	11.6	15.2	No
Crayfish	Diptera	Predator-prey	18.4	22.6	-4.2	No
Crayfish	Odonate	Predator-prey	**58.8**	25.3	33.5	No
Crayfish	Trichoptera	Predator-prey	**64.2**	13.3	50.9	No
Crayfish	Macrophyte	Negative	**100**	**100**	0	Yes
Macrophyte	*Lepomis*	Habitat	**58.9**	**72.3**	-13.4	Yes
Macrophyte	Gastropod	Habitat	**65.7**	**80.1**	-14.4	Yes
Macrophyte	Ephemeroptera	Habitat	25.8	17.2	8.6	No
Macrophyte	Odonate	Habitat	**65**	49.5	15.5	No
Macrophyte	Trichoptera	Habitat	**63.9**	14.9	49	No
Macrophyte	Amphipoda	Habitat	4.7	25.5	-20.8	No

Gastropod	Trichoptera	Competition	1.1	19.2	-18.1	No
Gastropod	Ephemeroptera	Competition	18.5	32.4	-13.9	No
Ephemeroptera	Trichoptera	Competition	10.7	4.6	6.1	No

FIGURE CAPTIONS

Figure 1. Signed digraph and qualitative community interaction matrix representing the full model (all potential interactions included) in Sparkling Lake. Numbers in parentheses in the digraph are species identification codes used in the interaction matrix; the effect of species j on species i (a_{ij}) occurs in the i^{th} row of the j^{th} column. Interactions between community members are directional; in the signed digraph interactions are negative (—●), positive (→), or no effect (no line), corresponding to -1, 1, and 0 in the community interaction matrix, respectively. All community members also include a negative self-dampening effect to represent density dependence (diagonal of the community matrix), not shown in the digraph for clarity of representation.

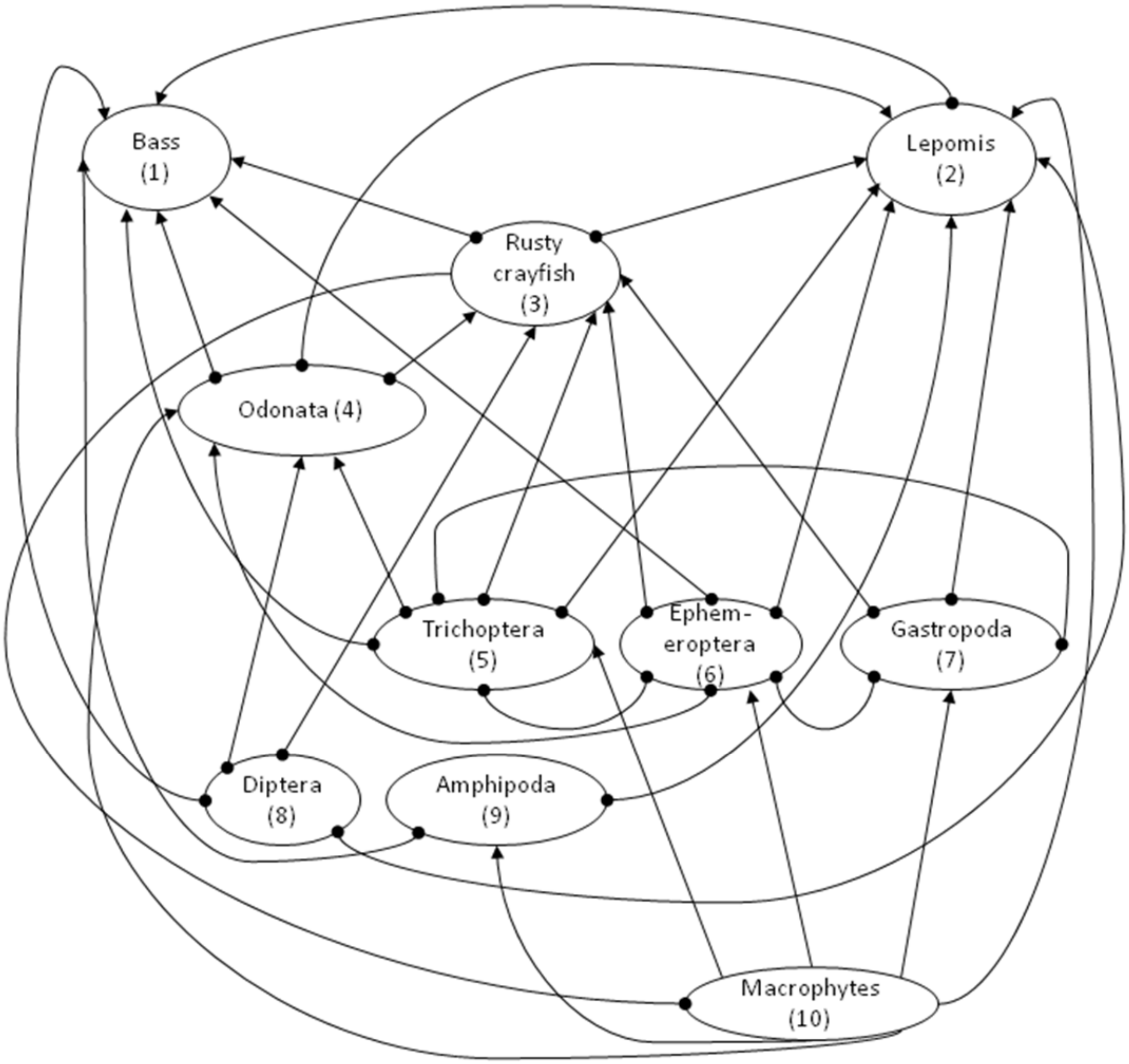
Figure 2. Flow chart outlining qualitative simulation approach.

Figure 3. Response (natural log scale) of all trophic species to the experimental rusty crayfish removal (see Table 2 for information on how each group was measured). Color of bars reflects the qualitative response of each group to the experimental removal of rusty crayfish used for validation of qualitative models: black=decrease, grey=increase, white=no change (DIptera in cobble habitat only). Bass and *Lepomis* were measured on the whole-lake scale and changes in the two habitats are identical. Other groups were measured separately in each habitat type.

Figure 4. Frequency of interactions occurring in valid models in cobble habitat. Only interactions occurring in ≥50% of valid models are shown; heavy lines represent interactions occurring in 75-100% of models.

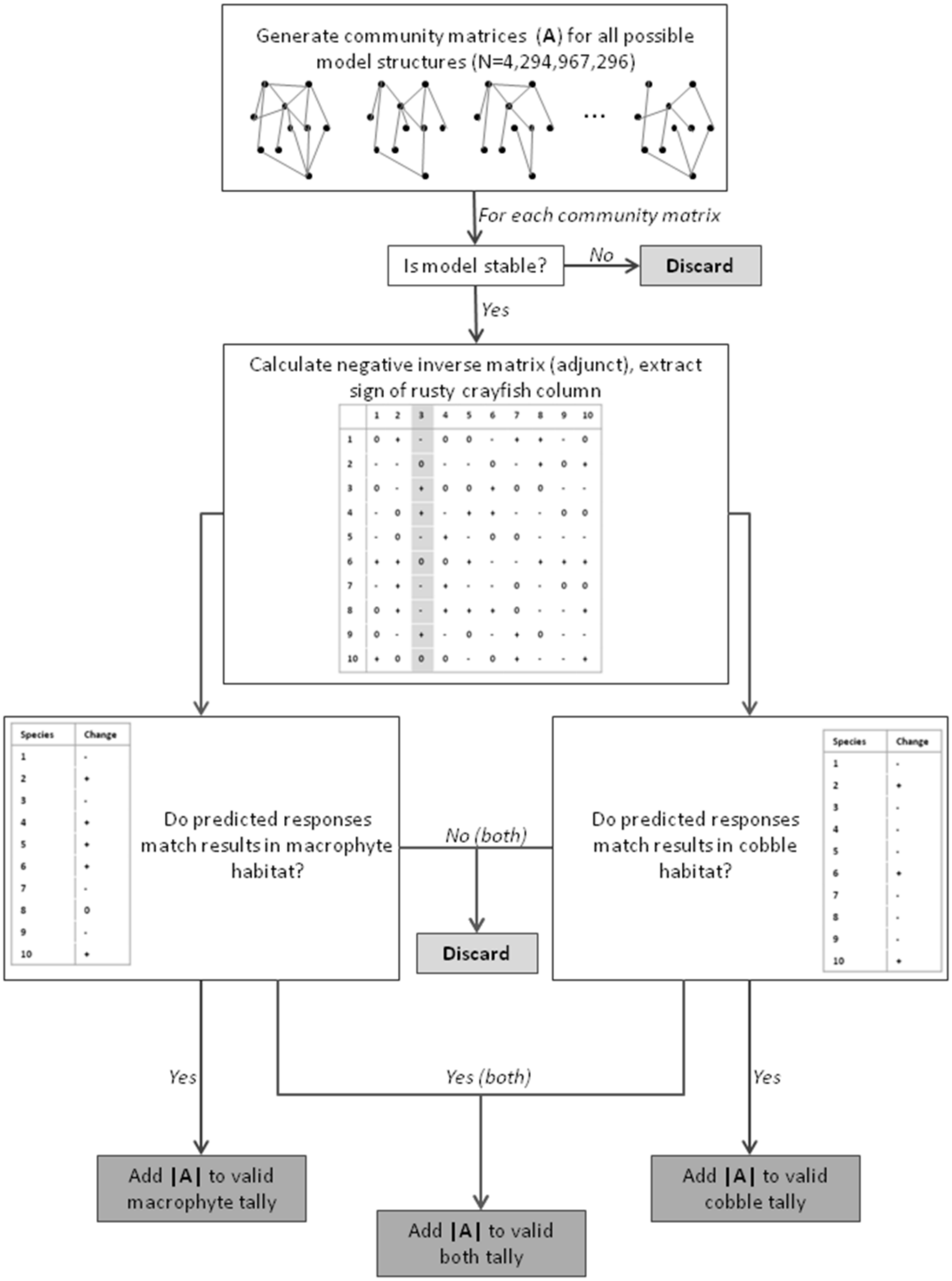
Figure 5. Frequency of interactions occurring in valid models in macrophyte habitat. Only interactions occurring in >50% of valid models are shown; heavy lines represent interactions occurring in 75-100% of models.

Figure 6. Core model of interactions occurring in >50% of valid models for both habitat types.



	1	2	3	4	5	6	7	8	9	10
1	-1	1	1	1	1	1	0	1	1	0
2	-1	-1	1	1	1	1	1	1	1	1
3	-1	-1	-1	1	1	1	1	1	0	0
4	-1	-1	-1	-1	1	1	0	1	0	1
5	-1	-1	-1	-1	-1	-1	-1	0	0	1
6	-1	-1	-1	-1	-1	-1	-1	0	0	1
7	0	-1	-1	0	-1	-1	-1	0	0	1
8	-1	-1	-1	-1	0	0	0	-1	0	1
9	-1	-1	0	0	0	0	0	0	-1	1
10	0	0	-1	0	0	0	0	0	0	-1

Figure 1.



	1	2	3	4	5	6	7	8	9	10
1	0	+	-	0	0	-	+	+	-	0
2	-	-	0	-	-	0	-	+	0	+
3	0	-	+	0	0	+	0	0	-	-
4	-	0	+	-	+	+	-	-	0	0
5	-	0	-	+	-	0	0	-	-	-
6	+	+	0	0	+	-	-	+	+	+
7	-	+	-	+	-	-	0	-	0	0
8	0	+	-	+	+	+	0	-	-	+
9	0	-	+	-	0	-	+	0	-	-
10	+	0	0	0	-	0	+	-	-	+

Species	Change
1	-
2	+
3	-
4	+
5	+
6	+
7	-
8	0
9	-
10	+

Species	Change
1	-
2	+
3	-
4	-
5	-
6	+
7	-
8	-
9	-
10	+

Figure 2.

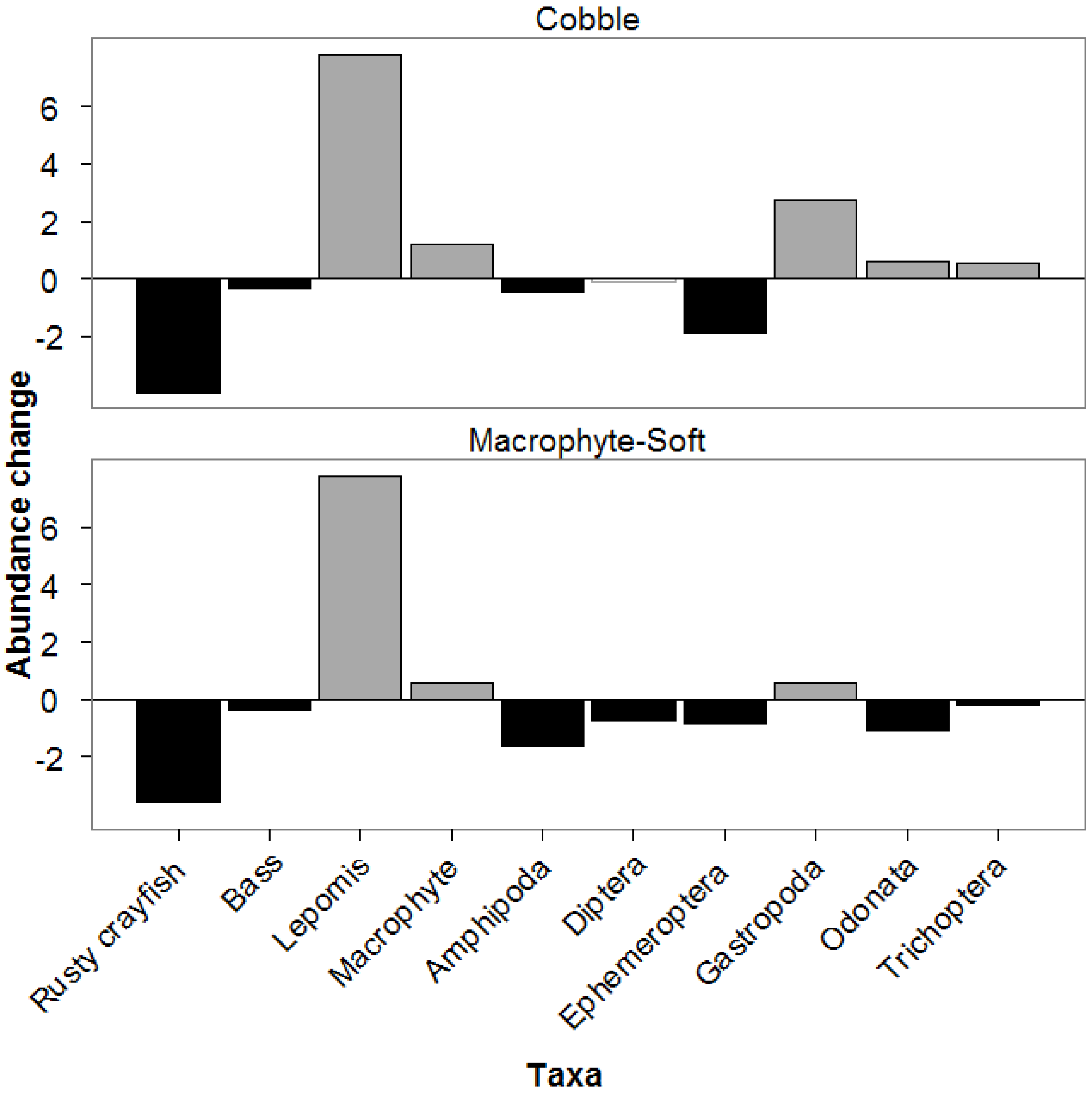

Cobble
Macrophyte-Soft
Abundance change
6
4
2
0
-2
Rusty crayfish
Bass
Lepomis
Macrophyte
Amphipoda
Diptera
Ephemeroptera
Gastropoda
Odonata
Trichoptera
Taxa

Figure 3.

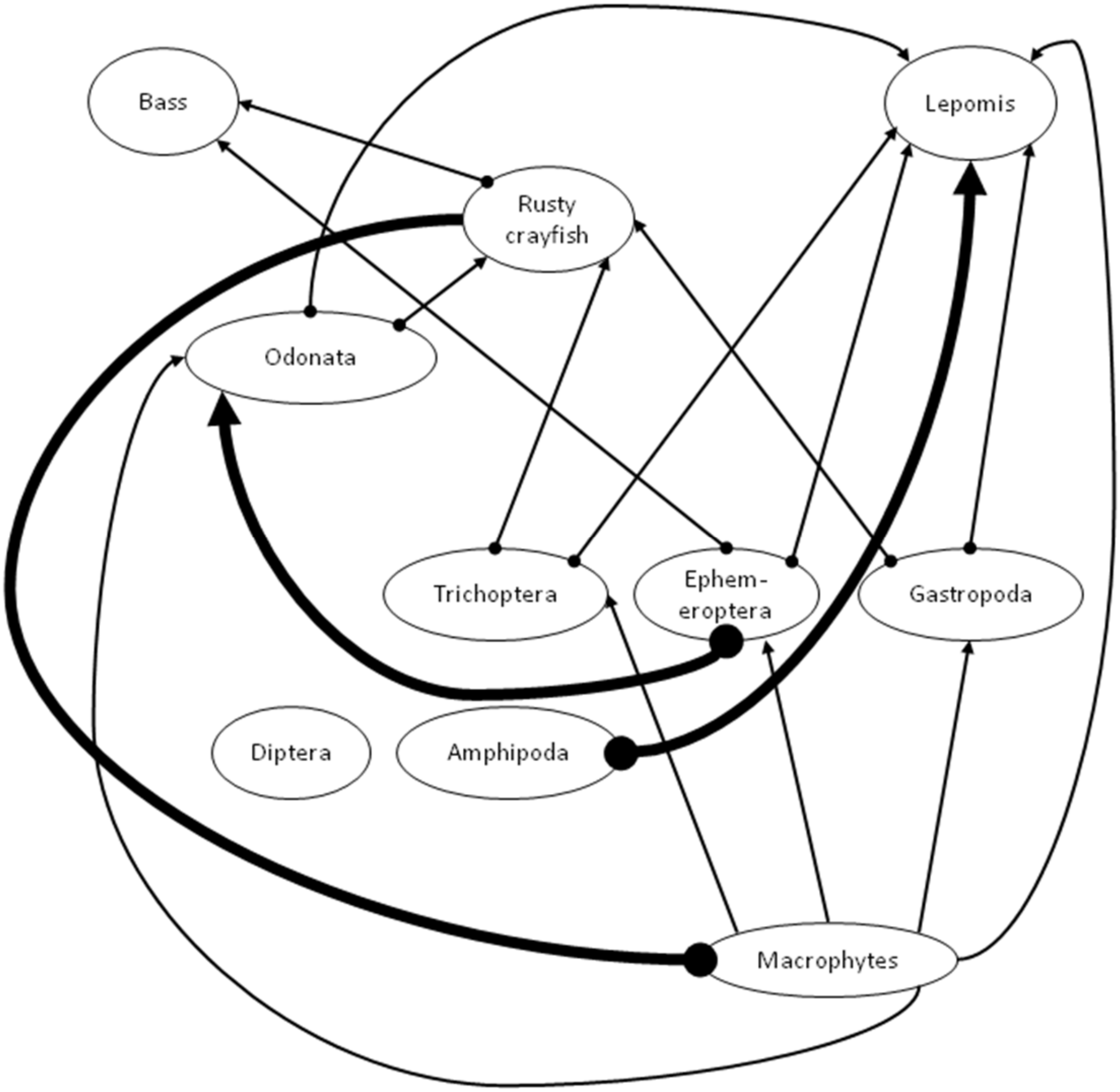

Bass
Lepomis
Rusty crayfish
Odonata
Trichoptera
Ephem-eroptera
Gastropoda
Diptera
Amphipoda
Macrophytes

Figure 4.

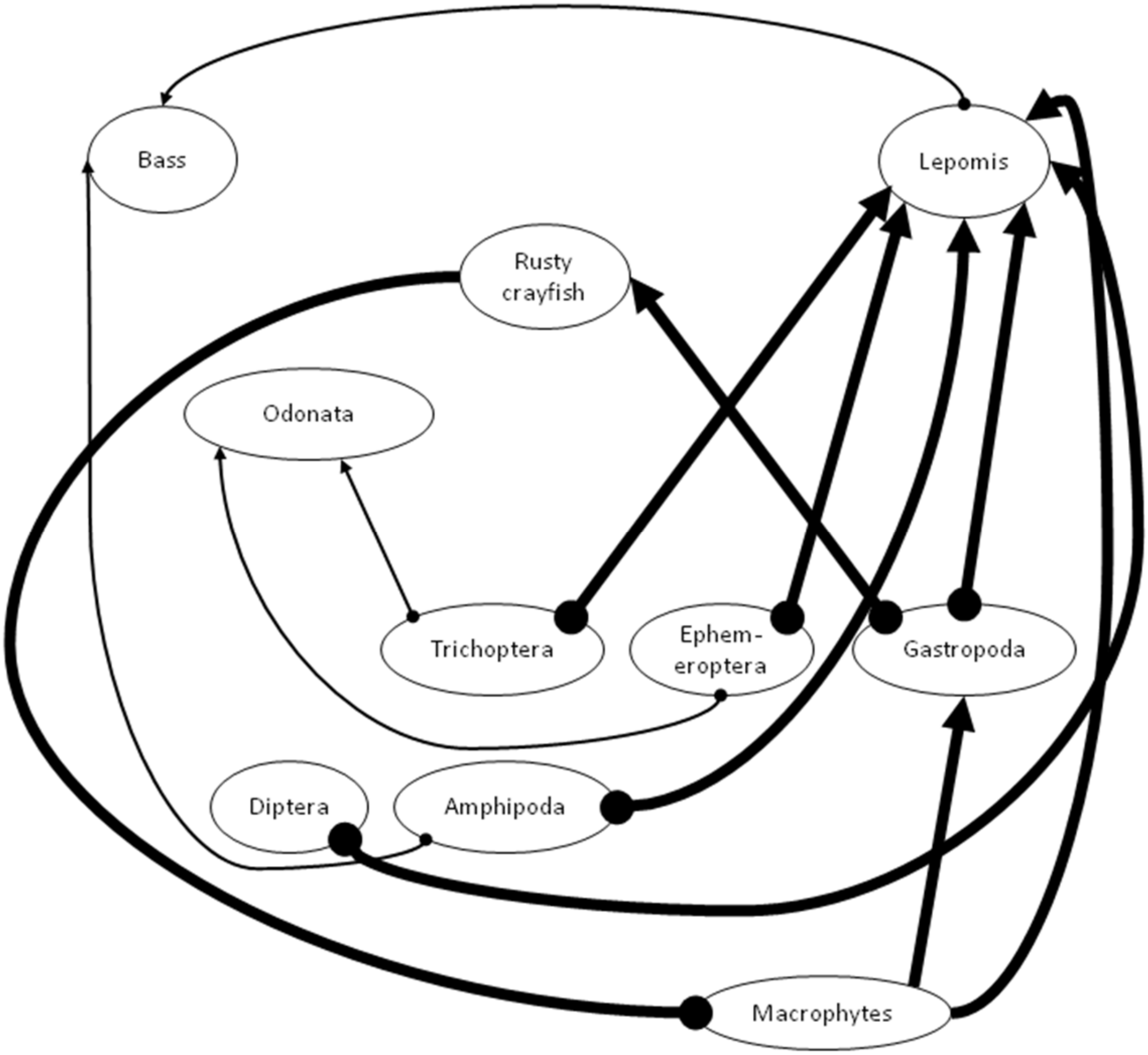

Bass
Lepomis
Rusty crayfish
Odonata
Trichoptera
Ephem-eroptera
Gastropoda
Diptera
Amphipoda
Macrophytes

Figure 5.

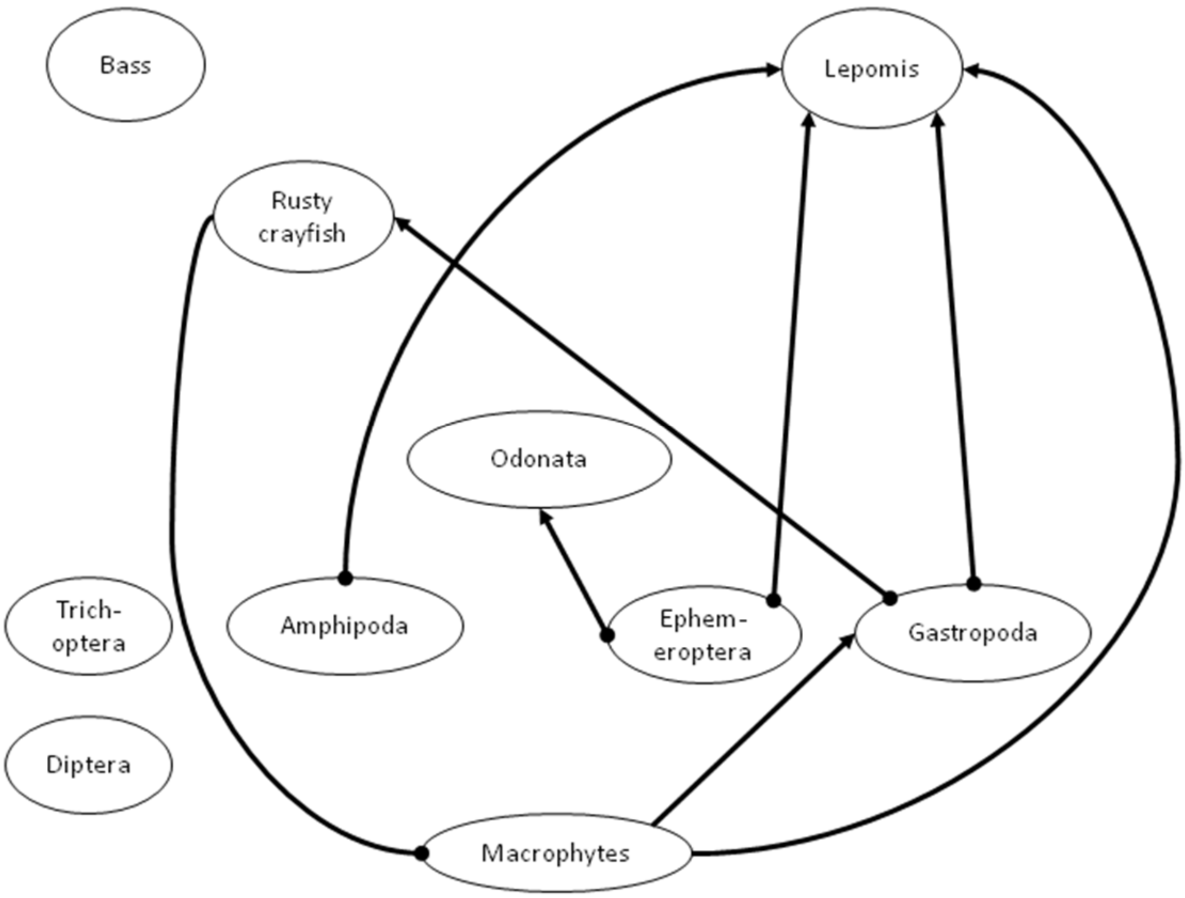

Bass
Lepomis
Rusty crayfish
Odonata
Trich-optera
Amphipoda
Ephem-eroptera
Gastropoda
Diptera
Macrophytes

Figure 6.

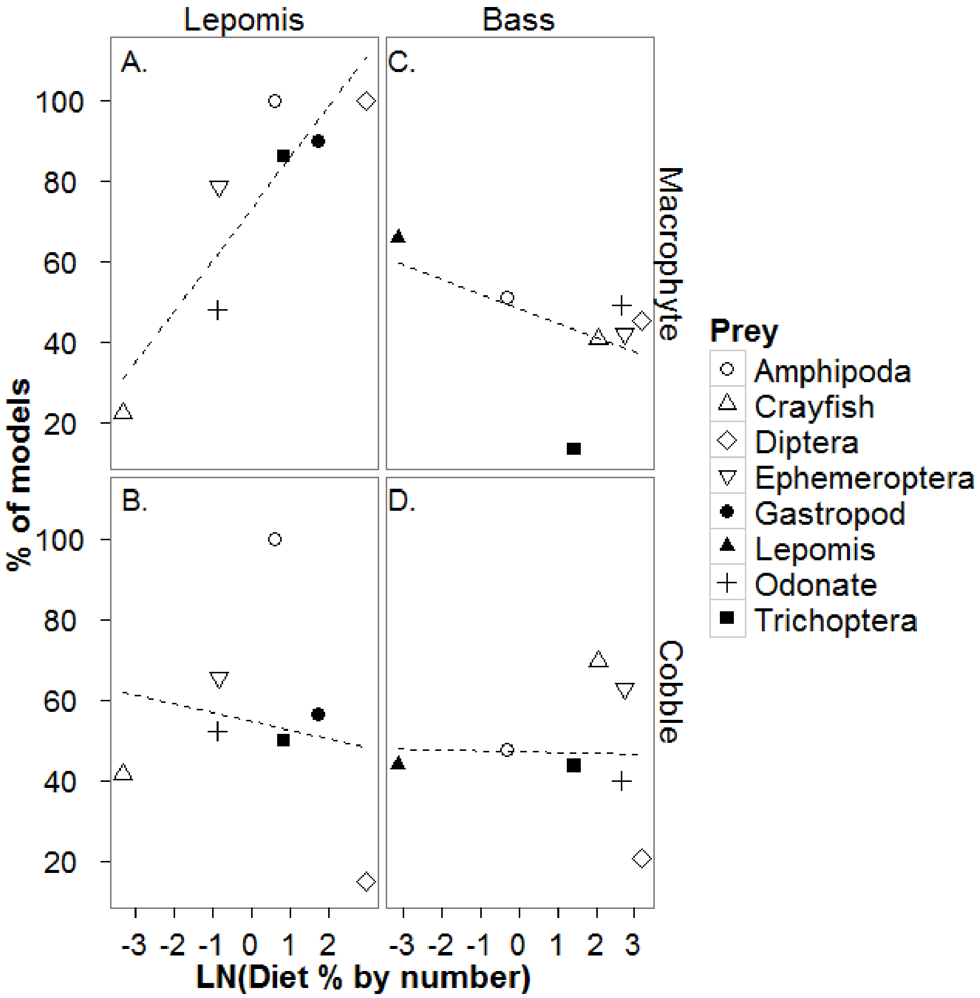

Lepomis
Bass
A.
C.
B.
D.
Macrophyte
Cobble
% of models
100
80
60
40
20
-3 -2 -1 0 1 2
-3 -2 -1 0 1 2 3
LN(Diet % by number)
Prey
○ Amphipoda
△ Crayfish
◇ Diptera
▽ Ephemeroptera
● Gastropod
▲ Lepomis
+ Odonate
■ Trichoptera

Figure 7.