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EFFECTS OF OMNIVOROUS CRAYFISH ON FISH POPULATIONS AND THE STRUCTURE OF LITTORAL COMMUNITIES

By

Nathan Jeffrey Dorn

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ABSTRACT

EFFECTS OF OMNIVOROUS CRAYFISH ON FISH POPULATIONS AND THE STRUCTURE OF LITTORAL COMMUNITIES

By

Nathan Jeffrey Dorn

Crayfish are the largest invertebrate predators in many freshwater systems, they are broadly omnivorous, and are capable of dominating secondary production and biomass. Crayfish are widely distributed in waterbodies throughout the globe and have been introduced to many ecosystems, otherwise beyond their dispersal capacities, for a variety of reasons. In this study, I explored the effects of crayfish on another large freshwater predator (sunfish) and on community structure of shallow water habitats.

The effects of crayfish on fish populations were explored with a literature review and two replicated experiments in ponds. Crayfish can have a number of relationships with fish, and interactions are not limited to the traditional studies of fish as predators and crayfish as prey. Other interactions have been less well studied, and one potentially important interaction is the effect of crayfish as predators of fish eggs.

To look for evidence of the effects of crayfish on reproductive success and nesting behavior I performed two experiments (1999 and 2001) with two species of common sportfish, the pumpkinseed sunfish (*Lepomis gibbosus*) and bluegill sunfish (*L. macrochirus*). Both species of sunfish nest in shallow littoral habitats of lakes and ponds and nests are guarded by the adult males. In both of the experiments, crayfish infiltrated nests, ate the eggs and had negative impacts on reproductive success of the sunfish. In the experiment with bluegill sunfish, crayfish stopped reproduction until predator-free

nesting habitats (exclosures) were added to the ponds later in the summer. After the exclosures were added, adult bluegill in each pond found the exclosures and were able to reproduce.

Crayfish had additional strong effects on overall community development (succession) in six ponds studied in 2001-2002. Through direct and indirect effects, crayfish had significant effects on the biomass of zooplankton and phytoplankton assemblages and peak levels of dissolved oxygen. Crayfish also had strong negative effects on macrophyte establishment, metaphyton abundance and composition, gastropod biomass, and the density of bullfrog (*Rana catesbiana*) tadpoles. Based on these results and those of other studies of crayfish in lakes and ponds, systems with abundant crayfish are expected to be structurally simple systems with few macrophytes and gastropods where filamentous green algae and some species of amphibians and fish will perform poorly, but other organisms may benefit.

In my last experiment I explored the relative impacts of native and exotic *Orconectes* crayfish grazing on a common plant type. Using feeding trials in cages I determined that adults of the exotic crayfish, *Orconectes rusticus* and the native *O. virilis* had similar grazing rates on *Chara* macroalgae in two ponds with and without bass, as long as no direct interactions with the bass were possible. However, when direct interactions were possible, *O. rusticus* had higher feeding rates than *O. virilis*. This result is consistent with differences in overall predation vulnerability of these species, and suggests that stronger per biomass effects of exotic crayfish might be obviated in the presence of predators.

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CHAPTER 1

INTRODUCTION: OMNIVORY AND FRESHWATER BENTHIC COMMUNITIES

One of the long-standing goals of ecology is to understand the mechanisms that regulate populations and thereby structure communities. The details of consumer-resource interactions underlie most of the direct and indirect biotic mechanisms thought to affect community composition (e.g., Paine 1966, Holt 1984, Ricklefs 1987). Although all animals are consumers, different animals species have different feeding habits; some animals have restricted diets (specialists) and others feed on several prey types (generalists). Generalist predators that feed across trophic levels are considered omnivores. The ubiquity and importance of omnivory (plant-animal omnivory, trophic omnivory, and others) has been recognized for some time in marine systems (e.g., Menge and Sutherland 1976, 1987) and has recently gained attention in a variety of ecosystems (e.g., Polis et al. 1989, Diehl 1993, McCann and Hastings 1997, Eubanks and Denno 1999). By feeding on multiple trophic levels omnivores can disrupt the general expectations of simple trophic cascades (Diehl 1993, Pringle and Hamazaki 1998), maintain or augment their populations through feeding on non-preferred prey (Polis and Strong 1996, Eubanks and Denno 1999), and stabilize community dynamics (McCann and Hastings 1997, Fagan 1997).

Menge and Sutherland (1987) and Diehl (1993) have suggested that large omnivores feed indiscriminately on small prey regardless of trophic or taxonomic status. Thus populations of intermediate consumers and lower resources may respond similarly to top-down control by large omnivores (Menge and Sutherland 1987, Diehl 1993). However, the strength of top-down control on specific organisms will certainly depend upon prey size, morphology, and anti-predator behaviors (Kerfoot and Sih 1987, Lima and Dill 1990, Diehl 1993), as well as environmental stress and habitat complexity (Menge and Sutherland 1987, Polis and Strong 1996).

Freshwater benthic communities have many omnivorous vertebrates and invertebrates with important feeding links to intermediate consumers and basal resources (e.g., Warren 1989, Vadas 1990, Havens et al. 1996, Pringle and Hamazaki 1998). Furthermore, because many large freshwater predators have relatively small early life-stages, even the largest predators (i.e., fish) may be susceptible to predation by intermediate consumers. Abundant omnivory and size-structured populations, coupled with a diversity of predator and prey sizes, morphs, and behaviors, make freshwater benthic communities rich systems for studying the direct and indirect effects of omnivores on populations and community structure.

CRAYFISH BACKGROUND

Crayfish are the largest invertebrate predators in freshwater benthic communities, and over 300 species can be found in a diversity of habitats in the United States and Canada (Taylor et al. 1996). Crayfish are omnivores in a traditional sense; they feed on living plants (both macrophytes and algae), detritus (and associated decomposers), invertebrates, and even vertebrate protein if available (Momot 1995). Young-of-year crayfish are relatively susceptible to fish predation and can provide an important food base for large fish (Chapter 2), but adult crayfish are relatively invulnerable (Stein 1977). Crayfish can attain high community biomass and production rates in many systems, and Momot (1995) has hypothesized that crayfish can eliminate vulnerable or preferred animal prey while maintaining their populations on less profitable food resources (detritus and plants).

Previous experimental work has documented strong direct and indirect effects of crayfish on other benthic invertebrates and primary producers (e.g., Creed 1994, Lodge et al. 1994, Nyström et al. 2001). Due to their large body size and omnivorous feeding habits, crayfish have the potential to influence the trajectory of community development (primary or secondary succession) by directly or indirectly affecting the success of a variety of species residing in littoral habitats.

Understanding the effects of crayfish on community structure and their interactions with populations of other large consumers, like fish, is also important for predicting and understanding the effects of crayfish invasions. Many crayfish species have been introduced to waterbodies beyond the reach of their natural dispersal abilities (Hobbs et al. 1989). Introductions have been both intentional - for the purpose of aquaculture, aquatic plant management, or as forage for fish, and accidental – as in the case of bait bucket introductions (Hobbs et al. 1989, Lodge et al. 2000), and have had a variety of negative consequences (Lodge et al. 2000).

DISSERTATION OVERVIEW

I am interested in the effects of crayfish on fish populations and the structure of littoral communities. In this dissertation I investigated these interactions through a literature survey of fish-crayfish interactions (Chapter 2), and several field experiments utilizing a set of semi-natural experimental ponds, which allowed entire populations of organisms to interact with and respond to each other (Chapters 3, 4, 5). I addressed the following questions through my research: (1) What are the known relations and interactions between crayfish and fish populations and what interactions have been poorly studied? (2) Can crayfish be significant predators of the early-life-stages (eggs, fry) of fish, and how do reproducing fish respond behaviorally to the presence of safe nest sites? (4) Can crayfish affect primary succession of pond communities, and in what ways do pond communities with and without crayfish differ? and (5) Do native and exotic *Orconectes* crayfish have impacts of the same nature and magnitude on macroalgae?

In Chapter 2 I reviewed the known interactions between crayfish and fish from the published literature. Much of the literature has documented the energetic importance of crayfish prey for predatory fish diets. Additional work has detailed the behavioral interactions between fish predators and crayfish prey. Far fewer studies addressed the following interactions that could potentially have negative consequences for fish populations: (a) competition between benthic fish and crayfish for shelter and food, (b) predation by crayfish on fish eggs and fry, and (c) the indirect effects of crayfish on fish populations through alteration of important macrophyte habitats.

In Chapter 3 I tested the hypothesis that crayfish could be significant predators on the early life-stages of fish by performing two field experiments. I measured recruitment success of populations of two species of nesting sunfish (*Lepomis*) with functionally different nesting strategies (solitary nesters versus colony nesters) in replicate ponds with and without crayfish. In the second experiment I added small crayfish-proof exclosures to the crayfish ponds to determine whether reproducing adult sunfish would respond favorably to a safe nesting site. The results from these experiments indicate that (1) crayfish can be significant egg predators of both species of sunfish and can cause reproductive failure at realistic crayfish densities, and (2) sunfish can find and will use safe nesting sites when they are available. These results provide a mechanistic explanation for the observed decline of fish populations following invasions (Magnuson et al. 1975, Guan and Wiles 1997, Covich et al. 1999).

Nystrom et al. (1996) suggested that crayfish could have important effects on the succession of pond communities. Their study relied on observations of ponds at one point in time 40 years after they were constructed. To evaluate the effects of crayfish on early stages of succession I conducted a 13-month experiment of succession in six recently constructed ponds with and without omnivorous crayfish. Previous experiments with crayfish have looked at the trophic effects of crayfish in smaller arenas on extant (equilibrium) communities. This experiment allowed me to consider the effects of a large benthic omnivore on the colonization and establishment of many species in whole pond ecosystems. The results from this experiment indicated that direct and indirect effects of crayfish deflected the dynamics of these communities. Populations and assemblages of zooplankton, phytoplankton, metaphytic algae, macroalgae (*Chara vulgaris*) periphyton, benthic invertebrates, and tadpoles as well as suspended sediments and production: respiration ratios were all affected by crayfish presence.

Crayfish are widely introduced throughout the Midwest and the world (Lodge et al. 2000), and the effects of exotic crayfish could be greater than the species they replace. In Chapter 5, I tested the grazing capacities of native (*Orconectes virilis*) and exotic (*Orconectes rusticus*) crayfish to determine whether native and exotic species would have different impacts on macroalgae (*Chara*). Because the exotic species (*O. rusticus*) was known to be less vulnerable to predation I measured the grazing capacities of each species inside cages placed in two ponds, with and without bass predators, to determine whether predator presence changed the relative grazing impact of the two species. The results of this experiment indicate that the two species respond differently to different predator environments; in the absence of predators the two species grazed similarly, but in presence of direct interactions with predators (the condition most like natural lakes) the exotic species had higher mass-specific grazing effects on macroalgae.

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CHAPTER 2

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CHAPTER 2

MORE THAN PREDATOR AND PREY: A REVIEW OF INTERACTIONS BETWEEN FISH AND CRAYFISH

with Gary G. Mittelbach

ABSTRACT

Crayfish are a major constituent of benthic invertebrate production in both lentic and lotic habitats. Crayfish also provide an important food resource for many fish. Because of their abundance and relatively large body size, the interactions between fish and crayfish can have profound effects on the rest of the benthic community. In this paper we will 1) review the well-studied trophic and ecological relationships between fish and crayfish and 2) posit other potentially important but less-studied interactions. Fish and crayfish have generally been viewed as predator-prey. Crayfish are not easy prey for many fish because of their large size and defensive armor, and a number of studies have shown that the relative size of fish and crayfish is a major factor affecting the predator-prey interaction between these species. Crayfish may also compete with small benthic fish for food and shelter. Further, crayfish have been implicated in the declines of fish populations due to direct predation on fish eggs, and crayfish may indirectly affect fish populations through their destruction of macrophyte beds, which are important juvenile fish habitats. Many of these more subtle interactions between fish and crayfish were first observed when exotic species of crayfish were introduced to a new system (either intentionally or accidentally). More experimental work and long-term data sets are necessary to discover the importance of these less-studied interactions between crayfish and fish. Careful consideration should be given to the multiple pathways of fish-crayfish

interactions when managing, farming, introducing, or studying these aquatic macroconsumers.

KEYWORDS: competition, crayfish, egg predation, fish, predator, prey

INTRODUCTION

Recent research in freshwater systems has documented a rich array of ecological interactions between fish and benthic invertebrates. These interactions include top-down effects of fish on benthos; e.g., effects of fish on invertebrate densities (Diehl 1995, Batzer 1998), invertebrate size-structure (Mittelbach 1988), species composition (Power 1992, McPeek 1990), behaviour (Wooster and Sih 1995, Lima 1998), and morphology (Johansson and Samuelsson 1994). Similarly, bottom-up effects of benthic invertebrates may significantly influence fish diets (Crowder and Cooper 1982), habitat use (Werner et al. 1983a), growth rates (Diehl and Kornijów 1998), and abundances (McIvor and Odum 1988). In many of these interactions, body size plays an important role. For example, most freshwater fish are size-selective foragers (Wootton 1990, Gerking 1994), often feeding preferentially on large invertebrates (Mittelbach 1988). Consequently, intense fish predation may shift the size-structure of benthic invertebrate communities towards smaller individuals and smaller species (Strayer 1991).

In most cases, fish are much larger than the benthic invertebrates they feed upon. When this is true, the relationship between invertebrate size and fish foraging preference is relatively simple – bigger is better. Larger invertebrate prey generally provide the highest energetic gain (Mittelbach 1981, Persson and Crowder 1998), and fish growth rates have been shown to be positively correlated with the abundance of large, benthic invertebrates (Mittelbach 1988). However, some benthic invertebrates may reach large enough sizes, or may be sufficiently well armored, that larger individuals are no longer vulnerable to most fish predators. When this is the case, trophic interactions between fish and benthos become more complex.

Crayfish (Decopoda) are among the largest freshwater benthic invertebrates. As they often dominate benthic invertebrate biomass, crayfish provide a rich prey resource for some freshwater fish. Due to their large size and defensive armor, crayfish are not easy prey for all fish, which complicates the trophic interactions. In this paper, we first document the importance of crayfish to benthic invertebrate production in many freshwater systems, and the importance of crayfish to the diets of benthic-feeding fish. We then examine predator-prey interactions between fish and crayfish. Lastly, we explore some less well-studied direct and indirect interactions between these two freshwater macroconsumers.

TROPHIC RELATIONSHIPS

Crayfish are often significant components of benthic invertebrate production (Rabeni et al. 1995, Momot 1995), and many studies report crayfish dominating benthic standing stock biomass (Huryn and Wallace 1987, Griffith et al. 1994, Momot 1995). Because crayfish are omnivores, they provide direct links from both primary production and detrital-based food webs to fish (Vannote and Ball 1972, Rabeni 1992, Roell and Orth 1993). Fish have been shown to be important consumers of annual crayfish production in many systems (Table 1), and fish predation may provide top-down control on crayfish densities. For example, Mather and Stein (1993) and Lodge and Hill (1994) found a significant inverse relationship between densities of predaceous fish and crayfish. Svärdson (1972) further showed that in Sweden, where eels (*Anguilla anguilla*) and crayfish (*Astacus astacus*) are largely allopatric, the introduction of eels generally leads to the local extermination of crayfish. Largemouth bass (*Micropterus salmoides*) have also been shown to signficantly reduce or eliminate crayfish from aquaculture ponds (0.1-4 ha) (Taub 1972, Rickett 1974). In contrast to the above studies, Gowing and Momot (1979) concluded that predation by brook trout (*Salvelinus fontanilis*) had little control of crayfish production in an inland Michigan (USA) lake. However, due to gape limitation, brook trout in this study were only able to feed upon juvenile crayfish, limiting their ability to control crayfish numbers. Additional long-term experimental studies using natural densities of crayfish and their predators are needed to determine the extent of "top-down" influences on crayfish abundances.

The importance of crayfish in diets of several fish species is summarized in Table 2. Some fish species feed heavily on crayfish (e.g., smallmouth bass, *Micropterus dolumieu*, rock bass, *Ambloplites rupestris*, and flathead catfish, *Pylodictis olivaris*), while other fish are more opportunistic and consume crayfish infrequently (e.g., walleye, *Stizostedion vitreum*, black bullhead, *Ictalurus melas*, northern pike, *Esox lucius*). Small, gape-limited fish or fully pelagic fish are likely to feed on only the smallest crayfish.

The importance of crayfish in fish diets increases with fish age and size. In general, YOY (young of the year) fish rarely consume crayfish due to limitations in mouth gape (Rabeni 1992, Roell and Orth 1993). For those fish species that feed extensively on crayfish, the percentage of crayfish in the diet increases during ontogeny (Keast 1977, Dehli 1981, Roell and Orth 1993). These ontogenetic diet shifts are due to changes in the relative vulnerability of crayfish as fish size increases (Stein 1977). The proportion of crayfish in a species' diet may also vary widely among systems (Table 2). For example, Gowing and Momot (1979) found that trout from lakes with high trout stocking densities consumed more crayfish than trout stocked into lakes at low density. Wells (1980) found that perch foraging over rocky substrate in Lake Michigan utilized crayfish to a greater degree than perch foraging over sandy bottoms. Crayfish are generally more common in rocky substrate (Janssen and Quinn 1985, Kershner and Lodge 1995) and therefore perch may consume crayfish in proportion to their abundance. Experiments in large enclosures or ponds are necessary to verify these contentions. Ward and Neumann (1998) suggested that largemouth bass consumption of crayfish changes with seasons (most eaten during summer-fall), and that bass consume more crayfish in systems where forage fish are scarce. Seasonal variation in average crayfish size and molting stage also affects their vulnerablity to fish predation. Most crayfish molt 1-3 times per growing season. Following a molt, even a large crayfish can be extremely vulnerable to predation (Stein 1977). Below we consider in more detail the factors that influence the predator-prey interaction between fish and crayfish.

TRADITIONAL PREDATOR-PREY STUDIES

Effects of body size and substrate

A number of studies have examined interactions between predatory fish and their crayfish prey. Stein and Magnuson (1976) and Stein (1977) report a series of experiments in which smallmouth bass preyed upon crayfish (*Orconectes propinquus*). In these experiments, crayfish size was inversely related to feeding preference with the smallest crayfish eaten first. Reproductive (F1) males and gravid females were the least vulnerable life stages, while recently molted crayfish were the most vulnerable. Stein (1977) also found that the interaction between fish and crayfish size was influenced by substrate size. If we assume that absolute vulnerability to fish predation cannot increase above that experienced on bare sand, we can hypothesize the interaction between crayfish size and substrate size looks something like Figure 1. At small substrate sizes (sand), small crayfish have the highest vulnerability to predation. When substrate (rock) size increases to a threshold value, the smallest crayfish (10 mm) experience a refuge from predation by using the substrate as shelter. Consequently, intermediate-sized crayfish (20 mm) are most vulnerable and eaten first. As substrate size increases still further, a greater number of these intermediate size crayfish can utilize the substrate. Largest crayfish can utilize only large rocks for shelter but maintain relatively low vulnerability regardless of the substrate size. Although this relationship is consistent with experimental evidence in gravel bottom pools, the ability of crayfish to burrow in soft sediments or clay may change the interaction substantially (see Vorburger and Ribi 1999).

Effects on fish on crayfish behaviours

In the presence of predatory fish, crayfish alter their microdistributions (Stein 1977, Hill and Lodge 1994) and activity levels (Stein and Magnuson 1976, Resetarits 1991). Field studies and experiments indicate crayfish use more cobble habitat (or otherwise structured habitat) and use less open sand in the presence of predaceous fish (Stein and Magnuson 1976, Stein 1977, Hill and Lodge 1994, Lodge and Hill 1994, Kershner and Lodge 1995, Mather and Stein 1993). In the absence of predatory fish, crayfish tend to prefer the substrate which provides the greatest food availability, while in the presence of predators crayfish prefer substrate with the most available refuge (Hill and

Lodge 1994). Regardless of the presence of fish predators, crayfish become more evenly distributed across sand, cobble, and macrophyte habitats at night (Hill and Lodge 1994).

Crayfish foraging activity is generally suppressed in the presence of predatory fish (Stein and Magnuson 1976, Resetarits 1991), while chelae displays and other behaviors reducing vulnerability increase (Stein and Magnuson 1976). Crayfish with large chelae (males) seem to be affected least by the presence of fish predators (Stein 1977, Stein and Magnuson 1976). Blake and Hart (1993) studied the effects of chemical and visual predator cues on crayfish activity levels. Crayfish (*Pacifasticus leniusculus*) given chemical stimuli of either perch (*Perca fluviatilis*) or eels (*Anguilla anguilla*) reduced activity levels during both night and day periods. When given visual stimuli without prior chemical cues, crayfish only changed behavioral patterns during the day. Hamrin (1987) also found that patterns of crayfish diel activity levels were altered by the presence of fish predators. However, in Hamrin's study, total crayfish activity actually increased in the presence of crepuscular fish predators. Hamrin's (1987) result runs counter to the findings of Stein and Magnuson (1976), Resetarits (1991), and Blake and Hart (1993). This result was probably due to predatory treatments that did not involve both visual and chemical cues. In the predator treatments, crayfish were placed in plexiglass tubes, which likely limited the chemical signals necessary for crayfish to alter (decrease) nighttime activity levels. In summary, the presence of predatory fish has negative affects on crayfish activity levels. Further, these reductions in activity have been shown to have significant negative effects on crayfish growth rates (Resetarits 1991, Hill and Lodge 1999). In addition, Hill and Lodge (1995) found increased macrophyte and macroinvertebrate densities in mesocosms where crayfish experienced the presence of bass.

Crayfish species are differentially susceptible to fish predation (Didonato and Lodge 1993, Garvey et al. 1994), and fish predation may facilitate invasions by exotic crayfish species (Hill and Lodge 1998, Söderbäck 1994). For example, in northern Wisconsin (USA), *Orconectes rusticus* (the rusty crayfish) has invaded lakes previously occupied by two congeners (*O. propinquus* and *O. virilis*) (Olsen et al. 1991, Hobbs et al. 1989). *O. rusticus* has excluded the native crayfish in these lakes and the evidence suggests that fish predation is a significant mechanism involved in the replacement of the native crayfish species by *O. rusticus* (Didonato and Lodge 1993, Garvey et al. 1994, Hobbs et al. 1989, Hill and Lodge 1998). In mixed species assemblages, *O. rusticus* is more successful at obtaining available shelters and is relatively less vulnerable to fish predation on open sand (Garvey et al. 1994). As a result, bass selectively feed on the exposed and relatively more vulnerable *O. virilis* and *O. propinquus,* while *O. rusticus* are avoided (and thereby persist). Overall, *O. rusticus* is able to maintain higher growth and lower mortality than the two native *Orconectes* in the presence of predaceous fish (Hill and Lodge 1999). This example is likely analogous to the replacement of *Astacus astacus* by the introduced *Pacifasticus leniusculus* in Swedish lakes where the data indicate preferential perch predation on the native *A. astacus* (Söderbäck 1994).

INTERACTIONS BETWEEN CRAYFISH AND SMALL BENTHIC FISH

Although small benthic fish like sculpins (European bullheads -*Cottus spp.*) or darters (*Etheostoma spp.*) are generally too small to feed on crayfish, these fish species share common adult sizes, food resources, and predators with crayfish. Therefore, crayfish and smaller benthic fish may interact competitively. However, these interactions are less well-studied than the standard predator-prey interactions of fish and crayfish. Studies of interactions between small benthic fish and crayfish include competition for limited shelters (Guan and Wiles 1997), competition for food (Miller et al. 1992), behavioral interactions in the presence of predators (McNeely et al. 1990), and combinations of these interactions (Rahel and Stein 1988, Wojdak and Miner unpublished manuscript).

In studies of competition for shelters, the results are mixed and dependent upon the species of fish and crayfish studied. Guan and Wiles (1997) found significant competition for shelter between the introduced crayfish *Pacifasticus leniusculus* and two benthic fish (*Cottus sp.* and *Neomacheilus sp.*) in a British lowland river. In laboratory experiments, crayfish excluded fish from shelters, and field surveys showed inverse correlations between fish and crayfish abundances (Guan and Wiles 1997). Rahel and Stein (1988) found similar results with darters (*Etheostoma sp.*) and the crayfish *O. rusticus*. In the laboratory, crayfish evicted darters from shelters and caused them to increase overall activity; this increased darter susceptibility to smallmouth bass predation. Wojdak and Miner (unpublished manuscript) found that an introduced fish species, the round goby (*Neogobius melanostomus*) had the opposite effect on the crayfish (*Orconectes rusticus*). In laboratory experiments, gobies competitively excluded crayfish from shelters and exposed the crayfish to increased bass predation. Thus, results of competition for shelter seem dependent upon the specific pair of species under study.

McNeely et al. (1990) found a complex behavioral interaction between *O. putnami* and the mottled sculpin (*C. bairdi*). In the presence of bass and crayfish, sculpins experienced less predation. This interaction involved a change in predator-avoidance behavior by the sculpin, dependent upon crayfish presence or absence. When crayfish were absent the sculpin utilized few shelters and employed a stationary behavior to avoid predator detection. In the presence of crayfish, sculpin increased use of shelter to avoid predation. The crayfish in this study were relatively invulnerable to predation and did not alter shelter use dependent upon bass presence or absence. However, the increased benthic activity of crayfish was thought to "draw the attention of the bass away from the sculpin" (McNeely et al. 1990).

Crayfish and equivalent-sized small benthic fish share common predators and shelters. From the above studies it is clear that competitive outcomes for common refugia are less than predictable. Complex behavioral interactions and agonistic exclusions act to make the outcomes of these interactions specific to particular fish-crayfish pairs. If introduced species of benthic fish and crayfish competitively exclude natives, this could lead to restructuring of the benthic food web as carnivorous benthic fish and omnivorous crayfish replace each other. Competition between benthic fish and crayfish for common food resources is a virtually unstudied area that deserves future research.

Trophic energy transfer, predator-prey interactions, and competition are the most obvious ways in which fish and crayfish may interact. However, there are a number of other potential pathways by which fish and crayfish populations may be linked. In the next section, we outline a few of the more subtle interactions that may occur between fish and crayfish. Much of the impetus for this section comes from studies that have examined the effects of exotic crayfish introductions (Hobbs et al. 1989) which have led to many insights about the roles of crayfish in freshwater communities (Lodge et al. 1998).

POTENTIAL NEGATIVE EFFECTS OF CRAYFISH ON FISH

Egg predation

In some northern Wisconsin lakes (USA), the decline of gamefish populations has been attributed to the invasion of the exotic crayfish *O. rusticus* (Hobbs et al. 1989). Egg predation has been proposed as one mechanism causing declines in bass, sunfish (Centrarchidae), walleye, and lake trout (*Salvelinus namaycush*). Observations indicate that sunfish only nest in areas where *O. rusticus* have been experimentally removed (K. Wilson, University of Wisconsin, Madison, USA -pers. comm.). In experiments, crayfish (*Orconectes spp.*) ate lake trout eggs (Savino and Miller 1991, Horns and Magnuson 1981), and rates of egg predation ranged from 2-5 $\text{eggs}\cdot\text{crayfish}^{-1}\cdot\text{day}^{-1}$, depending upon temperature, substrate, and crayfish species. Given this rate of predation, Savino and Miller (1991) concluded that predation by crayfish on lake trout eggs will only be important over a restricted set of conditions: high crayfish density and/or low egg density within cobble habitat.

The potential for crayfish to consume the eggs of warmwater fish may be greater. Bass and sunfish spawn at much warmer temperatures than lake trout, and Horns and Magnuson (1981) have shown that the rate of egg consumption by crayfish increases with temperature. Further, most bass and sunfish concentrate their eggs in shallow, littoral zone nests, which may make them more vulnerable to crayfish predation than the widely scattered eggs of trout or walleye. If crayfish can infiltrate these nests and/or feed unnoticed at night, egg predation on warmwater gamefish may be significant.

Destruction of macrophyte beds and effects on fish recruitment

Macrophytes are known to disappear in the presence of crayfish (Feminella and Resh 1989, Matthews and Reynolds 1992, Lodge et al. 1994, Olsen et al. 1991, Chambers et al. 1990). Some of the macrophyte destruction is due to active crayfish feeding, while a substantial amount is due to non-consumptive fragmentation (Lodge and Lorman 1987, Olsen et al. 1991). In this manner, crayfish may be viewed as ecosystem engineers - modifying the structural complexity of littoral zones through non-consumptive means (Lawton 1994, Jones et al. 1994).

For many fish species, macrophyte beds serve as important juvenile habitat (Mittelbach 1981). Dense stands of littoral-zone macrophytes provide shelter from predatory fish (Werner et al. 1983b), and also provide a source of vegetation-dwelling invertebrate prey (Osenberg and Mittelbach 1989, Persson and Greenberg 1990). Complex structural habitats (macrophyte beds) decrease the efficiency of piscivorous fish (Persson and Crowder 1998) affording protection for growing juvenile fish. When juveniles of different fish species take advantage of this littoral vegetated habitat, competition may occur (Mittelbach 1984, 1988). If macrophyte beds shrink following crayfish introductions, competition between juvenile fish for the remaining macrophyte refuge or associated invertebrate prey may increase. A loss of vegetated habitat may also lead to changes in competitive advantage between fish species (Persson 1991).

When exotic crayfish species such as *O. rusticus* and *Procambarus clarki* were introduced to water bodies, large losses in macrophytes were observed (Lodge and Lorman 1987, Feminella and Resh 1989, Lodge et al. 1994). Additional studies of *P. leniusculus* and *O. virilis* in Sweden and Canada respectively, support the hypothesis that exotic crayfish species will have large effects on macrophyte biomass, species richness, and associated invertebrate community structure/abundance when introduced (Nyström and Strand 1996, Chambers et al. 1990, Hanson and Chambers 1995). The link between macrophyte losses and effects on fish recruitment are logically sound, yet remain unexplored.

CONCLUSIONS

Fish and crayfish have traditionally been viewed as predator and prey. Recent studies, however, document a wealth of potential interactions between these macroconsumers. Many of these interactions were first observed when an exotic species of crayfish entered a system. Although predatory fish generally suppress crayfish activity, growth, and population densities, there are a number of examples where fish have been shown to have much smaller impacts on exotic crayfish. In one well-documented example, fish were found to accelerate the rate at which an exotic crayfish, *O. rusticus*, invades new lakes (Hill and Lodge 1999).

Although conclusive data are lacking, introduced benthic fish (e.g., gobies) and crayfish (*P. leniusculus*) may competitively exclude native fish and crayfish with potentially important consequences for structuring of benthic food webs. Future work in this area should 1) investigate the invasion ecology and competitive arenas between benthic fish and crayfish, and 2) examine the trophic effects of swapping carnivorous benthic fish and omnivorous crayfish in benthic food webs.

While most studies have focused on the predatory effects of fish on crayfish, there are a number of ways in which crayfish may negatively affect or control fish production. For example, crayfish eat fish eggs, and warmwater fish species may be especially vulnerable to crayfish egg predation. Crayfish also destroy macrophytes, which in turn reduces important habitat for juvenile fish (Mittelbach 1984, Persson and Crowder 1998). Future research in these areas should concentrate on the consequences of egg predation and macrophyte destruction (ecosystem engineering) for warmwater fish production. Between species differences in egg predation and macrophyte destruction should be examined to highlight potential consequences of crayfish introductions. Understanding the mechanisms of interaction between fish and crayfish is crucial if we are to be able to predict the consequences of species introductions, both intentional and accidental (Lodge et al. 1998).

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Table 1. Annual production (kg/ha/yr) of crayfish and percentage consumed by predatory fish in four natural systems.

System: lotic/lentic	Crayfish Annual Production (kg/ha/yr)	Percent of Annual Production consumed by fish	Fish species	Reference
Lentic				
3 Michigan lakes	17-141.8	1-40[a]	*Salvelinus fontinalis*	Gowing and Momot 1979
Lotic				
Missouri stream	415-505	33[b]	*Ambloplites rupestris* and *Micropterus dolumieu*	Rabeni 1992
Michigan stream	415	15	*Micropterus dolumieu*	Vannote and Ball 1972
		>35[c]	*Ambloplites rupestris*	
West Virginia Stream	70	31	*Ambloplites rupestris*	Roell and Orth 1993, Roell 1989 (from Rabeni 1992)
		35	*Micropterus dolumieu*	
		10	*Pylodictis olivaris*	

[a] dependent upon fish density, [b] converted from g dry wt/m^2 (Momot 1995), [c] estimated value from Vannote and Ball (1972).

Table 2. Results of gut content analyses in several freshwater systems where fish were found eating crayfish.

System and Location	Crayfish species	Fish species	Proportion of diet (wt mass)	Frequency in diet[a]	Reference
Lentic					
Kansas, USA	*Orconectes nais*	*Micropterus salmoides*		0.6-0.85	Rickett 1974[b]
Illinois, USA	*Orconectes virilis*	*Micropterus dolumieu*	44-49		Ross et al. 1995
Manitoba, Can	*Cambarus sp.*	*Micropterus dolumieu*		0.68	Fedoruk 1966
Michigan, USA[*]	*Orconectes virilis*	*Ambloplites rupestris*		0.42	Chriscinske et al. unpubl.
Manitoba, Can	*Cambarus sp.*	*Stizostedion vitreum*		0.03	Fedoruk 1966
Michigan, USA	*Orconectes virilis*	*Salvelinus fontinalis*	10-70		Gowing and Momot 1979
Michigan, USA[+]	*O. virilis, O. propinquus*	*Perca flavescens*		0.45	Quinn and Janssen 1989
Michigan, USA[+]	*Orconectes propinquus*	*Perca flavescens*	2-60		Wells 1980
Michigan, USA[*]	*Orconectes virilis*	*Perca flavescens*		0.3	Chriscinske et al. unpubl.
Norway	*Astacus astacus*	*Perca fluviatilis*		0.93	Dehli 1981
Kansas, USA	*Orconectes nais*	*Ictaluras melas*		0-0.16	Rickett 1974[b]
Lotic					
Michigan, USA	*Orconectes propinquus*	*Micropterus dolumieu*		0.97	Vannote and Ball 1972
W. Virginia, USA	various[c]	*Micropterus dolumieu*	60-85		Roell and Orth 1993
Michigan, USA	*Orconectes propinquus*	*Ambloplites rupestris*		0.66	Vannote and Ball 1972
W. Virginia, USA	various[c]	*Ambloplites rupestris*	55-80		Roell and Orth 1993
W. Virginia, USA	various[c]	*Pylodictis olivaris*	70-95		Roell and Orth 1993
s. England, UK	*Astacus pallipes*	*Esox lucius*		<0.1	Mann 1976

[a] proportion of fish found with at least one crayfish in their gut contents (empty stomachs excluded when possible). [b] experimental ponds stocked with fish and crayfish. [c] mixed diets of *Orconectes sanbornii*, *O. virilis*, and *Cambarus sciotensis*. [+] Lake Michigan [*] Lake Huron

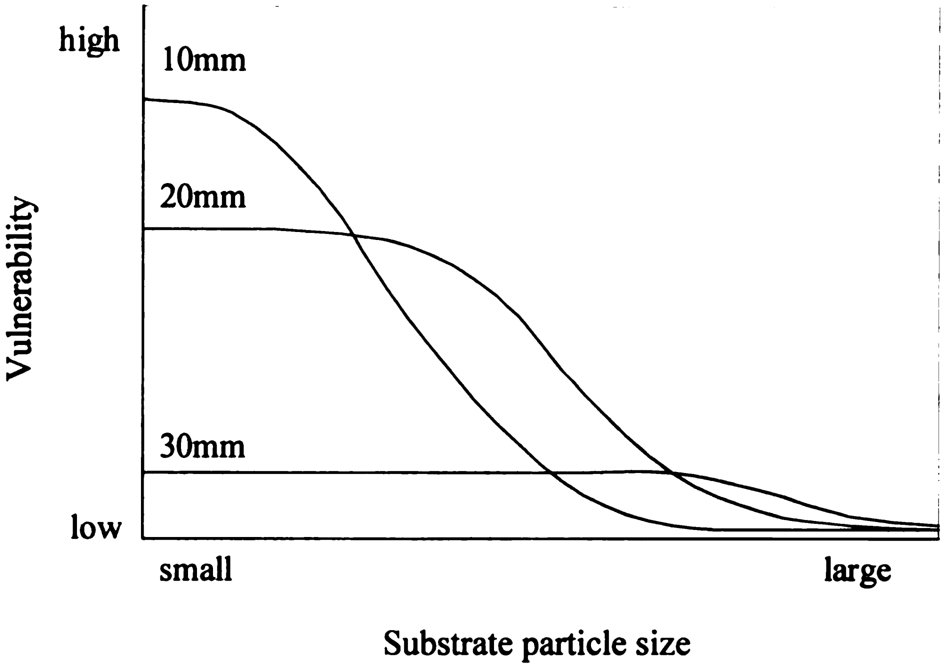

Figure 1. Hypothetical relationship between crayfish size (10-30 mm CL), substrate size, and vulnerability to fish predation.

CHAPTER 3

EGG PREDATOR EFFECTS ON FISH REPRODUCTIVE SUCCESS AND NESTING BEHAVIOR

with Gary G. Mittelbach

ABSTRACT

Early-life-stage predators can have profound effects on species population dynamics and community structure. The early life stages of fish are vulnerable to a suite of potential predators, yet relatively little is known about the impacts of egg- and fry-stage predators on fish reproductive success or breeding behavior. Crayfish are traditionally viewed as primary consumers and prey items for large fish, yet they are capable of feeding on substrate-bound fish eggs and fry and their introductions have been blamed for declining or disappearing fish populations in Europe and North America. We manipulated crayfish presence and absence in two replicated pond experiments and measured their effects on the reproductive success of two species of sunfish – bluegill (*Lepomis macrochirus*) and pumpkinseed (*L. gibbosus*). In both experiments, crayfish delayed (or prevented) successful reproduction, and the biomass of larval fish produced by the sunfish was significantly lower in the presence of crayfish. In the experiment with bluegill, crayfish inhibited all successful reproduction. However, when we added crayfish-proof exclosures to the experiment, the fish located the crayfish-free habitat and reproduced successfully. This work highlights the importance of egg/nest predation to fish reproductive success and nest site selection and it has important implications for understanding how early-life-stage predators may impact the spawning landscape of fish. These experimental results also provide evidence for egg predation as a mechanism that

can explain observed declines in fish populations following the invasion or purposeful introductions of crayfish.

KEYWORDS: bluegill, crayfish, egg predation, *Lepomis*, nest habitat, nest site choice, *Orconectes*, predator-prey, pumpkinseed, sunfish

INTRODUCTION

The early-life-stages of species are especially vulnerable to predators and high mortality on these stages can have strong effects on the recruitment dynamics of populations (Werner and Gilliam 1984, Martin 1993, Howe and Brown 2000). However, early-life-stage mortality events can be difficult to observe and quantify in the field, hindering our ability to identify important stage-specific predators and measure their impacts. Losses of recruits to predators begins at the egg and seed stage for animals and plants respectively. Egg/nest predation has been well-studied in avian systems, and nest predation (in combination with habitat features or fragmentation) has been cited as a major factor determining habitat-partitioning, species coexistence, community composition and recruitment failure for birds (Martin 1993, Robinson et al. 1995). Likewise, in grasslands and forests, seed predation can have profound impacts on plant populations and community structure (Schupp 1990, Howe and Brown 1999, 2000). The importance of egg/nest predators for fish behaviors, populations, and communities is comparatively unknown.

For many species of fish, the earliest egg and fry stages are closely associated with benthic substrates or vegetation for days to months (Breder and Rosen 1966). In these substrate-bound habitats the eggs and fry are vulnerable to a suite of predators that pose little or no threat to larger and more mobile life-stages. A variety of species are known to feed on the early-life-stages of fish (e.g., Gross and MacMillan 1981, Deblois and Leggett 1993, Mol 1996, Selgeby 1998, Dorn and Mittelbach 1999), however surprisingly little is known about the potential impact of any of these predators on species' reproductive success or spawning habitat use. This is in contrast to the well-studied effects of piscivorous predators on fish feeding behaviors and foraging habitat choice (e.g., Lima and Dill 1990, Mittelbach 2002).

Theory developed for avian systems predicts that predation rates on nests can be influenced by nest site characteristics (Schmidt 1999), and that favorable nests should therefore be defendable, cryptic, or located in habitats where brood predators are rare. If reproducing animals can discriminate amongst breeding sites, then nest defensibility, the spatial heterogeneity of nest/egg predators, or the presence of predator-free nest-space, may be important features determining the habitat choice and reproductive success of individuals and populations. While some animals seem to aggregate their nests for group defense (e.g., Tyler 1995, Wiklund and Andersson 1994), other animals breed in sites or habitats where the frequency of encounter with brood predators is low (e.g., Marzluff 1988, Clark and Shutler 1999, Schmidt 1999, Östlund-Nilsson 2000). For example, ducks and other waterfowl are commonly observed nesting in high densities on islands that lack mammalian nest predators (Clark and Shutler 1999). A few observations suggest that fish might be selecting breeding sites based on relative predation risk to their eggs (Beauchamp et al. 1992, Knapp 1993, Takemon and Nakanishi 1998, Östlund-

Nilsson 2000), but direct experimental tests of the effects of egg predators on the reproductive success and nesting habitat use of fish populations are lacking.

Crayfish (Decapoda) have historically been considered detritivores and herbivores (Momot 1995) and have been commonly introduced to lakes and streams as forage for fish, to reduce unwanted macrophytes (Hanson and Chambers 1995), or to provide human food (Gherardi and Holdich 1999). However, crayfish are relatively large invertebrates with polytrophic feeding habits, leading some to suggest that crayfish are important aquatic predators (e.g., Momot 1995) and potentially important predators of fish eggs (Hanson and Chambers 1995, Dorn and Mittelbach 1999). Recent studies from Europe and North America implicate introduced crayfish in the decline of fish populations in rivers, lakes, and streams (Guan and Wiles 1997, Covich et al. 1999, Nyström 1999, Wilson 2002, Bryan et al. 2002). The mechanisms for the negative effects of crayfish on fish are largely unknown, but predation on substrate-bound eggs or fry is one oft-cited hypothesis. In this paper we report the results from two field experiments designed to examine the impacts of crayfish egg predation on the reproductive success and nesting behavior of two species of North American sunfish: bluegill (*Lepomis macrochirus*, Rafinesque) and pumpkinseed (*Lepomis gibbosus*, Linnaeus).

Sunfish (Centrarchidae) are distributed throughout much of Eastern North America. The bluegill and pumpkinseed are two of the most common species, both are medium-sized fish (adults 10-20 cm standard length (SL)) and in southern Michigan they often account for >75% of total fish biomass in small lakes and ponds (Werner et al. 1977). Bluegill and pumpkinseed reproduce repeatedly over several weeks in the late spring/early summer after water temperatures reach 18-20°C. Large adult males construct depressions (nests) by fanning the substrate with their caudal fins. Males defend the nest, solicit eggs from females, and guard the brood until the young swim off the nest (6-10 days post egg deposition). Male pumpkinseeds tend to nest in a solitary manner while bluegill usually aggregate their nests into colonies. Colony nesting is thought to have evolved as a defense against egg predators (Gross and MacMillan 1981).

MATERIALS AND METHODS

We conducted two field experiments to examine the effects of crayfish on the reproductive success and nesting behavior of sunfish. The experiments were conducted at the Kellogg Biological Station's experimental pond facility in southwestern Michigan. The crayfish *Orconectes virilis* (Hagen) was stocked into previously crayfish-free ponds in our experiments. *O. virilis* is widely distributed throughout the eastern United States and Canada and is considered native to the upper midwest, however, it has been introduced to previously crayfish-free streams in Arizona (USA, Bryan et al. 2002) and lakes in western North America (Hepworth and Duffield 1987, Hanson and Chambers 1995). *O. virilis* can be found in several lakes around the Kellogg Biological Station, including the lake from which we collected the fish. For the experiments we collected crayfish in large numbers from ponds at the Michigan Department of Natural Resources research station in Saline, Michigan. The 1999 experiment examined the effects of crayfish on pumpkinseed reproductive success, while the 2001 experiment examined the effects of crayfish on bluegill reproductive success and nesting behavior.

1999 Pumpkinseed experiment

Six 30-year-old ponds (each 26 m dia.) were used for the 1999 experiment. These ponds had a heavy cover of macrophytes that reached to the pond surface by mid-summer and they were surrounded by a border of cattails (*Typha*). The ponds were drained in March 1999 and were allowed to sit empty for approximately 2 months, after which they were refilled to 1.6 m depth in May. In June, twelve adult pumpkinseeds (6 of each sex) were collected from a local lake and added to each pond (average standard lengths were 112-122 mm for males and 104-114 mm for females). Three of the 6 ponds were stocked with crayfish (mean carapace length (CL) of 38.5 mm) at 1.5 individuals/m^2 (26 g wet mass/m^2) prior to fish addition, and three ponds served as no-crayfish controls (hereafter referred to as "crayfish" or "no-crayfish" ponds). Crayfish reproduction in the ponds was extremely low in our experiments, as most females had already dropped their young prior to stocking. We used standardized trapping techniques (Lodge et al. 1986) on 3-4 dates throughout each summer to quantify crayfish activity-density. Crayfish were trapped overnight (15-18 hr sets) using 2-4 Gee minnow traps (Nylon Net Co.) per pond with openings adjusted to 4 cm. Traps were baited with 120 g of beef liver and set in the ponds (at least 5 m apart) at 17-18:00 on each trap date.

Nighttime observations of active nests and crayfish predation were made from the shoreline at 2-4 day intervals from the beginning of the experiment (12 June) through 14 July. In both experiments, an active nest was defined as any unmolested nest containing eggs or fry. Nesting observations were analyzed using repeated measures ANOVA (SAS 5.0, SAS Institute).

Young-of-the-year (YOY) fish were sampled in July and September 1999. In July (when fish were very small) we sampled with a wall seine (2.3 x 2.9 m with 1.8-mm-mesh fabric) attached to two wooden poles and operated by two swimmers (as in Rettig and Mittelbach 2002). The seine was placed in the middle of the pond and swum through the water towards shore, seining one radius of the pond. In September, when YOY fish were larger, the ponds were sampled with a bag seine (23 m long with 3.2-mm-mesh) covering approximately 15% of the pond area in one seine haul. All collected fish were euthanized with MS222 and preserved in 10% formalin or 95% ethanol. We calculated total biomass sampled for each pond using average lengths (N=35 fish) and pond specific length-wet mass regressions. Biomass, mean individual mass, and numbers of YOY were analyzed using ANOVA (Systat 9.0).

We used otolith analysis to examine the effects of crayfish on the timing of successful larval production. Otoliths (fish ear bones) were removed from a random sample of at least 35 YOY collected from each pond in September, and prepared using standard methods (Stevenson and Campana 1992). Briefly, sagittal otoliths were extracted and placed in a clear glue (Crystalbond Adhesive 509, Aremco Products Inc.) on a microscope slide. The otoliths were polished when necessary and viewed under a compound microscope at 10-40x magnification. Daily rings (Taubert and Coble 1977) on the right otolith were counted twice and averaged to determine fish age. If the two counts differed by >2 days, we made a third count and used the average of the two most similar counts. A few fish (<5) were discarded due to the inability to clearly read the daily rings. Differences between treatments in YOY age were analyzed using both parametric tests of pond-specific averages and a non-parametric test of the summed distributions.

We also checked for differences in YOY growth rates between treatments by regressing fish mass against fish age in each pond, and then using ANOVA to compare the fitted slopes of the regression lines (estimates of the increase in mass per day).

2001 Bluegill experiment

The six ponds used in the 1999 experiment were renovated during the summer of 2000 as part of an overall pond renovation at the experimental pond facility. Sediments and plastic liners were removed and replaced, with each pond receiving ~ 25 cm of a homogeneous sand and clay mixture. Ponds were filled to 2 m deep (29 m dia.) in November of 2000 and were allowed to colonize naturally with algae, macrophytes, and invertebrates from nearby ponds. At the beginning of the experiment the ponds had substantial populations of zooplankton, benthic invertebrates, clouds of filamentous metaphytic green algae (*Zygnema* and *Cladophora spp.*), and sparse macrophytes. Forty-five reproductive bluegill were stocked into each pond in June 2001. The populations stocked into each pond included 15 females (range of pond mean lengths = 129-131 mm SL), 15 large males (129-131 mm SL) and 15 small males (67-69 mm SL). The two male sizes correspond to the two commonly observed reproductive strategies described by Gross (1982) as “parentals” (larger nest-builders and guarders) and “sneakers”. Crayfish were stocked at a similar density as in the 1999 experiment (1.45/m^2), however the crayfish were smaller (mean CL = 29 mm) and therefore the biomass was lower (9.5 g/m^2).

A complete census of nesting activity in each pond was conducted every 2-3 days from 12 June - 3 August by divers using mask and snorkel or SCUBA. On each sampling date, the entire pond bottom was censused for active nests as well as evidence of nest attempts. Successful reproduction, as measured by recruitment to the free-swimming larval stage, was quantified with nighttime (22:00) ichthyoplankton net tows pulled across the surface of the pond once per week. Nighttime tows were employed to reduce the effects of net avoidance. Equal sampling effort was applied to each pond. The ichthyoplankton net (0.5-mm-mesh with opening of 68 cm diameter) was towed 27 m at 0.75 m/s, and captured larval fish (<8-10 mm SL) in the upper 68 cm of the water column. Larvae were preserved in 10% formalin, enumerated, and a random sample was measured for standard length.

On 5 July, one crayfish-proof exclosure was added to each of the three crayfish ponds. The exclosures measured 1.9 m^2 in area with walls made of 50-cm tall aluminum flashing and bottoms of fiberglass screen (1.2-mm-mesh). Each exclosure was filled with approximately 5 cm of substrate taken from the pond bottom. Exclosures were placed approximately 4 m from the center of the pond (away from the area of previously attempted nesting).

RESULTS

1999 Pumpkinseed experiment

Crayfish did not have a significant effect on the number of active nests observed in the ponds through time (rmANOVA treatment and treatment*time effect p values >0.36). On several nights in June and early July, crayfish were observed feeding on pumpkinseed eggs or fry inside nests (>10 crayfish in a single nest on one occasion).

Pumpkinseeds attempted to defend their nests by rushing at the crayfish with open mouths, and occasionally biting the crayfish on top of the carapace. In response, crayfish would either raise their chelae in defense, or back away from the nest. Crayfish activity-density over the summer averaged 1.9 individuals per trap-night (S.E.=0.2, N=3 dates).

YOY fish biomass sampled in July and September was significantly lower in the crayfish ponds than in no-crayfish ponds (July $F_{1,4}=11.76$, $p=0.027$; September $F_{1,4}=10.39$, $p=0.032$; Figure 1a). One crayfish pond failed to produce any YOY fish by the July sampling date. Nest destruction was observed several times in that pond and the first successful reproduction occurred in late July. The mean number of fish sampled per pond was lower on average in crayfish ponds (Figure 1b), but was not statistically different (July $F_{1,4}=1.43$, $p=0.3$; September $F_{1,4}=1.1$, $p=0.35$; Figure 1b). YOY fish in crayfish ponds were significantly smaller in July ($F_{1,4}=21.06$, $p=0.01$) and were generally smaller in September as well ($F_{1,4}=3.68$, $p=0.128$; Figure 1c).

Results of the otolith analysis indicated that YOY fish were born later in ponds containing crayfish (Figure 2). The distribution of YOY birthdates was significantly different when analyzed with a non-parametric Komolgorov-Smirnov two-tailed test of distributions (max. diff. = 0.575 two-sided $p<0.001$). The median birthdate also differed by about 12 days between treatments (ANOVA $F_{1,4}=7.175$ $p=0.055$).

YOY fish mass correlated positively with age in all six of the ponds, however there was no significant difference between the slopes of the regressions for the two treatments ($F_{1,5}=0.401$, $p=0.56$), suggesting the YOY fish grew at similar rates in crayfish and no-crayfish ponds.

2001 Bluegill experiment

In the no-crayfish ponds, active nests (e.g., those with eggs or larvae) were first discovered on 14 June (2 days after addition of females), and bluegill in those ponds continued to nest actively until 3 July (3-4 bouts of reproduction). By 14 June in crayfish ponds, bluegill had excavated nests in a similar spatial arrangement to the active nests observed in the no-crayfish ponds, and they kept them swept clean through mid-July. However, no nests with eggs or fry were observed in the crayfish ponds during the first 4 weeks of the experiment (Figure 3a), and on two dates (14 and 29 June) we found crayfish destroying nests in two of the ponds. In each case, more than 30 crayfish were found swarming 4-5 nests that contained a few remaining bluegill eggs. Overall crayfish activity-density was higher in 2001 than in 1999 (2001 average activity=9.44 crayfish per trap-night, S.E.=0.92, N=4 dates).

On 5 July we added one crayfish-proof exclosure to each crayfish pond to determine whether adult bluegill would be able to reproduce when given a crayfish-free nesting habitat. Eleven days later (16 July) active nests were observed inside the exclosure in one pond. Within a few more days, male bluegill in the other ponds were observed nesting within the exclosures; nesting activity continued until 3 August (Figure 3a). No crayfish were observed inside the exclosures and active nests were never found outside of the exclosures. After nesting commenced in the exclosures, male bluegill stopped sweeping off nests at the sites of previous nest attempts.

Larval bluegill were first collected in the no-crayfish ponds 14 days after the start of the experiment (26 June), and abundant larvae were caught in tow samples for the following 3 weeks (Figure 3b). After 16 July, most larval fish in the no-crayfish ponds had grown to a size (>10 mm Standard Length (SL)) at which they were able to avoid capture by our towed ichthyoplankton net. However, divers in the no-crayfish ponds continued to observe YOY fish throughout the remainder of the experiment. In the crayfish ponds, no larval fish were captured prior to the addition of the exclosures (Figure 3b). However, bluegill larvae were caught in the crayfish ponds 18 days after the exclosures were added (23 July), and larval recruitment was especially strong on 30 July.

DISCUSSION

Effective species management and conservation requires scientists and managers be able to identify important stage-specific interactions within and between species. It has been well recognized that seed and nest predators can have profound impacts on the population dynamics and community structure of plants and birds (Schupp 1990, Martin 1993, Robinson et al. 1995, Howe and Brown 2000). Egg predators can also have major impacts on population reproductive success of amphibians and reptiles (Petranka and Kennedy 1999, Chalcraft and Andrews 1999). While a host of freshwater animals, including many species recently introduced to the Great Lakes region (Segelby 1988, Chotkowski and Marsden 1999, Lodge et al. 2000), are known to eat the early life-stages of fish, little is known about the impacts of any of these organisms on fish reproductive success, spawning behavior, or population size. Some attempts have been made to quantify the impact of egg predators by extrapolating estimates of predator feeding rates (e.g., Mol 1996, Fitzsimons et al. 2002), however, no experimental studies have examined fish reproduction in the presence and absence of putative egg/fry predators. Our results indicate that egg predation can be extremely important to the reproductive success of sunfish.

While our experimental ponds are small relative to most natural lakes, they are good mimics of the shallow habitats where *Lepomis* sunfish breed and the densities and average activity-densities (i.e., trap CPUE) of crayfish in our experiments were well within the ranges observed for *Orconectes* crayfish in Midwest (USA) lakes, ponds, and streams. For example, Momot et al. (1978) report densities of 1.2-21.2 *Orconectes* crayfish/m^2 (4.6-95.2 g/m^2) from a variety of systems, and *O. virilis* in particular was found at densities of 1.9-6.1 crayfish/ m^2 (4.6-21.2 g/m^2) in low productivity marl-bottom Michigan lakes for several consecutive years. Activity-density (trap CPUE) of crayfish should give a good metric for comparing the potential impacts of crayfish across systems because it incorporates densities and system-specific foraging behavior, which could be influenced by food levels (hunger) and predators. Activity-densities of *Orconectes* crayfish in lakes can range up to 30 or more (adult crayfish) per trap (Capelli and Magnuson 1983, Collins et al. 1983, Olsen et al. 1991, Lodge and Hill 1994, Richards et al. 1996). Although many lakes with *O. virilis* have activity densities < 2/trap (Capelli and Magnuson 1983), a number of lakes have been found with activity-densities of 3.6 to 11.6/trap (Capelli and Magnuson 1983, Olsen et al. 1991). The invasive *O. rusticus* and another congener (*O. proprinquus*) can be found at much higher activity-densities (Olsen et al. 1991, K. Wilson 2002 and personal communication).

The difference in YOY biomass between the crayfish and no-crayfish ponds in the 1999 pumpkinseed experiment was caused by a combination of YOY size and density. The smaller average size of pumpkinseed YOY in the presence of crayfish was consistent with differences in age; YOY fish were born later on average in the ponds with crayfish. There was no evidence of differential YOY growth between the pond types. The observed later YOY birth dates could be the result of pumpkinseeds becoming more successful over time in the presence of crayfish, either by adjusting their spawning behaviors or changing nest site selection. Although we observed crayfish completely destroying nests on several occassions, male pumpkinseeds were persistent in their reproductive attempts and variable in their nest site use. In some cases we found nests in extremely shallow water (<20 cm), next to the bank, or in small aggregated groups. These nesting behaviors may have led to the eventual successful production of larvae in the presence of crayfish and suggest that pumpkinseeds may adjust their nest site selection or behavioral strategies in response to crayfish egg predation.

Further evidence of changing nest site selection in response to crayfish was observed in the 2001 bluegill experiment when no YOY were produced in the crayfish ponds until after the addition of crayfish exclosures. Active nests were never found in the crayfish ponds before the addition of crayfish exclosures and crayfish were observed eating fish eggs on two occasions. The successful reproduction we observed following the addition of crayfish-exclosures indicates that adult fish had sufficient resources to reproduce, but simply lacked a safe nesting habitat. It is interesting to note that in the no-crayfish ponds bluegill reproduction followed the normal course of reproduction observed in local lakes; most nesting occurs during 3-4 weeks in June and ceases early in July. However, in the crayfish ponds reproduction occurred much later and only after we added the crayfish exclosures. Clearly, bluegill have the ability to breed later into the season. Active nesting may have ceased in the no-crayfish ponds due to competition between YOY fish and adults for zooplankton prey. Macrozooplankton in the no-crayfish ponds disappeared quickly after the YOY fish were produced while large zooplankton in the crayfish ponds remained abundant until the fish reproduced later in the summer (Chapter 4).

Interactions of crayfish and fish populations

Crayfish have been introduced to waterbodies throughout the globe for purposes of augmenting fish forage or controlling macrophytes (Hobbs et al. 1989, Hanson and Chambers 1995). In addition to purposeful introductions, crayfish have also been inadvertently introduced to waterbodies through vectors like the bait trade (Lodge et al. 2000). While recent work indicates strong impacts of crayfish on macrophyte, macroinvertebrate, and amphibian populations (Chambers et al. 1990, Lodge et al. 1994, Gamradt and Kats 1996, Nyström 1999), there have been relatively few studies examining the effects of crayfish on fish populations (Dorn and Mittelbach 1999). Introduced crayfish have been implicated in the demise of fish populations in European rivers (Guan and Wiles 1997, Nyström 1999) and North American lakes (Lodge et al. 1985, Covich et al. 1999, Wilson 2002), and *O. virilis*, the crayfish used in our experiments, is believed to have negative impacts on native fish populations in Arizona streams (Bryan et al. 2002). In a recent study of crayfish feeding rates and densities, Fitzsimons et al. (2002) indicate that *Orconectes* crayfish could be important egg predators of a coldwater, broadcast-spawning fish species (Lake trout - *Salvelinus namaycush*) as well. Our experimental results provide the best evidence to date, and the only experimental work, indicating that crayfish are important egg predators of fish.

Egg predators and breeding habitats

In addition to their impact on reproductive success, egg/nest predators may also affect nesting strategies or breeding site selection. Colonial breeding in birds and fish is probably the best-known example of an anti-predator nesting strategy (Wiklund and Andersson 1994, Tyler 1995), but strategic nest placement can also lower predation risk (Martin 1993, Schmidt 1999). For *Lepomis*, nest site selection is traditionally assumed to be a response to habitat structure (Breder and Rosen 1966, Colgan and Ealey 1973, Bietz 1981, Popiel et al. 1996). However, if egg predators have significant effects on fish reproductive success, and fish are able to recognize areas of high and low egg predator risk, then habitat selection may occur as a response to spatial variation in predation risk as well (Gross and MacMillan 1981). Crayfish are most abundant in cobble habitats which provide a refuge from predaceous fish (Lodge and Hill 1994), leading to heterogeneous distributions of this egg predator in lakes with multiple habitats. Likewise, small fish (various species) and bullheads (*Ictalurus spp.*), which are known egg predators of sunfish (Gross and MacMillan 1981, Popiel et al. 1996), are most abundant in vegetated habitats (Gross and MacMillan 1981, Werner et al. 1983). Bluegill and pumpkinseeds would therefore reduce exposure to both types of predators if they nested in relatively open habitats, which matches their observed breeding sites in lakes and ponds (Colgan and Ealey 1973, Gross and MacMillan 1981, Breder and Rosen 1966).

Our 2001 experiment suggests that bluegill can discriminate between safe and risky nesting habitats. No crayfish were observed inside the exclosures in the crayfish ponds and active nests were never found outside of the exclosures. There also was no evidence of fish attempting to nest in any other areas of the pond (except for the original, abandoned, nest sites) suggesting that bluegills selected nesting locations inside the exclosures (which occupied <1% of the pond bottom) to avoid crayfish egg predation. Other aspects of the exclosure besides the absence of crayfish may have stimulated nesting, and we cannot rule this out directly because we did not have a crayfish-permeable control structure. However, if bluegill were attracted to some physical feature of the exclosure then we might have expected nesting attempts on both sides of the exclosure walls (inside and out), which did not occur.

Other researchers have observed correlations between spawning sites or preferred nest sites and lower levels of egg predation risk (e.g., Beauchamp et al. 1992, Knapp 1993, Clark and Shutler 1999, Östlund-Nilsson 2001). However our study is the first to experimentally manipulate egg predator presence, offering fish an environment with variable predation risk. Observations of birds (Martin 1993, Schmidt 1999, Clark and Shutler 1999) and experiments with mites (Janssen et al. 2002) indicate that other animals may lower exposure to egg predators by breeding in selective habitats. Waterfowl are known to nest in high densities on islands lacking mammalian nest predators (Clark and Shutler 1999). However, in this case, it is not known if birds are actively choosing to nest on islands in response to predator absence or whether selection has simply favored a return to safe or natal nesting habitats. On a landscape scale, predator-free nesting habitats or islands could be extremely important for the long-term reproductive success of populations. Future experimental work is needed to fully evaluate the relative roles of brood predators, environmental structure, and other factors in determining the breeding site choices of fish and other animals.

Viewing and Managing the Spawning Landscape

Little is known about the impacts of early-life-stage predators on the reproductive success or population size of any fish. Observational studies based on extrapolation of egg and fry survival rates or predator feeding rates suggest that egg and fry predators may strongly influence reproductive success and population size in both marine and freshwater systems (e.g., Deblois and Leggett 1991, Wisenden 1994, Mol 1996, Fitzsimons et al. 2002). The introduction of new species or types of predators may be especially critical for fish populations.

If introduced predator species have different patterns of habitat use or higher overall densities, then their appearance may change the spawning landscape in ways that become more hazardous for early-life-stages of fish. For example the introduced crayfish, *Orconectes rusticus* has displaced *O. virilis* and another congener, *O. propinquus*, in many Midwestern lakes (Lodge et al. 2000). *O. rusticus* and *O. virilis* have similar feeding habits but *O. rusticus* is less vulnerable to fish predators and is thought to utilize open non-cobble habitats to a greater degree than the species they replace (Capelli and Magnuson 1983, Lodge et al. 1985). Open habitats generally have low crayfish densities could provide adequate nesting areas the activity-density of crayfish increases on those habitats. In some invaded lakes, crayfish activity-densities on non-cobble habitats exceed 20/trap (K. Wilson, personal communication, unpublished data), which is more than twice the activity-density we measured in our 2001 experiment when bluegill reproduction failed completely. After *O. rusticus* invaded Trout Lake (WI), crayfish activity-density increased several-fold and populations of bluegill and pumpkinseeds virtually disappeared (Wilson 2002). Similar reports of disappearing sunfish populations in association with crayfish invasions have occurred in the past (e.g., Magnuson et al. 1975), and our experiments point to egg predation as an important mechanism capable of explaining these observations. In many southern Michigan lakes around Kellogg Biological Station, *O. virilis* is present at low densities, probably due to poor environmental conditions (anoxia, soft organic sediments), and seems to have little impact on populations of *Lepomis* sunfish. However, in hard-bottom lakes with abundant crayfish (native or introduced) *Lepomis* populations may suffer unless safe spawning sites exist.

Future considerations of available or appropriate spawning habitat should consider a “fish-eye view” of both the physical habitat structure and the distribution of early-life-stage predators. Because fish breed consistently in particular habitat types, spawning habitat has been generally identified and quantified using metrics of physical structure or other abiotic variables (e.g., Takemon and Nakanishi 1998, Bernier-Bourgault and Magnan 2002). However, egg and fry predator densities can vary from site to site as well (Wisenden 1994, Fitzsimons et al. 2002), and natural selection should produce inverse correlations between breeding activity and egg predator abundance. In the Great lakes, lake trout spawn on reefs and other rocky areas and are believed to respond to appropriate structural and abiotic features of the habitat (Marsden et al. 1995a). Egg predators have historically been considered unimportant (e.g., Wagner 1981), but there has been increasing interest in determining the impacts of egg/fry predators on reproductive success and spawning habitat use (Marsden et al. 1995b, Fitzsimons et al. 2002). Beauchamp et al. (1992) reported that the self-sustaining population of lake trout in Lake Tahoe (CA) spawned in a non-traditional habitat - over macroalgae (*Chara delicatula*) located on deepwater mounds surrounded by even deeper (>100 m) water. Egg predators were uncommon on the mounds (few sculpins – *Cottus* spp. and no crayfish) and it was postulated that trout spawned on these sites, rather than in other deep rocky areas, in response to the paucity of egg predators (Beauchamp et al.

1992). Spawning habitat use of lake trout, sunfish (this study), cichlids (Wisenden 1994, Takemon and Nakanishi 1998), and other species of fish in other contexts, may be a reflection of their behavioral and/or selected responses to variable densities of important egg predators as well as physical habitat variables.

Adding artificial structures to lakes and other systems to enhance fisheries, restore degraded habitats, or meet a variety of other types of goals is a common management practice (e.g., D'Itri 1985, Jude and Deboe 1996). It has also been a goal in some cases to introduce these structures as breeding habitats for fish (Peck 1986). Unfortunately, some organisms, including crayfish and benthic fish (e.g., gobies (*Neogobius spp.*) and sculpins), that inhabit these structures are considered both fish forage (Janssen and Quinn 1985, Jude and Deboe 1996) and egg predators (Chotkowski and Marsden 1999, Fitzsimons et al. 2002). These benthic predator species are believed to be limited in distribution and density by available shelters (Janssen and Quinn 1985, Lodge and Hill 1994), and by adding structure where there was previously little, managers and others may be inadvertantly enhancing egg predators (see also Jude and DeBoe 1996). If artificial structures (e.g., reefs, docks, riprap, and breakwalls) allow crayfish or other egg predator populations to colonize new habitats or increase overall densities (due to increased juvenile survival), then the predation rates on fish eggs and fry will increase.

Although early-life-stage predators of fish have been overlooked compared to their counterparts in terrestrial ecosystems (e.g., avian nest predators, seed predators), our findings indicate that egg/nest predators can be very important to fish breeding behaviors and reproductive success. Specifically, aquatic resource managers assessing the impacts of past or future introductions of crayfish should consider their potential negative effects on fish populations, as well as their potential benefits as fish prey. In general, egg/nest predators may play an important role in determining the overall quality of the reproductive landscape. Hopefully, the results of this study and others will give managers a better "search-image" for identifying factors that determine quality spawning habitat and for recognizing potentially hazardous management plans that may damage the reproductive landscape for fish and other taxa.

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Figure 1. Production of young-of-year (YOY) pumpkinseed (*L. gibbosus*) in ponds with and without crayfish (*O. virilis*) during summer 1999. (a) Mean total biomass (numbers x mean size) of YOY sampled with standardized seining. (b) Mean number of YOY captured in seines. (c) Mean wet mass (g) of sampled YOY. Error bars represent one standard error and p-values are from one-way ANOVAs (N = 3).

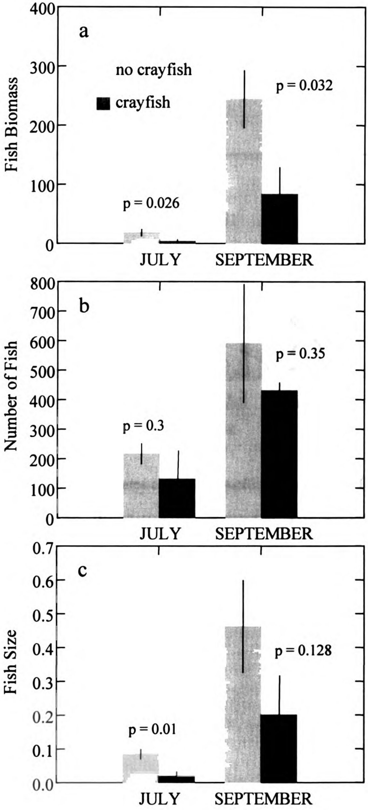
a
no crayfish
crayfish
Fish Biomass
400
300
200
100
0
p = 0.032
p = 0.026
JULY
SEPTEMBER
b
Number of Fish
800
700
600
500
400
300
200
100
0
p = 0.35
p = 0.3
JULY
SEPTEMBER
c
Fish Size
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
p = 0.128
p = 0.01
JULY
SEPTEMBER

Figure 1

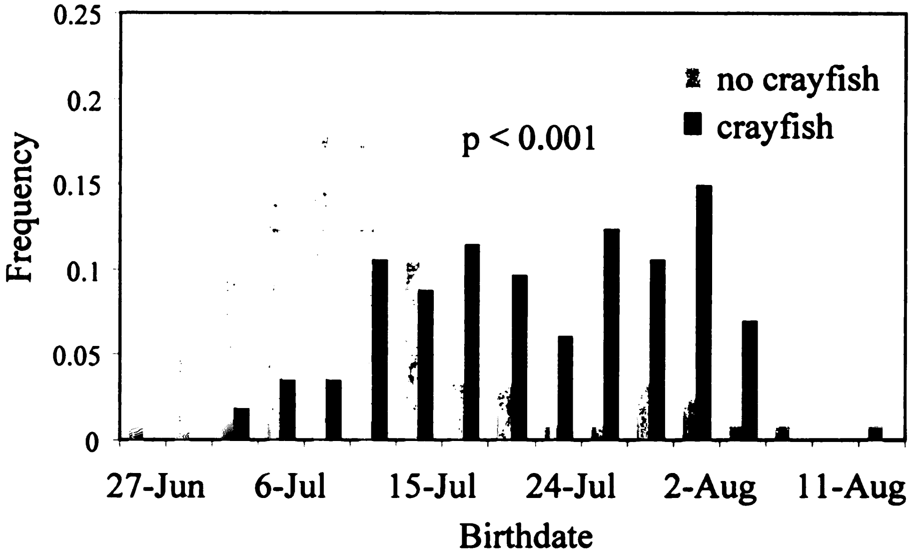

Figure 2. Distribution of birthdates of YOY pumpkinseed collected from ponds with and without crayfish in 1999. Birthdates were estimated by enumeration of otolith daily growth rings. Distributions were compared with a non-parametric Komolgorov-Smirnov test.

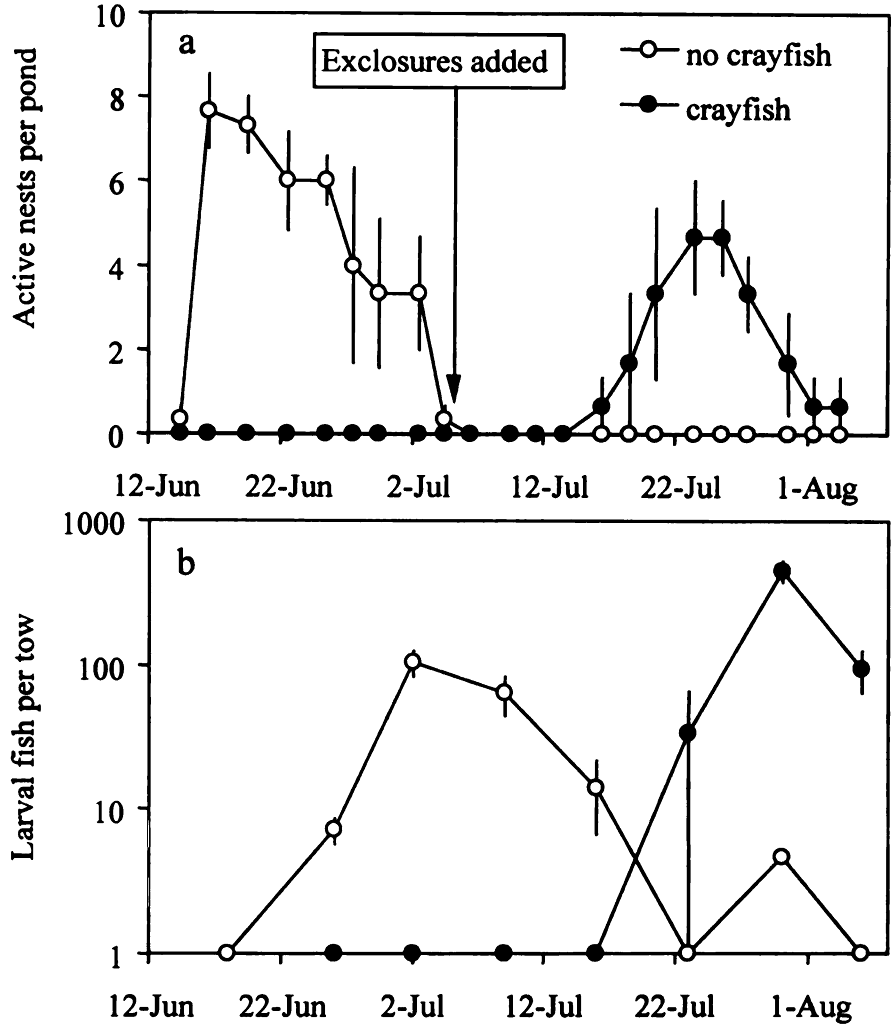

Figure 3. Timeline of bluegill (*L. macrochirus*) nesting and larval recruitment in ponds with and without crayfish (*O. virilis*) during summer 2001 (N = 3). (a) Mean number of active bluegill nests (nests with eggs or fry) per pond. (b) Mean number (+1) of free-swimming YOY bluegill caught per standardized ichthyoplankton tow/pond. Error bars denote one standard error. Exclosures were added to crayfish ponds on 5 July.

CHAPTER 4

OMNIVOROUS CRAYFISH DEFLECT SUCCESSIONAL PATHWAYS IN POND COMMUNITIES: AN EXPERIMENTAL STUDY

with Jeremy M. Wojdak

ABSTRACT

Studies of succession in freshwater habitats have been primarily limited to the seasonal succession of planktonic communities in lakes, whereas successional dynamics in the littoral zone has been largely ignored. In this study we followed the development of benthic and planktonic communities in six newly created, replicate, experimental ponds in the presence and absence of crayfish, an important benthic omnivore. Over the period June 2001 – June 2002, we measured the following community and ecosystem properties; zooplankton and phytoplankton abundance, water quality (dissolved oxygen, particulates, light), abundance of benthic primary producers, and success of invertebrate and vertebrate populations.

Zooplankton biomass was higher in crayfish ponds throughout the study, primarily the result of failed fish recruitment due to egg predation by crayfish. Patterns of phytoplankton biomass did not reflect the expected cascade in 2001, and were higher in the crayfish ponds as well. The higher levels of phytoplankton biomass observed in crayfish ponds in 2001 was probably due to resuspended nutrients (crayfish ponds had lower light and higher suspended solids). Peak dissolved oxygen levels were lower in the crayfish ponds throughout the study, indicating that they had a lower primary production: respiration ratio. In control ponds, *Chara* and a few macrophyte species covered 34% of pond bottoms by June 2002, whereas *Chara* and macrophytes were completely absent from crayfish ponds. Crayfish also had pronounced effects on the metaphyton and periphyton communities in the ponds, a result of both direct consumption of algae and indirect interactions through other herbivorous species. For example, exclusion by crayfish of two important grazer groups (tadpoles and gastropods) was associated with higher periphyton levels in the crayfish ponds at the end of 2001. Total benthic invertebrate biomass did not respond to crayfish presence, but *Caenis* mayflies and chironomids had altered size-distributions. These results indicate that omnivorous crayfish can have strong impacts on succession and community structure of shallow freshwater ecosystems.

KEYWORDS: *Chara*, *Cladophora,* crayfish, community, gastropod, *Gleotrichia*, herbivory, metaphyton, omnivory, *Orconectes*, periphyton, succession, tadpole

INTRODUCTION

Community structure of insular systems like ponds and lakes may be strongly influenced by the colonization and extinction of key species (Magnuson 1976). For example, the presence or absence of fish can have profound impacts on trophic-level biomass relationships, nutrient cycles, species composition, and size-structure of producers and consumers in lakes (Leibold 1989, McPeek 1990, Carpenter and Kitchell 1993, Mittelbach et al. 1995, Schindler et al. 2001). Zimmer et al. (2001, 2002) show that in wetlands naturally undergoing periodic fish colonization and extinction events, the presence or absence of fish has consistent influences on community structure and water quality. While effects of fish on community structure are fairly predictable, other largebodied consumers, particularly herbivores or omnivores, also may have strong impacts on succession and community structure in shallow freshwater environments.

Experimental studies in terrestrial and marine intertidal communities have demonstrated the important role of herbivores and omnivores in determining successional outcomes. For example, herbivores may speed up succession (e.g., Sousa 1979, Lubchenco 1983), slow it down (e.g., Brown 1985, Sarnelle 1993, Howe and Brown 2001, Cadenasso et al. 2002), or even deflect its path (*sensu* Godwin 1929, Hixon and Brostoff 1996, Gibson and Brown 1992). Deflections, as distinguished from changes in rates, follow different pathways to different endpoints (Hixon and Brostoff 1996), which Godwin (1929) called "specialized climaxes" and others refer to as alternate stable states (Petraitis and Dudgeon 1999). Understanding the biotic factors that determine the consistency or contingency of successional dynamics remains a central goal in community ecology (Walker 1987, Berlow 1997), reinforced in part by its important ramifications for ecosystem restoration (Palmer et al. 1997). However, while experimental studies of succession are common in terrestrial and marine intertidal systems, relatively few studies have used controlled experiments to examine the factors influencing succession in freshwater systems, outside of studies examining the seasonal succession of plankton in lakes (e.g., Sommer 1989, Sarnelle 1993).

Small lakes and ponds undergo succession over many time scales. For example, temperate systems show seasonal succession in species composition and relative abundances due to annual variation in temperature and/or precipitation. Over decades, lakes and ponds may undergo succession due to eutrophication, accumulation of sediments, or changes in regional hydrological regimes (at the extreme drying up and refilling). Over very long time scales (hundreds or thousands of years), most lakes and ponds gradually fill in and eventually disappear. Lakes and ponds are also subject to the chance colonization and/or extinction of species (Magnuson 1976, Zimmer et al. 2001) and as a consequence we might expect these species to influence successional pathways. Here, we focus on the potential role of crayfish in influencing pond succession.

Crayfish are relatively large invertebrates with polytrophic feeding habits (Momot 1995). Their diets include algae, aquatic vascular macrophytes, detritus, invertebrates, fish eggs, and carrion, and they can attain relatively high biomass and production rates in some systems (Momot 1995). The presence, absence, and relative abundance of crayfish in shallow water ecosystems can be influenced by colonization through overland watercourses, changes in water levels, deletions or introductions of predaceous fish, habitat modification, winterkill, acidification, and disease, as well as human introductions (Lodge and Hill 1994, Gherardi and Holdich 1999). Over longer time scales of primary succession in temperate zones, rates of glacial retreat and recolonization rates will determine if and when systems colonize with crayfish.

In a survey of 42 ponds, Nyström et al. (1996) found that systems with more crayfish had sparser and less diverse macrophyte communities, lower benthic invertebrate biomass, shifts in invertebrate community composition, and lower organic matter content of the sediment. From this correlative study, Nyström et al. (1996) hypothesized that crayfish may have important impacts on the succession of shallow aquatic ecosystems. We tested this prediction experimentally, by examining the effects of crayfish on pond successional dynamics in six replicate ponds at the Kellogg Biological Station (KBS) in southwestern Michigan, USA.

METHODS

Setup

The 18 ponds at the KBS experimental pond facility (each 29 m dia., 2 m maximum depth) were constructed in 1972. The pond site is about 800 m (and uphill) from the nearest source of crayfish and there has been no natural colonization by crayfish. In October 2002, nine of the 18 ponds were renovated by first draining the ponds and then bulldozing out the existing sediments and plastic liners. The ponds were then relined with plastic and covered with a sand-gravel-clay sediment mixture (20-25 cm deep). Ponds were filled in November 2000 with water from an on-site reservoir and allowed to colonize naturally with organisms from nearby ponds (except for the planned addition of fish and crayfish, described below). We followed the first-year successional dynamics of these ponds, with and without crayfish. Because of their identical construction and close proximity to one another (31-36 m between pond centers), the ponds provide an excellent experimental opportunity to examine the direct and indirect effects of crayfish on early pond succession.

Crayfish (*Orconectes virilis*, Hagen) were collected from the Michigan Department of Natural Resources Fisheries Research Station in Saline, Michigan and were stocked into three of the six ponds at approximately 1.4 individuals $\cdot$ m^{-2} (9.3 g $\cdot$ m^{-2}). Because I suspected gradients from the front of the pond array to the back (especially in bird and turtle use of the ponds), the treatments were interspersed across the array. Crayfish were stocked on 31 May (after their yearly reproductive cycle) at an average carapace length (CL) of 29 mm. We monitored crayfish trap capture rate (an estimate of density or activity-density) using standardized (e.g., Lodge and Lorman 1986) baited minnow traps set overnight (2-4 traps · pond^{-1} · night^{-1}). Stocking densities and trap capture rates of crayfish in our experiment were well within the natural range of crayfish densities in ponds as well as *Orconectes* crayfish for a number of systems (e.g., Abrahamsson 1966, Momot et al. 1978, Capelli and Magnuson 1983, Olsen et al. 1991). Stocking densities in our ponds were considerably lower than the density of *O. virilis* that develops naturally (i.e., without supplemental feed) in the source ponds (10-15 crayfish · m^{-2}, J. Gapczynski personal communication). Furthermore, in three low-productivity marl-bottom lakes in Michigan, *O. virilis* were found found at densities of 1.9-6 crayfish · m^{-2} (4.6-21.2 g ·m^{-2}) for 5 consecutive years (Momot et al. 1978, Momot and Gowing 1977).

In late May and early June 2001, 30 large (129-131 mm standard length, SL) and 15 small (67-69 mm SL) bluegill sunfish (*Lepomis macrochirus*, Rafinesque) were added to each pond. The bluegill were seined from a local lake and added in equivalent sex ratios and sizes to each pond (see Chapter 3). At the time fish and crayfish were added to the ponds, the ponds had already been colonized by plankton, benthic invertebrates, filamentous metaphyton (e.g., *Cladophora* and *Zygnema*), and a few macrophytes.

Measurements

Plankton

Zooplankton and phytoplankton were sampled six times during the spring and summer between 14 June, 2001 to 6 June, 2002. We used an integrated tube sampler (1.5 m deep, 7 cm diameter – similar to Steiner 2002) to sample zooplankton from 5-7 locations around the pond on each date. A total of 16 L of water was collected on each sampling date. The water was filtered through a 80-µm sieve and zooplankton were preserved in acid Lugols. Zooplankton were enumerated and identified to genus with the exception of copepods, which were identified as calanoids or cyclopoids. The major cladoceran taxa were *Daphnia* (>99% *D. pulex*), *Ceriodaphnia*, *Diaphanosoma*, *Simocephalus*, *Bosmina*, and *Chydorus*. From each sample, we measured the body lengths of up to 50 haphazardly-chosen individuals of each taxon and converted lengths to biomasses using published length-dry weight regressions (e.g., Burns 1969, Dumont et al. 1975).

To estimate phytoplankton biomass, we collected a 300 ml water sample (0.4 m deep) from a single location near the middle of each pond. For each pond and date, 100-200 ml of water was filtered onto Gelman A/E glass fiber filters (pore size 1.0 µm). The filters were extracted in 20ml of 95% ethanol at 7°C for 18-20 hours. Chlorophyll *a* ($\mu g \cdot L^{-1}$) concentration was determined using narrowband fluorometry (Welschmeyer 1994).

Dissolved oxygen, light, and seston

On each plankton sampling date, we also measured peak dissolved oxygen levels using a YSI Model # 600 XL-100-M oxygen meter within an hour of sunset. Measurements were taken at 0.3 m increments from 0.3 to 1.8 meters deep. The measurements were averaged across depths for the analysis, however the depth profiles were shallow and did not exhibit any regular differences between the treatments. Water clarity was measured using a light meter (LI-COR model # LI-185B) in 2001 and a small secchi disk (16 cm diameter) in 2002. In 2001 we calculated the light extinction coefficient between the surface and 2 meters depth as (ln(watts at surface) – ln (watts at 2 m))/2. Light extinction was measured once (11 July) in 2001 - secchi disk depth was measured twice (May and June) in 2002. Total particulate matter and the component organic and inorganic fractions were measured on 26 July 2001. Water from each pond was collected and particulate matter was filtered onto preweighed and combusted Gelman A/E glass fiber filters. Dry mass was determined after drying the filters for 40 hrs at 60° C and ash content was determined after combusting in a muffle furnace for 50 minutes at 500° C.. The concentration ($mg \cdot L^{-1}$) of total particulates (dry weight – filter weight), particulate inorganic matter (ash weight – filter weight), and particulate organic matter (difference between total and inorganic) were calculated for each pond. Particulates were not measured in 2002.

Benthic community

Primary Producers

We visually estimated percent cover of macroalgae (*Chara vulgaris*) and vascular macrophytes (always rare) in June of both summers by diving into the ponds (SCUBA) and using quadrats. Seven haphazardly placed 0.25 m^2 quadrats were dispersed throughout the pond in shallow areas (0.2-1.8 m deep) and five quadrats were dispersed throughout deeper (1.8-2 m) areas (reflecting the proportionally greater shallow habitat in the ponds). Two divers made independent estimates of percent cover (to the nearest 5%) for each quadrat sample. The independent measurements agreed well ($R^2 = 0.92$, slope = 1), and were averaged for each point measurement to calculate mean percent cover in each pond. In June of 2001 we used the same quadrat method to estimate the abundance (% cover) of mats of metaphytic green algae (unattached algae dominated by filamentous-green forms like *Cladophora* and *Zygnema*) found on the pond bottom. Metaphyton mats were present in the ponds before the treatments were applied in 2001 and these mats (individually up to 8 m^2) would regularly rise and fall between the bottom and the surface on sunny days.

We characterized the composition of the metaphyton community on 24 August, 2001 by collecting samples of metaphyton from the surface of each pond. Samples were homogenized and then enumerated on a Zeiss Axioskop microscope at 400 X magnification. At least 300 natural units were counted for each sample. Identification was to genus whenever possible.

Periphytic algal biomass (algae attached to hard substrates like gravel and sand) was quantified by placing 12 ceramic tiles (31.5 cm^2) in the center (2 m deep) and 24 tiles on the sloping north shore (0.75 m deep) of each pond on 14 June 2001. The tiles colonized naturally and three tiles were collected on each sample date (1 deep, 2 shallow) from each pond. Each tile was extracted in 40 ml of 95% ethanol for 18-20 hours. Chlorophyll *a* concentration (expressed as $\mu g \cdot cm^2$) was determined using a fluorometric techniques similar to that used for the phytoplankton.

Invertebrates

Benthic invertebrates were sampled on 13 June 2002 using a D-shaped sweep net (27 cm wide, with 1-mm mesh). One sweep was taken from 3 of the 4 quarters of each pond at 0.5 m depth (one randomly chosen quarter-pond was ignored). The net was placed on the substrate at each sample point and moved at a constant rate for 0.75 meters sampling an area of approximately 0.2 m^2. The three samples were pooled and then sorted by placing the contents in white, enameled pans and picking out the live invertebrates by hand. Invertebrates were preserved in 80% ethanol and later counted and identified under a dissecting scope to family or genus. For analyses, invertebrate taxa were combined into four categories based on their abundance: chironomidae, *Caenis* (mayflies), gastropods, and other (including Trichoptera, Odonata, Heteroptera, and

Hydrachnida) . To estimate biomass and compare size-structure, a random sample of at least 25 individuals of each major taxa was measured from each sample when possible. Length-dry mass regressions (unpublished) developed for local organisms were used to estimate total invertebrate biomass and the biomass of each group. For taxa that were abundant in all ponds (*Caenis* and chironomids), we compared their population size structures by lumping all measured individuals from a treatment into a single size-frequency distribution.

Vertebrates

Bluegill reproduced in the ponds and we quantified the abundance of young-of-year (YOY) fish in 2001 using a ichthyoplankton net (0.5-mm mesh with a 68-cm dia opening) towed across the pond at nighttime at regular sampling intervals (see Chapter 3 for details). We also made repeated observations of bluegill nesting behavior using SCUBA. Only qualitative estimates of fish abundance were made in 2002. The abundance of bullfrog (*Rana catesbiana*) tadpoles was quantified in August 2002 using baited minnow traps set overnight in each pond.

Metaphyton choice feeding experiment

To determine whether selective grazing by crayfish caused a shift in metaphyton composition from filamentous greens to dominance by the filamentous blue-green *Gleotrichia*, we performed a feeding preference assay following the methodology of Peterson and Renaud (1989). On 2 August, 9 male crayfish (CL range = 40-42 mm) were placed in individual plastic containers (25 cm dia., filled 3.5 cm deep with pond water) and offered similar wet masses (mean = 9.0 g) of drained and weighed filamentous green metaphyton (mostly *Cladophora*) from a control pond and blue-green *Gleotrichia* from a crayfish pond. Crayfish ponds had abundant *Gleotrichia* at this time of the year and all control ponds had green metaphyton mats similar in appearance to the *Cladophora* used in the feeding trials. The crayfish were starved for 6.5 hours prior to the start of the feeding trials. Both algal types were added simultaneously to the nine containers with crayfish, and to an additional nine control containers without crayfish. The use of controls allows for statistical incorporation of variation in autogenic mass change (Peterson and Renaud 1989). After 20 hours of feeding, the crayfish were removed and the remaining algae was sorted, drained, and reweighed.

Crayfish migration between ponds

In the late-summer/ early-fall of 2001 a few crayfish invaded the control ponds from nearby crayfish ponds by moving overland (a common behavior for this species in the ponds where we collected them – J. Gapczynski, pers. comm). We attempted to remove the invading crayfish by hand using SCUBA, however, a few individuals eluded us and reproduced in the control ponds in mid to late May of 2002. Initially the small YOY crayfish had little effect on the status of the treatments. However, by mid-July they had reached relatively large sizes (some > 20 mm CL), were trappable with baited minnow traps, and were having noticeable impacts on *Chara* (visible herbivory). Thus, our treatments effectively homogenized by mid July 2002 and we were forced to end the experiment.

Statistical Analyses

Data were log-transformed when necessary to normalize distributions or to meet assumptions of homogeneity of variances. Phytoplankton, zooplankton, oxygen levels, secchi disk depth, and periphyton measures were analyzed through time and between treatments using repeated measures ANOVA (rm-ANOVA hereafter) with SAS 8.0 (SAS Institute). Data from 2001 and 2002 were analyzed separately for each response variable (3-4 measures in 2001 and 1-2 measures in 2002) because there was no correspondence of dates between years. We analyzed our data using Proc Mixed, a general linear mixed model, which allowed us to optimize the covariance structure for each analysis. Akaike's Information Criterion was used to choose the best structure for each data set - compound symmetry was the best structure for most of our analyses. If significant time x treatment interactions were found, the data were sliced by time (lsmeans option in Proc Mixed) to look for treatment differences on individual dates.

One-way ANOVAs were used to analyze percent cover of *Chara* and metaphytic green algae, invertebrate biomass, amphibian abundance, light extinction coefficients, and particulate matter. Non-parametric Komolgorov-Smirnov two-sample tests were used to compare the size-frequency distributions of *Caenis* and chironomid larvae. Data from the laboratory feeding assay with *Cladophora* and *Gleotrichia* metaphyton were analyzed with a t-test of differences which incorporates variation from an equal number of controls into a test of differences in proportional mass change (Peterson and Renaud 1989).

RESULTS

Crayfish abundance

Mean crayfish abundances ranged from 4.7-12.3 · trap^{-1} in 2001 (N = 4 dates) to 0.33-2.1 · trap^{-1} in 2002 (N = 3 dates). Differences in crayfish abundances were due to natural mortality as well as a lack of reproduction in 2001. This species of crayfish has a maximum lifespan of three years and reproduction occurs once per year in the spring.

The crayfish added to the ponds were age 1 and 2, and cohort biomass and numbers of *O. virilis* in lakes (with similar standing stock biomass) naturally declines from age 1 to 2 and 2 to 3 (Momot and Gowing 1977). In fact, cohort numbers often decline by 70-89% from year 2 to 3 (Momot and Gowing 1983). There was no reproduction in 2001 because individuals were introduced to the ponds after their spring reproductive cycle. Crayfish did reproduce in 2002 in the crayfish ponds, but the small YOY did not reach large enough sizes to recruit to traps by mid-summer.

Plankton

Total zooplankton biomass was highest (~0.9 mg dry mass $\cdot$ L^{-1}) early in the summer of 2001, then declined over time (time effect $F_{3,12} = 38.88$, $p < 0.0001$, Figure 1). Zooplankton biomass was similar between treatments on the first sample date of the experiment in 2001 ($F_{1,15.6} = 0.07$, $p = 0.7948$), but was significantly higher in the crayfish ponds on the last 3 dates of 2001 (sliced by date: $F_{1,15.6} > 11.5$, $p < 0.004$). Zooplankton composition was very similar between treatments on the first date in 2001 (larval fish recruited into the water column). However, the zooplankton composition quickly shifted to copepod dominance in the control ponds by the second sample date, while cladocerans (large and small) remained relatively more abundant for longer in the crayfish ponds (Table 1). In 2002, zooplankton biomass remained significantly higher in the crayfish ponds (treatment effect $F_{1,4} = 14.43$, $p = 0.019$).

In 2001, phytoplankton biomass (μg chlorophyll *a* $\cdot$ L^{-1}) was significantly higher in the crayfish ponds (treatment effect $F_{1,4} = 14.99$, $p = 0.018$) and increased through time (time effect $F_{3,12} = 17.19$, $p = 0.0001$) (Figure 2). Treatments reversed direction in 2002, with phytoplankton biomass being higher in the control ponds (treatment effect $F_{1,4}$ = 24.55, p = 0.077).

Dissolved oxygen, light, and seston

Mean peak dissolved oxygen (mg $O_2 \cdot L^{-1}$) was higher in control ponds than in crayfish ponds in 2001 ($F_{4,12}$ = 5.62, p = 0.048) and tended to be higher in 2002 as well ($F_{1,4}$ = 13.1, p = 0.059, Figure 3). Although the treatment effect was not significant in 2002 the largest single difference came on the last date (June 2002) when the crayfish ponds were undersaturated and all control ponds were supersaturated with oxygen.

Light extinction coefficients were higher in crayfish ponds in 2001 ($F_{1,4}$ = 30.23, p = 0.0053) which was consistent with diver observations of reduced visibility in crayfish ponds throughout the summer. Light extinction coefficients, however, were not related to water column chlorophyll *a* concentrations (r = -0.11, p =0.82). In 2002, water transparency (measured by secchi disk depth) was not different between treatments (rm-ANOVA treatment and treatment x time interaction p-values > 0.72).

Total particulate matter (mg $\cdot L^{-1}$) was significantly higher in crayfish ponds ($F_{1,4}$ = 33.4, p = 0.004, Figure 4) in 2001. Both the organic and inorganic fractions were larger on average in the crayfish ponds (organic $F_{1,4}$ = 10.3, p = 0.033, inorganic $F_{1,4}$ = 10.6, p = 0.031), and the inorganic fraction accounted for a much greater proportion of the total in crayfish ponds (49.8%) compared to control ponds (10.3%).

Benthic community

Primary producers

From June 2001 to June 2002, the percent cover of *Chara* in control ponds increased from < 1% cover to an average of 34% cover (Table 1). *Chara* failed to establish in any of the crayfish ponds - small patches of *Chara* were occasionally observed in these ponds, but none persisted. The lack of a significant treatment effect on *Chara* abundance in 2001 was due to high variability among control ponds during initial colonization.

There were pronounced difference in the development of the metaphyton community in ponds with and without crayfish. Mats of metaphytic green algae (mainly *Cladophora* and *Zygnema*) were found in the control ponds in June 2001, but were absent from the crayfish ponds (Table 1). Late summer (August) samples of the metaphyton community showed that all ponds had become dominated by blue-green forms (at least 64% of all cells in cell-counts), but *Gleotrichia* was only found in the crayfish ponds where it was the dominant metaphytic taxa (Table 2). By 2002, metaphyton was rare or absent in both pond types, however, small amounts of *Gleotrichia* were observed in the crayfish ponds in June 2002. In our feeding trials, crayfish simultaneously offered *Cladophora* metaphyton from a control pond and *Gleotrichia* from a crayfish pond preferentially consumed the *Cladophora* (60% mean reduction in wet mass) and virtually ignored the *Gleotrichia* (Figure 5, t-test of differences $p < 0.0001$).

Periphyton biomass changed through time but was dependent upon treatment (Figure 6; time effect ($F_{2,8} = 9.77$, $p = 0.0071$) and time x treatment interaction ($F_{2,8} = 5.54$, $p = 0.0104$)). The control ponds had more periphyton early in July (sliced by date: $F_{1,3.04} = 11.22$, $p = 0.0431$), but the crayfish ponds were significantly higher in August ($F_{1,5.69} = 9.54$, $p = 0.023$). In 2002, the treatments maintained the same rank as at the end of 2001 (all crayfish ponds had higher chlorophyll *a* measures than all control ponds), but they did not differ significantly ($F_{1,4} = 3.3$, $p = 0.144$).

Invertebrates

Crayfish significantly reduced gastropod biomass (*Gyraulus*, *Lymnaea*, and *Physa*) ($F_{1,4} = 21.2$, $p = 0.01$; mean dry mass in $mg \cdot m^{-2}$ (S.E.): control ponds = 8.4 (3.1), crayfish ponds = 0.34 (0.34)), but had no effect on the biomass of other taxa or on the biomass ($mg \cdot m^{-2}$) of all benthic invertebrates combined ($F_{1,4} = 2.17$, $p = 0.21$). Chironomids (larvae and pupae) and *Caenis* (nymphs) showed significant differences in size between treatments, with chironomid sizes shifted towards smaller individuals in crayfish ponds (Komolgorov-Smirnov 2-sample test $p = 0.008$, Figure 7a), and *Caenis* shifted towards larger individuals in the presence of crayfish ($p < 0.0001$, Figure 7b).

Vertebrates

Crayfish were significant predators on bluegill eggs and larvae and detailed observations of their effects on bluegill reproductive success are reported in Chapter 3. In brief, bluegill reproduced throughout June 2001 in the control ponds, but due to egg predation by crayfish, they were unable to reproduce successfully in the crayfish ponds until crayfish-proof exclosures were added on 5 July 2001 (Chapter 3). Adult bluegill began spawning in the crayfish-proof exclosures in mid-late July and produced a pulse of larval fish late in the summer (See timing of first successful recruitment in Figure 1). Small larval bluegill densities ranged from $1\text{-}10 \cdot m^{-3}$ in the control pond from mid-June to mid-July (Figure 1) and they were quickly outgrowing the sizes that we could catch with our ichthyoplankton net. Larval bluegill were never caught in the crayfish pond during that same period (Chapter 3). We observed bluegill (juveniles and adults) in all the ponds in spring 2002, indicating that the fish survived the winter. However, we do not have detailed measures of their 2002 abundances.

Crayfish had a similarly dramatic effect on bullfrog reproductive success. In more than 70 person-hours of observation with mask and snorkel and from shore, we never found a bullfrog tadpole in any of the crayfish ponds. Tadpoles were abundant, however, in 2 of the 3 control ponds in 2001 and in all 3 control ponds during 2002. Baited crayfish traps placed in all six ponds in August, 2002 captured an average of 7.2 bullfrogs per trap (S.E. = 0.72) in the control ponds and 0.0 in the crayfish ponds ($p < 0.0001$).

DISCUSSION

Crayfish had pronounced effects of the development of benthic and planktonic communities in our experiment ponds and these effects were due to a combination of direct and indirect interactions. We discuss these effects below, first in the context of our experiment and then in a more general framework, combining our results with those of other studies of crayfish to examine the role of crayfish on littoral zone community development in a wider range of freshwater systems.

Crayfish abundance

Although our initial crayfish stocking densities were reasonable considering densities in oligo-mesotrophic north-temperate lakes (Momot et al. 1978, Capelli and Magnuson 1983, France 1985, Olsen et al. 1991, see METHODS) crayfish abundance declined in the crayfish ponds from 2001 to 2002. Density changes from 2001 to 2002 were a result of natural mortality and a lack of reproduction in 2001 (see Results). However, even if our stocking densities were at or slightly above the carrying capacity of the ponds, our observations of the control ponds that were invaded in 2002 indicate that the outcome would have been very similar had we started the ponds with small numbers of adults and let the population grow naturally. When the ponds were drained in September of 2002, the YOY that were born into one of the control ponds had attained a population size of approximately 500 very large YOY (20-30 mm CL), the pond bottom was barren (in June it had 33% cover of *Chara*), and the pond was extremely turbid (personal observations).

Plankton and water quality

Crayfish had a strong, positive effect on zooplankton biomass, driven by their negative impacts on fish recruitment (Chapter 3). Interestingly, this effect on zooplankton biomass did not cascade down to affect phytoplankton abundance in 2001. This could be a consequence of bottom-up effects of crayfish via sediment (and nutrient) resuspension. Crayfish also consumed or excluded benthic macroalgae and macrophytes, and together these effects of crayfish may have indirectly augmented phytoplankton production rates. Despite our effort to avoid visible metaphyton in the phytoplankton samples, it is also possible that some of the samples from 2001 were contaminated by metaphyton or other suspended benthic algae. However, the blue-green metaphyton bloom in the crayfish ponds did not begin until late July and therefore could not account for differences earlier in the summer. If the samples were highly contaminated with filamentous green algae early in the summer it should have favored higher values in the control ponds (where *Cladophora* mats were abundant). In 2002, zooplankton continued to be more abundant in the crayfish ponds, whereas phytoplankton differences reversed such that crayfish ponds had significantly less phytoplankton. Higher zooplankton biomass in crayfish ponds could reflect lower numbers of juvenile fish in 2002, and our qualitative observations suggest this was the case. Phytoplankton levels in 2002 were consistent with expectations of top-down control by zooplankton, and may have been realized in 2002 (vs. 2001) if the lower abundance of crayfish had weaker indirect effects on phytoplankton production (note: water transparency was not different in crayfish vs. control ponds in 2002).

Peak levels of dissolved oxygen indicated that crayfish had an impact on the ecosystem production: respiration ratio in the ponds. Lower peak dissolved oxygen could have been caused by increased light limitation, exclusion (consumption) of primary producers, and/or increased respiration of decomposers (through organic matter processing or aeration of the sediments). Crayfish are clearly important in processors of organic matter in streams (Usio 2000, Schofield et al. 2001, Creed and Reed *in press*), but further work is necessary to determine the mechanisms by which crayfish influence production: respiration ratios in lentic ecosystems. If this impact were to remain consistent through time, crayfish ponds should accumulate organic matter at a slower rate than ponds without crayfish (Momot 1995, Angeler et al. 2001), consistent with the observations by Nyström et al. (1996), that ponds of similar age with more crayfish had lower organic matter content in the sediments. Future work on crayfish should pay attention to this type of engineering role of crayfish that could have important long-term effects on ecosystem development.

Benthic community structure

Crayfish had strong direct effects on the benthic primary producers in our experiment. *Chara* macroalgae and filamentous alga *Cladophora* are known to be eaten by crayfish (Creed 1994, Nyström and Strand 1996) and they were strongly reduced by crayfish in our ponds. The shift in the metaphyton to dominance by the blue-green

Gleotrichia was most likely driven by selective consumption of *Cladophora* by crayfish. The results from our choice feeding assay demonstrated that crayfish preferred *Cladophora* over *Gleotrichia*, and in our casual observations walking around the pond edges we noted that crayfish commonly passed over opportunities to feed on *Gleotrichia*. It is also possible that the shift in metaphyton communities could have been influenced by sediment (and nutrient) resuspension. These results suggest that *Gleotrichia* is a relatively unpalatable or unprofitable form of algae, and that the metaphyton communities underwent a compositional shift due to strong top-down grazing.

Observations of plant succession in other KBS ponds (without crayfish) indicate that succession usually proceeds from green metaphyton mats (year 1) to mostly *Chara* (year 2) and then to increasingly more diverse vascular macrophytes in subsequent years (G. G. Mittelbach, personal communication). The appearance and dominance of *Gleotrichia*, and the exclusion of green-algae metaphyton mats and *Chara*, indicate that crayfish have dramatically altered the expected successional sequence of benthic primary producers in these ponds.

Strong trophic cascades from omnivorous crayfish to snails (or tadpoles) to periphyton have been observed in short-term experimental studies (Lodge et al. 1994, Nyström and Åbjörnsson 2000, Nyström et al. 2001), and our results suggest that a similar cascade may have occurred in the ponds. Tadpoles and gastropods were abundant in the control ponds during mid-summer 2001 but were absent or rare in crayfish ponds at the end of 2001 and in 2002. Crayfish are well-know predators of gastropods (Lodge et al. 1994, Nyström et al. 1999, 2001), but the mechanism responsible for the absence of bullfrog tadpoles in crayfish ponds is unclear. Ponds containing *Lepomis* sunfish are normally good habitat for bullfrog tadpoles because sunfish eliminate the invertebrate predators (e.g., Odonates) that feed on bullfrog tadpoles (Werner and McPeek 1994, Smith et al. 1999). Crayfish may have inhibited bullfrog breeding by eliminating the egg attachment sites; bullfrogs attached their egg masses to *Cladophora* metaphyton mats and pond margins in control ponds, but the mats were eliminated from crayfish ponds (also see Nyström 1999). It is also possible that crayfish had a direct effect on tadpole abundance by consuming egg masses laid along the pond margins or that bullfrogs avoided breeding in ponds due to the presence of crayfish. Crayfish will consume eggs of many amphibians including *Rana* frogs (Axelsson et al. 1997).

Periphyton biomass was significantly higher in the crayfish ponds in August 2001, consistent with a trophic cascade from crayfish to tadpoles and snails to periphyton. Periphyton biomass in 2002 was also higher in all crayfish ponds than the control ponds, but these differences were not significant. Because crayfish exclude some, but not all, benthic grazers and also consume periphyton, the long-term effects on periphyton biomass are difficult to predict (Nyström et al. 1996).

Crayfish did not influence the total biomass of invertebrates or the biomass of other taxa besides snails. However, crayfish had significant effects on the size-structure of chironomid and *Caenis* populations. Chironomids, which were smaller in crayfish ponds, are relatively immobile taxa (like snails) that are easily preyed upon by crayfish. Creed and Reed (*in press*) report similar effects of crayfish on the size-structure of chironomids which suggest crayfish are selectively feeding on larger chironomids. In contrast, *Caenis* larvae were larger in crayfish ponds. Mayflies are more mobile taxa and are probably not strongly influenced by crayfish predation (Nyström 1999, Nyström et al.

1999). Elimination of other grazers (tadpoles and snails) may have had indirect positive effects on *Caenis* growth rates in crayfish ponds. The higher periphyton biomass in the crayfish ponds at the end of 2001 suggests there may have been more resource available for *Caenis*. Nyström et al. (1999) suggested the same indirect mechanism was responsible for increased mayfly biomass in their mesocosm experiment.

General implications for community development

In Figure 8 we offer an illustration of systems with and without abundant crayfish to serve as 1) a pictorial summary of our results, combined with results from other studies and 2) a diagram of expected outcomes of succession. These expectations are most appropriate for ponds, shallow lakes, and littoral zones or shallow bays of deep lakes. The exact manifestation of the effects will be influenced by regional species pools, predators, and abiotic variables (pH, habitat, conductivity; Lodge and Hill 1994), and may be altered by presence or absence of other strong interactors (e.g., zebra mussels – *Dreissena polymorpha*, Stewart et al. 1998, Perry et al. 2000). But, for the purposes of general discussion, we will consider two similar littoral environments that differ only in the presence or absence of crayfish. It should be noted that not all crayfish are equal, and introduced species can sometimes become much more abundant than the species they replace (e.g., Wilson 2002). These expectations can therefore potentially apply to ponds or lake margins colonized by at a variety of successional stages.

In systems with few or no crayfish (Figure 8A) we would expect a community with more abundant and diverse macrophytes and snails. Crayfish decrease the biomass and species richness of macrophytes (including *Chara*)(Dean 1969, Feminella and Resh 1989, Chambers et al. 1990, Lodge et al. 1994, Nyström et al. 1996, Wilson 2002, this study, and others) and most species of snails are greatly reduced or excluded from systems with abundant crayfish (Lodge et al. 1994, 1998a, Nyström and Pérez 1998, Nyström et al. 2001, this study). However, heavily armored snail taxa (e.g., *Goniobasis, Campeloma*) can sometimes be found in areas with abundant crayfish (NJD - personal observations, Lodge et al. 1994).

The strong effects of crayfish on bullfrogs (this study) and on newts (Gamradt and Kats 1996) indicate that crayfish can have dramatic negative impacts on amphibian populations. Direct and indirect interactions are probably responsible for these effects (Gamradt and Kats 1996, Gamradt et al. 1997, Nyström 1999, Nyström and Åbjörnsson 2000).

Other effects on invertebrate communities have been represented in Figure 8 by the differences in size-structure of the sediment dwelling chironomids (this study, Creed and Reed *in press*) and mayflies (this study, biomass effect – Nyström et al. 1999). These differences reflect both direct effects of size-selective predation by crayfish (chironomids) and indirect positive effects (through exclusion of other grazers) on mobile insect grazers (mayflies).

Figure 8 indicates that crayfish can influence fish recruitment through egg predation (Nyström 1999, Fitzsimons et al. 2002, Chapter 3), but this effect is just one of many routes by which crayfish can influence fish populations and communities (Dorn and Mittelbach 1999). Small crayfish (especially YOY) are important prey items and could thereby positively affect some predatory species of fish (Rickett 1974, Stein and Magnuson 1976, Dorn and Mittelbach 1999). However, adult crayfish are relatively invulnerable to fish predators (Stein 1977) and large populations of crayfish (mostly exotic introductions) have been blamed for failed recruitment and fish population declines in ponds, lakes, rivers, and streams (Buck and Thoits 1970, Magnuson et al. 1975, Hepworth and Duffield 1987, Hobbs et al. 1989, Guan and Wiles 1997, Covich et al. 2000, Bryan et al. 2002, Wilson 2002).

Based on our results, zooplankton and/or phytoplankton may be expected to be more abundant in shallow systems with abundant crayfish. Depression of larger plants, predation on fish eggs (which limited abundance of zooplanktivores), and resuspension of nutrients could all impact the plankton. In other studies, bioturbation by crayfish relocated large amounts of sediment (Stazner et al. 2000) and resuspended significant amounts of phosphorous (Angeler et al. 2001, Ottolenghi et al. 2002). Of all the expected effects illustrated in Figure 8, the effects on plankton and fish recruitment are probably the most system- and species-specific, and we suggest them as hypotheses for future investigations.

Effects of animals on succession

Increasing attention is being paid to the role of consumers (mostly herbivores) on successional dynamics of plant communities (e.g., Lubchenco 1983, Bowers 1993, Sarnelle 1993, Hixon and Brostoff 1996, Howe and Brown 2001, Cadenasso et al. 2002). Herbivores can alter the rate of succession, and in some cases herbivores can even change the trajectory of succession (e.g., Hixon and Brostoff 1996, Gibson and Brown 1992). Although many have considered invertebrate herbivores to be inconsequential to succession dynamics of terrestrial plant communities, Carson and Root (1999) demonstrated that insects can have a strong impact on the rate of succession in oldfields. They hypothesized that well-defended or outbreaking species of invertebrates will have important effects on vegetation dynamics. In freshwater ecosystems, crayfish are the largest invertebrate consumers, they grow to predator-invulnerable sizes (Stein 1977), they can attain high community biomass (Momot 1995), and they are some of the most important macrophyte herbivores (Lodge et al. 1998b).

Most freshwater ponds and lakes have an insular nature (Magnuson 1976). Different ponds and lakes colonize with different assemblages of consumer species, and the major disturbances extinguishing or introducing consumer species occur episodically over relatively long time scales. Development and persistence of community structure in ponds and lakes may depend on the introduction, persistence, and size of consumer populations that exert major structuring effects. Although herbivores commonly change the rate of succession, the broad diets of omnivores and their potential to maintain their populations on alternate resources while suppressing populations of other more vulnerable or preferred species (Polis and Strong 1996) make them prime candidates to deflect the trajectory of community development (Knowlton 1992). In freshwater ecosystems fish are the largest predators, many of them are omnivorous (Vadas 1990) and they have strong impacts on community structure as evidenced when they are introduced or extinguished from a system (e.g., Mittelbach et al. 1995, Zimmer et al. 2001). Deletions and introductions of omnivorous crayfish (native or exotic) can have similarly large impacts on community structure.

Studies of crayfish deletions in Europe due to the crayfish plague (*Aphanomyces astaci* Schikora) have yielded observations consistent with the expectations from our experiment. In Sweden, the native crayfish *Astacus astacus* disappeared from 5 ponds (3 m deep, ≥ 2 ha) that had contained crayfish for 44 years. Pond bottoms that had been previously barren when crayfish were present developed a heavy cover of *Chara* and vascular macrophytes one year after the population crashed (Abrahamsson 1966). In addition, "(t)he number of molluscs and leeches increased markedly and immense numbers of young tadpoles appeared in the ponds." Nyström (1999) indicated that the same 5 ponds have been recolonized by a North American crayfish, *Pacifasticus leniusculus* (not susceptible to the plague), and have shifted back to the crayfish dominated (low macrophyte) condition. Similar changes in *Chara* and mollusc populations were documented when the plague eliminated native European crayfish from littoral zones of larger lakes (100 and 430 ha) in Ireland (Matthews and Reynolds 1992). Consistent effects of introductions have been observed in wetlands and lakes in the United States (e.g., Feminella and Resh 1989, Magnuson et al. 1975, Dean 1969).

In conclusion, our data indicate that crayfish can have dramatic impacts on the succession of pond communities through a variety of direct and indirect effects. Crayfish colonization of ponds or littoral habitats has the potential to drastically change community structure to a macrophyte-poor and algae-dominated, structurally simpler system, having lower productivity: respiration ratios and higher sediment resuspension rates, where some species may benefit, but others are excluded or do poorly. More broadly, our results indicate that succession and community structure of shallow freshwater ecosystems is dependent upon colonization or extinction events of important benthic invertebrate consumers.

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Table 1. Relative abundance (mean % of total biomass) of zooplankton groups in ponds with and without crayfish. Large cladocerans = *Daphnia* and *Simocephalus*; small cladocerans = *Bosmina*, *Ceriodaphnia*, *Chydorus*, and *Diaphanosoma*; copepods = calanoids and cyclopoids.

		2001				2002	
mean %	treatment	6/14	7/5	7/26	8/24	5/7	6/6
Large Cladocerans	control	58	23.9	9.3	0	1.3	7.3
	crayfish	63.3	40	6.3	0	2.4	2.4
Small Cladocerans	control	0.6	3.6	6.8	2.8	0	4.2
	crayfish	2.6	37.3	58	0.9	5.8	52.4
Copepods	control	41.3	72.5	83.9	97.2	98.7	88.5
	crayfish	34.1	22.6	35.5	99.1	91.8	45.2

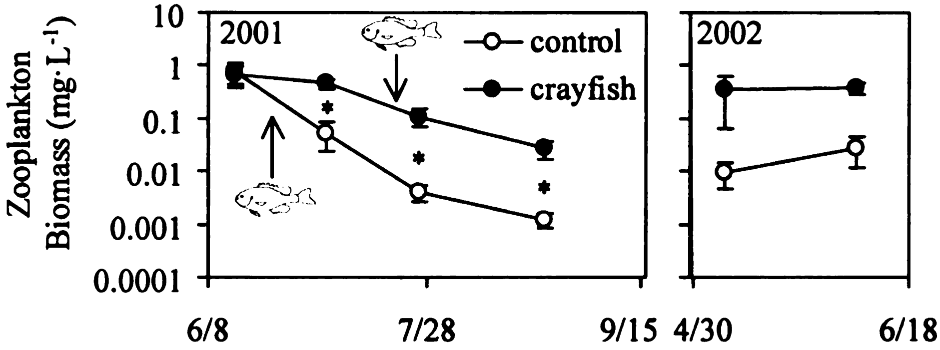
Table 2. Percent cover of green metaphyton (*Cladophora* and *Zygnema* algal mats) and *Chara* on the bottom of 6 ponds.

		Mean % cover		ANOVA results	
Date	Plant	control ponds	crayfish ponds	$F_{1,4}$	P
June, 2001	Green metaphyton	7.4 (1.5)	0 (0)	103.8	0.0005
June, 2001	*Chara*	0.73 (0.37)	0 (0)	3.99	0.117
June, 2002	*Chara*	34 (12.9)	0 (0)	63.57	0.0013

Table 3. Percent abundance (% of cells in counts) of algal genera in metaphyton samples taken from 6 ponds in late August 2001. All taxa that made up $\geq$ 5% of all cells in at least one pond are included in the table.

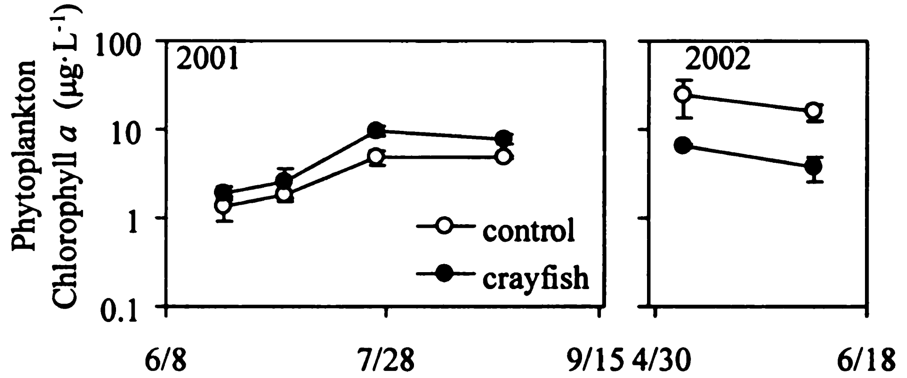
		Control ponds			Crayfish ponds		
Form	Genus	1	2	3	1	2	3
b-g. fil.	*Gleotrichia*	0	0	0	29.5	87.3	51.6
b-g. fil.	*Leptolyngbya*	29.4	28.8	13	25	p	15.5
b-g. fil.	*Nostoc*	0	0	25.9	0	0	0
b-g. fil.	*Pseudoanabaena*	10	16.2	10	p	p	p
b-g. fil.	*Phoridium*	0	23.6	10.7	0	0	0
b-g. fil.	*Cylindrospermum*	14.7	0	0	0	0	0
b-g. fil.	*Calothrix*	0	18.8	0	0	0	0
b-g. col.	*Aphanocapsa*	7.4	p	p	0	0	p
g. fil.	*Mougeotia*	p	p	10.4	0	0	0
diatom	*Navicula*	16.4	p	6.1	16.9	p	p
diatom	*Achanthidium*	p	0	8	10	p	12.4
diatom	*Cocconeis*	0	0	0	0	0	9.2

b-g. fil. = blue-green filamentous, b-g. col. = blue-green colonial, g. fil. = green filamentous. p = present with abundance of < 5%. 0 = not present in the sample.



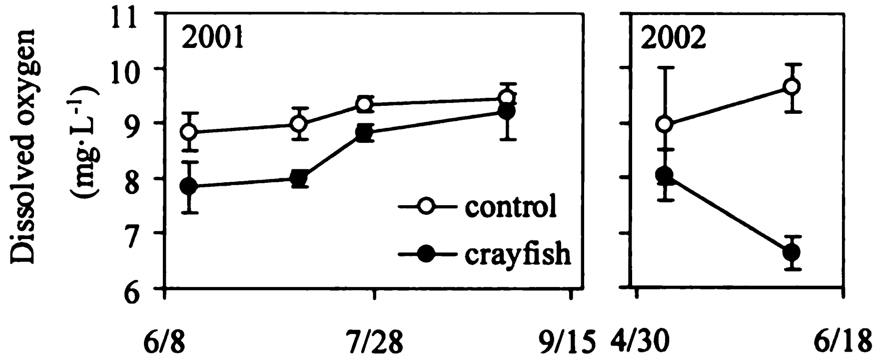
Effect	df	F	P	df	F	P
Treatment	1,4	29.1	**0.0057**	1,4	14.4	**0.0191**
Time	3,12	38.9	**<0.0001**	1,4	4.18	0.1104
Treatment x Time	3,12	5.63	**0.0121**	1,4	0.01	0.9214

Figure 1. Mean zooplankton biomass in ponds with and without crayfish (*Orconectes virilis*) with results from repeated measures ANOVA. The fish symbols and arrows indicate the estimated timing of the first successful fish recruitment in each treatment for consideration of trophic interactions between larval fish and zooplankton. Error bars denote one standard error. Asterisks indicate significant treatment effects (p-values < 0.004) on individual dates when treatments were sliced by time.



Effect	df	F	P	df	F	P
Treatment	1,4	15.0	**0.0180**	1,4	24.6	**0.0077**
Time	3,12	17.8	**0.0001**	1,4	2.19	0.2131
Treatment x Time	3,12	0.48	0.7032	1,4	8.42	0.6270

Figure 2. Mean phytoplankton abundance (µg chlorophyll *a* · L^{-1}) in ponds with and without crayfish (*Orconectes virilis*) and statistical results from repeated measures ANOVA. Error bars denote one standard error.



Effect	df	F	P	df	F	P
Treatment	1,4	5.62	**0.048**	1,4	13.1	0.059
Time	3,12	8.46	**0.038**	1,4	16.7	0.513
Treatment x Time	3,12	0.95	0.591	1,4	12.1	0.104

Figure 3. Mean peak dissolved oxygen in ponds with and without crayfish (*Orconectes virilis*) with results from repeated measures ANOVA. Error bars denote one standard error.

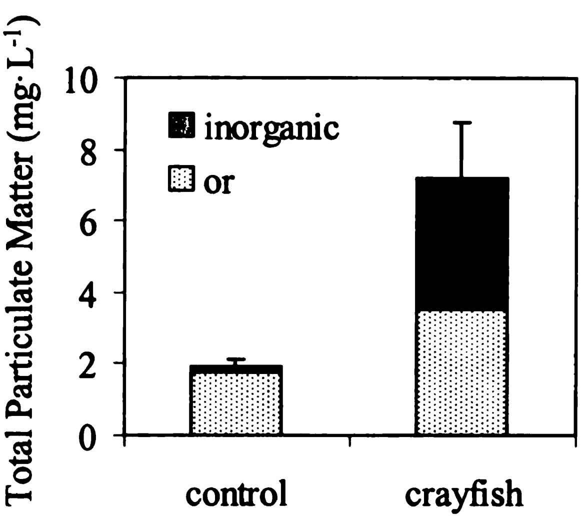


Figure 4. Average total particulate matter (TPM) in the water column of ponds with and without crayfish (*Orconectes virilis*) in July of 2001. Error bars are one standard error and refer to the standard errors of the entire bar. The ponds differed for all three measures of particulates (total, organic, and inorganic, p-values < 0.04, see text).

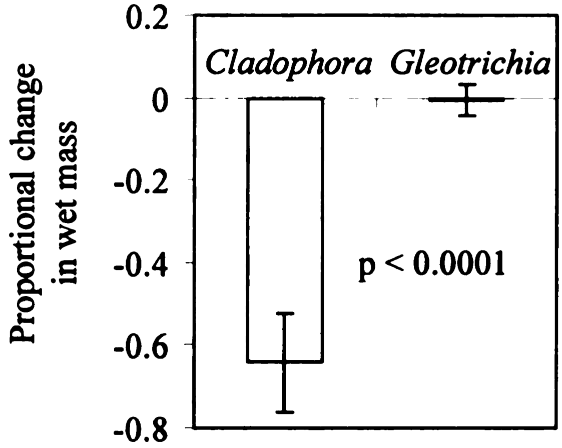
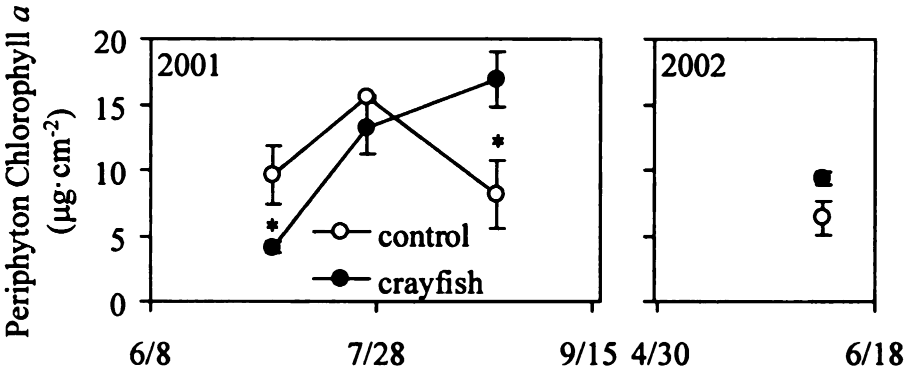


Figure 5. Results from a choice feeding assay where crayfish were simultaneously offered the dominant algal metaphyton from control and crayfish ponds (*Cladophora* and *Gleotrichia*). Error bars denote one standard error. The p-value is from a t-test of differences incorporating mass changes from control buckets in the analysis to control for variability due to autogenic mass change (see Peterson and Renaud 1989).



Effect	df	F	P	df	F	P
Treatment	1,4	0.19	0.7081	1,4	3.30	0.144
Time	3,12	9.77	**0.0071**			
Treatment x Time	3,12	8.54	**0.0104**			

Figure 6. Mean abundance of periphyton (algae attached to hard surfaces; μg chlorophyll $a \cdot cm^{-2}$) in ponds with and without crayfish (*Orconectes virilis*) with statistical results from rm-ANOVA (2002) and one-way ANOVA (2002). Error bars denote one standard error. The asterisk indicates a significant ($p < 0.05$) treatment effect in June and August 2001 (slicing by time).

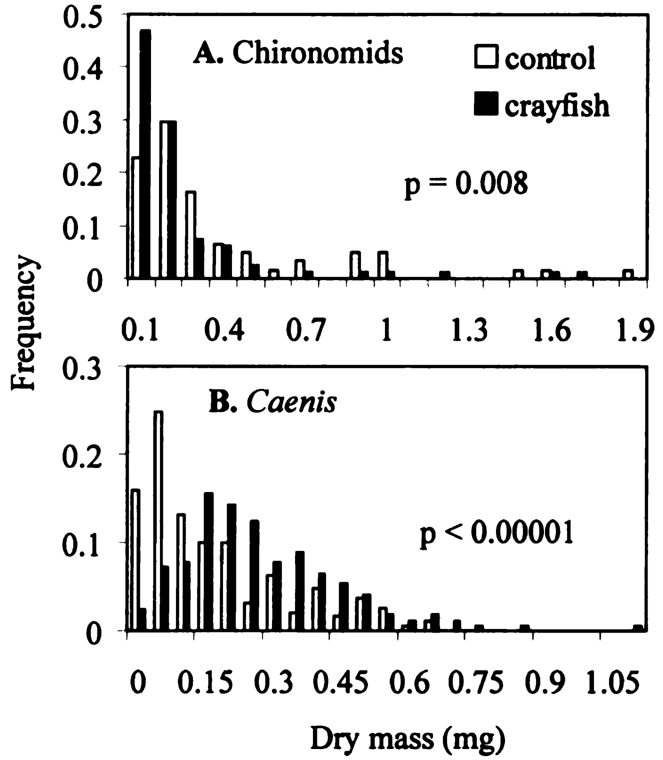


Figure 7. Size-frequency histogram of chironomids (A) and *Caenis* mayflies (B) collected from ponds with and without crayfish. The p-value is from a Komolgorov-Smirnov two sample test of distributions (chironomids: control n = 61, crayfish n = 81; *Caenis*: control n = 189, crayfish n = 168).

Figure 8. A comparison of the generalized community structure expected in lentic shallow water systems with or without abundant omnivorous crayfish (Decapoda).

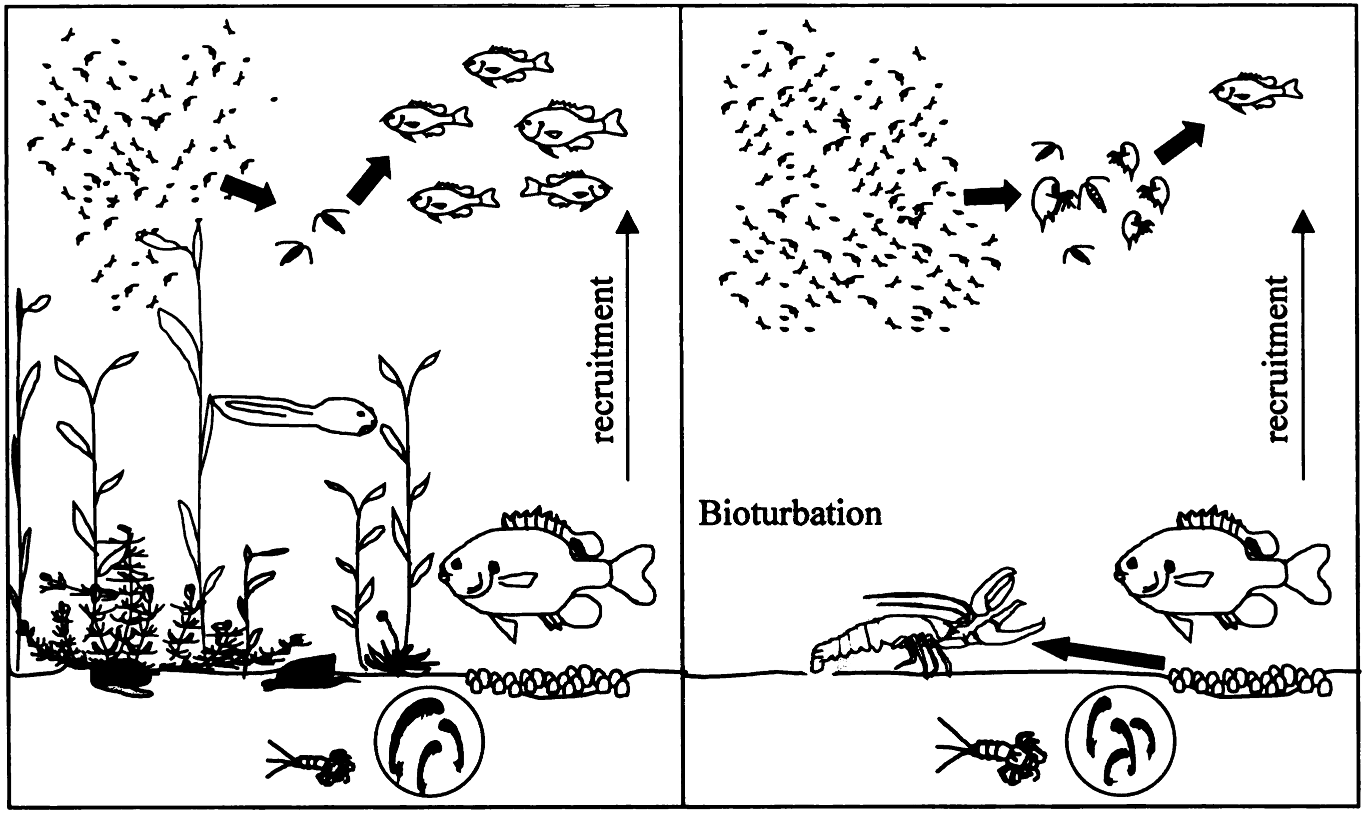


Figure 8

CHAPTER 5

COMPARING GRAZING RATES OF NATIVE AND EXOTIC *ORCONECTES* CRAYFISH: THE IMPORTANCE OF FISH PREDATORS

ABSTRACT

The invasive crayfish *Orconectes rusticus* has been replacing native *Orconectes virilis* in lakes in the Midwest for several decades, and invaded lakes have suffered losses of macrophyte biomass and diversity. Previous comparative experimental studies indicate that per capita grazing capacities of these species do not differ. However, previous experiments did not incorporate the effects of important predators (i.e., bass) which may affect the two species differentially, because *O. rusticus* is relatively less vulnerable to bass predation. I measured the grazing capacities of adult *O. virilis* and *O. rusticus* feeding on macroalgae (*Chara vulgaris*) in ponds with and without bass to determine whether predators influence the relative grazing rates of these species. Mass-specific consumption did not differ between species in the absence of predators or in the presence of non-lethal bass threats (when cages were closed). When covers were removed (open cages) and crayfish experienced direct encounters with bass, the two species responded differently to the predator contexts. *Orconectes rusticus* ate more than *O. virilis* in the bass pond and *O. virilis* fed slightly more than *O. rusticus* in the control pond. These results suggest that bass predators can have important effects on relative impacts of native and non-native crayfish.

KEYWORDS: *Chara*, crayfish, herbivory, invasive, *Micropterus*, native, *Orconectes rusticus*, *Orconectes virilis*, predator

INTRODUCTION

The predatory impacts of native and exotic animal species are commonly compared in experimental settings in order to predict or to understand the relative effects of invasions (e.g., Olsen et al. 1991, Nyström and Strand 1996, Dick et al. 2002, Loher and Whitlatch 2002). The usual protocol involves stocking similar numbers of each species into controlled experimental arenas and measuring effects on other trophic levels. Often these experiments do not incorporate the predators of the focal organisms, although interactions with predators are widely known to influence animal foraging behavior (Werner et al. 1983, Gilliam and Fraser 1987, Lima and Dill 1990). If the two species respond differently to a natural predator, then the results from an experiment without predators may have limited relavence to field conditions with predators.

Over the past several decades *Orconectes rusticus* (rusty crayfish) has invaded many lakes in the Midwest. Introduced primarily through the live bait trade, *O. rusticus* has displaced other *Orconectes* crayfish (*O. virilis* and *O. propinquus*) and become a dominant part of the fauna in many lakes (Capelli 1982, Hobbs et al. 1989, Olsen et al. 1991, Hazlett et al. 1992, Hill and Lodge 1999). The mechanisms responsible for the takeover have been well-documented and include competition for shelter, selective predation by fish, and hybridization (Capelli and Munjal 1982, Didonato and Lodge 1993, Garvey et al. 1994, Hill and Lodge 1999, Perry et al. 2001).

Orconectes rusticus and *O. virilis* (the native species it replaces) have similar feeding habits, similar adult size, and are both known to actively consume and destroy macrophytes and macroalgae (*Chara vulgaris*) (Lodge and Lorman 1987, Chambers et al.

1990, Lodge et al. 1994). Several studies have reported that macrophyte beds have been reduced in biomass and/or species richness in lakes invaded by *O. rusticus* (e.g., Capelli 1982, Lodge et al. 1985, Covich et al. 1999). Lab and field experiments indicate that the two species have similar grazing abilities (Olsen et al. 1991, Hazlett et al. 1992), which has led to the conclusion that the greater effects of *O. rusticus* on macrophytes must be due to higher densities of crayfish in invaded lakes (Olsen et al. 1991, Hazlett et al. 1992). However it is also possible that the experimental context in which these studies were done obscures differences between the species

Previous comparative experiments with these crayfish have been performed in closed cages or aquaria that did not include direct interactions with predatory fish. Bass (*Micropterus* spp. and *Ambloplites* spp.) are common and important predators of crayfish (Rickett 1974, Stein 1977, Dorn and Mittelbach 1999) and the non-lethal effects of largemouth bass (*Micropterus salmoides*) presence is known to reduce the grazing rates of *Orconectes* crayfish (Hill and Lodge 1995). *Orconectes rusticus* is also relatively less vulnerable to fish predation than native crayfish species because of it's greater defensive armor and less-risky behavior (Didonato and Lodge 1993, Garvey and Stein 1993, Garvey et al. 1994). If relative vulnerability affects feeding behaviors, then *O. rusticus* should be expected to feed at higher rates in the presence of predatory fish.

In this experiment, I measured the grazing capabilities of adult *O. virilis* and *O. rusticus* feeding on the macroalgae *Chara vulgaris*. In the first feeding trial I measured grazing in closed cages in two ponds – with and without bass predators. With the cages closed, crayfish could see and detect the presence of chemical cues from the bass (Wilmann et al. 1994, Hazlett and Schoolmaster 1998), but experienced no direct risk of predation. In a second trial I used the same setup but I removed the covers from cages in both ponds so that bass were able to explore the cages and directly threaten the crayfish. The second trial incorporated natural predator-prey interactions and also allowed for emigration (escape) from the habitat. My aim was to determine whether there was any evidence that *O. rusticus* has greater mass-specific grazing abilities than *O. virilis*, and whether relative effects of the two species depend upon experimental context (predator effects). I hypothesized that: 1) the relative effects of the species would not differ in the control pond, 2) overall crayfish feeding rates would be lower in the pond with bass than in the control pond, 3) consumption by *O. rusticus* would be greater than by *O. virilis* in the presence of bass predators.

MATERIALS AND METHODS

The feeding trials were conducted in two experimental ponds at the Kellogg Biological Station Experimental Pond Facility in Southwestern Michigan. The ponds (29 m diameter, 2 m deep) were less than 2 years old, never contained fish, and had been colonized with approximately 20-40% cover *Chara vulgaris*. Because the predator context was not replicated (treated as a block) it is potentially confounded with other differences between the ponds. However, these ponds were in the early stages of succession and had similar biotic and abiotic (i.e., bathymetry, water source) features except for bass introductions.

In June 2002, I constructed 32 circular cages from 50-cm tall metal flashing. The cages measured 1 m^2 in area and had an aluminum screen bottom so that crayfish could not escape by burrowing under the walls. Each cage had a cover made of a nylon fish net (1 cm mesh) stretched out inside a circular piece of black tubing that completely sealed the top of the cage. The covers kept the crayfish from swimming or crawling out but allowed them to see and sense their environment (bass vs. no predators). Sixteen cages were placed in the deepest areas of each pond and equal amounts of sand were added to each to serve as substrate. Three PVC shelters (5 cm diameter, 12-14 cm long) were added to each cage to give the crayfish a place to refuge.

Animals

Seven large (mean Total Length (s.d.) = 339 mm (32), Range = 285-388 mm) largemouth bass (*Micropterus salmoides*) seined from a nearby lake were added to one of the ponds on 11 July. Because the crayfish in this experiment were rather large, they may not have been very vulnerable even for large bass predators. However, Lodge and Hill (1995) found that bass presence had a negative impact on crayfish grazing even though the predator-prey size relations were such that crayfish were too big to be in serious danger.

Orconectes virilis and *Orconectes rusticus* were collected by hand and with baited traps in West Grand Traverse Bay (Lake Michigan). Because I did not want to introduce viable populations of *O. rusticus* to the ponds, only males were used in this study. All crayfish were Form II males when they were added to the cages, but some of both species molted during the first trial so the crayfish were a mixture of Form I and Form II males during the second trial. Each species was added (in groups of 3; 3 crayfish $\cdot$ m^{-2}) to 8 cages in each pond after being measured (Carapace length – CL) and weighed (g wet mass). Although carapace length (CL) did not differ significantly between the species (mean (s.d.), *O. virilis*: 37.2 mm (2.2); *O. rusticus*: 35.9 mm (2.9)), O. virilis cages had slightly more total crayfish mass (mean mass = 48.8 g vs. 46.7 g; t-test p = 0.08).

Because of differences in crayfish mass between species, and because some crayfish were lost from the open cages, I calculated crayfish grazing rates on a mass specific basis ($g \cdot g^{-1}$) for each cage in each experiment. In cases where crayfish densities were lower in a cage at the end than at the start of the experiment, I calculated average crayfish mass during the experiment, assuming either a constant number or a constant proportion of crayfish was lost per day.

Trial 1 – No predator vs. *Non-lethal threat (closed cages).*

In the first grazing trial the cages were closed (covers on). On 17 July, *Chara vulgaris*, with associated epiflora and epifauna (hereafter *Chara*), was collected from the ponds, lightly rinsed, and allowed to drip dry (in masses of 50-80 g) for approximately 20-30 seconds before being weighed. Each cage received 300-335 g of *Chara*, and care was taken to spread it out so that it could not be dominated by a single crayfish. During the feeding trial, observations were made on two days to record any molting and make certain crayfish had not completely consumed the *Chara*. Crayfish were allowed to graze for 7 days at which time the remaining *Chara* was carefully collected by a diver using SCUBA. After the *Chara* was reweighed, mass-specific consumption ($g \cdot g^{-1}$) was calculated as (initial wet mass – final wet mass) $\cdot$ crayfish wet mass^{-1}. Both trials were analyzed as a randomized block designs (with replication inside blocks) in SAS with Proc glm (SAS 8.0, SAS institute). Having replicate cages in each pond allowed me to look at the interaction of predator context (pond) and species.

Trial 2 -- No predator vs. *Direct threat (open cages).*

Immediately at the end of the first trial, I started a second trial with the same groups of crayfish. In Trial 2, all the cage covers in the bass pond were removed to allow bass predators access to the insides of the cages (i.e., to threaten or eat crayfish). In addition, the crayfish could potentially crawl or swim out by their own volition. Although I never observed crayfish climbing up the cage walls, occasionally an individual *O. rusticus* was observed hanging upside-down from the covers during Trial 1.

In the control pond, I left covers on half of the cages to determine whether or not the crayfish changed grazing behavior simply depending on the presence of a cover (i.e., if they stopped grazing and devoted their efforts to escaping). The treatment combination of *O. rusticus* without a cover was replicated only three times because a few crayfish were lost during setup due to mortality and an escape.

The second trial lasted two days (compared to seven days for Trial 1) and 48-60 g of *Chara* was added to each cages. Care was taken to make sure the *Chara* was spread out within the cage. At the end of the trial the number of remaining crayfish was counted at the same time the *Chara* was removed. When I calculated consumption in Trial 2, I corrected the crayfish mass to account for crayfish that disappeared from the cages. Because I did not want to scare the crayfish out of cages by my presence, I did not make any counts of crayfish during the experiment. Instead I calculated the average number of crayfish in each cage assuming a constant proportional daily disappearance rate (i.e., exponential decay). The disappearance rates were calculated independently for the two species in each pond. The results of the final analysis do not change if the disappearance rate is calculated based on a constant number instead of a constant proportion. The average number of crayfish in each cage during the experiment was used to calculate the average mass of crayfish and the mass-specific consumption for each cage. I analyzed the control pond alone as a 2 x 2 factorial ANOVA with crayfish species and presence of cover as the two factors to look for effects of a cover on consumption (i.e., changes in behavior). In the analysis of both ponds I used only the open cages, but the results do not change if all cages are used.

RESULTS

Trial 1 -- No predator vs. *Non-lethal threat (closed cages).*

No crayfish escaped the cages during the seven day trial indicating that the covers were effective at keeping the crayfish inside. *Chara* wet mass declined by an average of 72%, and there were no differences in the amount of *Chara* consumed per gram of crayfish between the two species. *O. virilis* and *O. rusticus* also had consumed similar amounts of *Chara* in the two ponds (Figure 1, Table 1). Removing cages in which crayfish molted during the trial from the analysis did not change the results nor did removing the interaction term from the analysis.

Trial 2 – No predator vs. *Direct threat (open cages).*

When the covers were removed, crayfish were open to close encounters with the bass in the predator pond (direct predator threat) and all crayfish in open cages had the opportunity to escape. Of 48 total crayfish in the bass pond cages at the beginning of the trial, 65% remained at the end of the experiment (17 total missing). Comparing the species in the bass pond, 25% (6 of 24) of *O. virilis* and 46% (11 of 24) of *O. rusticus* were missing. A larger percentage of total crayfish (52%) disappeared from open cages in the control pond than in the bass pond and this was due to the large number of missing *O. virilis* (58%; 7 of 12). The percentage of *O. rusticus* that disappeared (44%; 4 of 9) was similar in the bass and control ponds.

When the control pond was analyzed for effects of the mesh cover on consumption, Cover and the Cover x Species interaction terms were not significant ($F_{1,11} = 0.26$, $p = 0.61$; $F_{1,11} = 0.041$, $p = 0.84$), indicating that crayfish in the control pond were grazing similarly in the presence and absence of a cover.

Crayfish lower feeding rates in the second experiment and that was probably a result of different *Chara* stocking densities and functional responses. In the overall analysis the main effects of species and pond were not significant, however the two species responded in markedly different ways to the opening of the cages in the two ponds (Figure 2, Table 1; interaction term $p = 0.02$). Individual T-tests within the ponds indicated that the remaining *O. virilis* had non-significantly ($p = 0.15$) higher consumption in the control pond, while the remaining *O. rusticus* ate significantly more in the bass pond ($p = 0.04$).

DISCUSSION

In previous feeding assays with these two species, *O. rusticus* had a higher per capita feeding rate on snails (Olsen et al. 1991), but there was no difference in feeding rates on macrophytes (Olsen et al. 1991, Hazlett et al. 1992). Olsen et al. (1991) performed their experiment in laboratory aquaria with no predators present. Hazlett et al. (1992) do not provide information about predators in the stream where they conducted their experiment but their closed cages would not have allowed for direct interactions between crayfish and fish predators. In Trial 1 of this study, I found no differences in grazing between the species in a predator free pond and in a pond with non-lethal bass threats. These contexts are most similar to the contexts used in previous studies (Olsen et al. 1991, Hazlett et al. 1992).

Interestingly, there was no main effect of pond (bass presence) in either experimental trial. Bass presence has been shown to influence crayfish grazing rates in other studies (e.g., Hill and Lodge 1995). However, the average crayfish in my experiment was larger than the largest crayfish in the study by Hill and Lodge (1995), and Didonato and Lodge (1993) showed that larger crayfish are less vulnerable to natural assemblages of fish predators.

Although there was no overall effect of bass lowering crayfish grazing, the crayfish species responded differently to the two predator contexts when cages were opened and crayfish experienced direct encounters with the bass (Trial 2). *O. virilis* ate slightly more than *O. rusticus* in the control pond, but *O. rusticus* ate substantially more in the bass pond. By allowing for natural predator-prey interactions, the bass pond in Trial 2 incorporated more environmental reality than previous comparisons and the results suggest that adult *O. rusticus* can have substantially greater grazing effects on macroalgae than the native *O. virilis* in the presence of direct encounters with bass. The slightly higher average consumption by *O. virilis* in the control pond is not inconsistent with the findings of Olsen et al. (1991) and Hazlett et al. (1992). In both studies *O. virilis* had slightly, albeit statistically non-significantly, greater macrophyte destruction rates than *O. rusticus*.

During Trial 2 in the bass pond, *O. rusticus* ate more and it tended to disappear from the cages more than *O. virilis* (46% *O. rusticus* vs. 25% *O. virilis* were missing). Missing crayfish could have been eaten by bass or may have escaped. It is possible that *O. rusticus* foraged more actively, became more exposed to predation, and experienced greater mortality. However, this seems unlikely as *O. rusticus* has been shown to be less vulnerable to fish predation in experimental pools and lakes (Didonato and Lodge 1993, Garvey et al. 1994). Furthermore, a similar percentage of *O. rusticus* (44%) disappeared from cages in the control pond where there were no predators. This suggests that *O. rusticus* was probably escaping rather than being consumed. The fact that more than half of *O. virilis* escaped from cages in the control pond and only 25% were missing in the bass pond suggests that *O. virilis* decreased overall activity (feeding and escape activities) when exposed to direct predation threats. *O. rusticus* appeared more active in the presence of direct predator threats; it ate more and escaped more often than *O. virilis*.

In conclusion, these results indicate that *O. rusticus* can have larger mass-specific grazing effects than *O. virilis*, and that the relative grazing impacts of these species may depend on predators. Because most lakes have bass or other predatory fish, the observed negative effects of introduced *O. rusticus* on macrophytes may be due to higher grazing rates per unit biomass (compared to native crayfish species) as well as higher overall population densities (Olsen et al. 1991). In general, experiments comparing feeding rates among species should consider incorporating the effects of predators into the experimental design.

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Table 1. Analysis of variance results for two grazing trials comparing native (*Orconectes virilis*) and introduced (*Orconectes rusticus*) crayfish feeding on macroalgae (*Chara vulgaris*) in two ponds (with and without bass). Mass-specific consumption was measured for groups of crayfish grazing inside cages.

Trial 1. No bass vs. Non-lethal threat (closed cages)			
	df	F	P
Pond	1	0.18	0.677
Species	1	0.09	0.765
Pond x Species	1	0.23	0.634
Error	28		
Trial 2. No bass vs. Direct bass threat (open cages)			
Pond	1	0.23	0.637
Species	1	0.001	0.984
Pond x Species	1	6.36	**0.021**
Error	19		

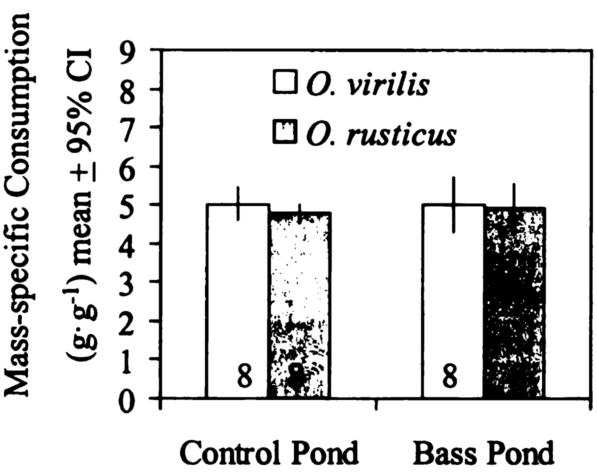

Figure 1. Mass-specific consumption of *Orconectes* crayfish feeding on *Chara* in closed cages inside ponds with and without bass. Crayfish in the bass pond were exposed to non-lethal threats (i.e., sight and smell) of largemouth bass (*Micropterus salmoides*). The numbers inside the bars indicate the number of replicates. Wet masses were used in calculations of consumption.

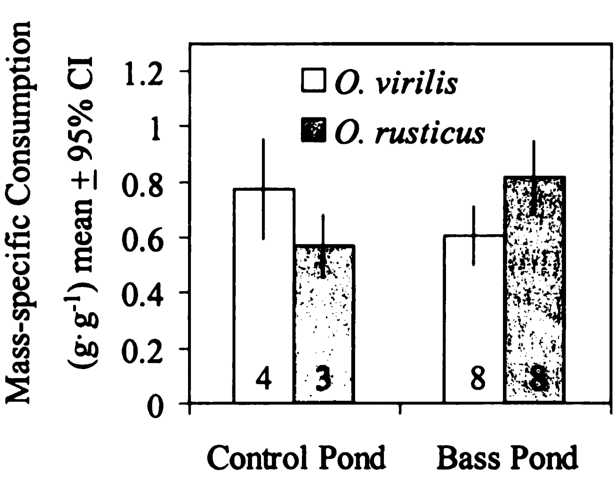

Figure 2. Mass-specific consumption of *Orconectes* crayfish feeding on *Chara* in open cages inside ponds with and without bass. Crayfish in the bass pond were exposed to direct interactions with largemouth bass (*Micropterus salmoides*). The numbers inside the bars indicate the number of replicates. Wet masses were used in calculations of consumption.