Reciprocal Relationships Between Exotic Rusty Crayfish, Macrophytes, and *Lepomis* Species in Northern Wisconsin Lakes

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ABSTRACT

The non-native rusty crayfish (*Orconectes rusticus*) has invaded many lakes of northern Wisconsin, profoundly changing littoral zones in the process. There are other lakes that have been invaded, but do not exhibit these changes. We hypothesized that endogenous feedbacks could form involving rusty crayfish, the macrophytes they destroy, and *Lepomis* species whose abundance is positively related to macrophyte abundance and also consume juvenile crayfish. We assessed this proposal with long-term data from one lake, a regional comparative study, and a case study of *Lepomis* predation on crayfish. Through time and across lakes, abundances of rusty crayfish, littoral macrophytes and species of the genus *Lepomis* were related in a fashion that indicated a set of feedbacks that regulate the abundance of all three. Intense predation on juvenile crayfish by abundant *Lepomis* is capable of maintaining some crayfish populations at low abundance. Thus, some lakes display profound ecological changes where crayfish achieve high abundance, and others sustain crayfish at low abundance. Consequently, lakes invaded by rusty crayfish may take on the appearance of alternative ecological regimes. Direct experimentation is necessary to determine if, and under what conditions, a lake can exist in either regime.

Key words: rusty crayfish; *Orconectes*; macrophytes; *Lepomis*; bluegill; pumpkinseed; exotic.

INTRODUCTION

Exotic species introductions are a prominent issue facing ecologists and managers alike. Species introductions are increasing worldwide, particularly in aquatic ecosystems (Cohen and Carlton 1998; Lodge and others 1998; Ricciardi and Rasmussen 1998). Thus, substantial effort has been dedicated to investigating factors that determine successful invasions and invader impacts in recipient ecosystems (Carlton 1996; Lodge and others 1998; Kolar and Lodge 2001). The ability of scientists to predict impacts can be compromised by species that cause major changes in one ecosystem but not in another (Lodge 1993; Forys and Allen 1999; Kolar and Lodge 2002). In theory, this dichotomy should provide a

unique opportunity to identify ecological conditions that encourage or constrain invasions and invader impacts. However, such opportunities are rare given the difficulty of finding multiple ecosystems that have been invaded, and perhaps more difficult, finding systems where relevant characters were studied throughout the invasion process.

Rusty crayfish (*Orconectes rusticus*) invasions into northern Wisconsin lakes may provide an opportunity to determine biotic factors that contribute to their success as invaders. Rusty crayfish have invaded many lakes in this region, and have been intensively studied for over 30 years. Previous studies have documented that rusty crayfish often rapidly replace sympatric congeners and become extremely abundant in many lakes (Capelli 1982; Olsen and others 1991), but do not become abundant in others (Lodge and Hill 1994; Garvey and others 2003). Foraging by abundant rusty crayfish can negatively affect several trophic levels, including primary producers (Mason 1974; Lodge and Lorman 1987; Lodge and others 1994; Luttenton and others 1998). Aquatic macrophytes appear to be especially susceptible to rusty crayfish foraging (Lodge and Lorman 1987; Lodge and others 1994; Wilson and others 2004). Macrophytes provide an important source of shelter and food for some juvenile fishes (Mittelbach 1981; Werner and others 1983; Werner and Hall 1983). However, links between rusty crayfish, macrophytes, and predatory fishes that could affect the abundance of all three groups have not been thoroughly explored by previous researchers.

A recent report documents the decline of bluegill (*Lepomis macrochirus*) and pumpkinseed sunfish (*L. gibbosus*) following rusty crayfish invasion in Trout Lake, Vilas County, Wisconsin (Wilson and others 2004). Explanations for this decline are limited. One hypothesis is that macrophyte destruction by rusty crayfish plays an important role in *Lepomis* decline because macrophytes provide refuge and foraging sites that are important determinants of juvenile *Lepomis* growth and predation mortality (Mittelbach 1981; Werner and Hall 1983; Olson and others 1998). Preliminary field observations indicated that bluegill and pumpkinseeds readily consume juvenile crayfish. Thus, the possibility exists that rusty crayfish foster ecological conditions for their success by destroying habitat for an agent of crayfish mortality. Our goal was to investigate these conditions as a means to identify factors that could encourage or constrain rusty crayfish invasions and their impacts.

No researchers have simultaneously investigated links between rusty crayfish, *Lepomis*, and macrophytes. These links are numerous and could lead to the reciprocal regulation of all three groups. Thus, we used data sets of rusty crayfish, *Lepomis*, and macrophyte abundance that spanned temporal, spatial, and organizational scales to help to clarify the importance of these links and lead to a greater understanding of biotic factors that contribute to or constrain rusty crayfish impacts in lake ecosystems.

METHODS

We used two data sets to define abundance relationships between rusty crayfish, macrophytes, and members of the genus *Lepomis*. We also tested the idea that predation by *Lepomis* species could be a critical constraint that maintains crayfish at low abundance. To accomplish this task, we used a long-term data set from Trout Lake, a comparative study of an additional 57 lakes, and a case study of *Lepomis* predation on crayfish in four lakes.

Long-term Data Set from Trout Lake

We determined long-term trends for crayfish, fish, and macrophytes using data from Trout Lake, Vilas County, Wisconsin (46°01′N, 59°40′W) extending the analysis by Wilson and others (2004). Crayfish and fish data are available from 1981 to 2004; macrophyte data are available starting in 1983. Over this period, water chemistry and clarity has not changed observably. All data, methods, and equipment descriptions are available online from the Northern Temperate Lakes Long Term Ecological Research (NTL-LTER) project website, http://www.limnology.wisc.edu. Crayfish were captured with steel mesh minnow traps modified to have a 2.5 cm diameter opening and baited with approximately 120 g of beef liver as per the crayfish sampling protocol of Capelli and Magnuson (1983) and Olsen and others (1991). For comparison with *Lepomis*, crayfish abundance was calculated as the mean catch per trap (CPUE) from all six LTER sampling sites in Trout Lake. *Lepomis* abundance was estimated by catch rates from fyke nets and beach seines. We combined the catch of *Lepomis* of all sizes from all six sites for each method. Macrophyte abundance was defined as total plant dry mass from 1.5, 2.5, and 4 m depths from the four sites where macrophyte data was collected in the southern basin of Trout Lake. We compared site-specific macrophyte data to site-specific mean crayfish trap catches because rusty crayfish effects on macrophytes occur at the local scale (Wilson 2002).

Comparative study of crayfish, fish, and macrophyte abundance

Crayfish, fish, and macrophytes were sampled from 57 lakes in Vilas County, Wisconsin to define correlative abundance relationships. Sampling occurred on 15–20 lakes each summer between 2001 and 2004; each lake was sampled once. Fish and crayfish sampling occurred in July of each year; macrophyte sampling occurred in August. On each lake, two 100 m long littoral sites per compass quadrant were randomly selected for sampling. Crayfish, fish, and macrophytes were sampled at the same eight locations. Fish were sampled once by electrofishing the length of each site between the 0.5 and 1.5 m depth contours at night. Fish abundance was estimated as the mean catch per site of six common piscivorous and benthivorous species: largemouth bass (*Micropterus salmoides*), smallmouth bass (*M. dolomieu*), rock bass (*Ambloplites rupestris*), walleye (*Sander vitreum*), yellow perch (*Perca flavescens*), and combined members of the genus *Lepomis* (bluegill *L. macrochirus*, pumpkinseed *L. gibbosus*, and hybrid bluegill × pumpkinseed). Crayfish were captured with baited traps identical to those used in Trout Lake. Three traps were placed at each site 15 m apart in 1 m of water and retrieved after 24 h. Crayfish were quantified as the whole-lake mean catch per trap (CPUE) for comparison with predator abundance. Site-specific total crayfish catch was compared with site-specific macrophyte cover. For comparisons with *Lepomis* and macrophytes, we separated rusty crayfish from the fantail crayfish (*Orconectes virilis*) and northern clearwater crayfish (*Orconectes propinquus*) to identify potential species effects. In general, *O. virilis* and *O. propinquus* are not known to effect the major changes in littoral zones caused by *O. rusticus*, and become severely reduced or disappear where rusty crayfish become abundant (Lodge and others 1985, 1994; Wilson and others 2004). For comparisons with the fish community, we combined crayfish species thereby considering the conservative hypothesis that any crayfish species can affect lake food webs (Lodge and Hill 1994; Momot 1995; Dorn and Wojdak 2004).

Macrophyte abundance was recorded as the mean percent cover of an assemblage of species that occupy the water column (for example, *Elodea* spp., *Nymphaea* spp., and *Potamogeton* spp.) and are likely to afford shelter for juvenile fishes. Species that form small basal rosettes (for example, *Eleocharis* spp., *Isoetes* spp., and *Juncus* spp.) were excluded. Species included in and excluded from this analysis were chosen irrespective of vulnerability to crayfish foraging (Wilson 2002), and are discussed in depth in Alexander (2005). Macrophyte cover was recorded within 0.25 m² quadrats along a single depth transect at each site. Quadrats were placed every meter along the depth transect up to a depth of 2 m. Thus, all sites did not have equal sampling effort (depending on littoral slope) but at least 25 samples were collected at all sites.

Lepomis Predation on Crayfish

We compared crayfish populations against predation rates by *Lepomis* in Arrowhead, Big, Trout, and Wild Rice lakes in Vilas County, Wisconsin. Preliminary investigation in 2002 and 2003 revealed that Arrowhead and Wild Rice lakes had low crayfish densities, whereas Big and Trout lakes had much higher densities. This allowed us to compare the relative effect of *Lepomis* predation in lakes with contrasting crayfish populations. All four lakes were studied by other researchers and found to contain rusty crayfish prior to 2000 (Wilson 2002). Rusty crayfish were the only species found in each lake, indicating that species replacement had already occurred, and that negative effects of rusty crayfish should be well-established (Wilson 2002). All four lakes have similar water chemistry and nutrient concentrations, although Big and Trout lakes are larger than Arrowhead and Wild Rice (Table 1). There is also no clear trend in the relative abundance of cobble, the most important habitat for crayfish refuge and production (France 1985; Lodge and Hill 1994; Garvey and others 2003) (Table 1).

Crayfish Population Estimates

Lakes were sampled between July 7 and July 14 of 2004 shortly following the release of juvenile crayfish from brooding females. Crayfish were sampled with SCUBA on cobble substrate only during daylight hours. SCUBA surveys offer an accurate picture of the crayfish population without the size and sex biases of crayfish traps (France 1985; Olsen and others 1991; Lamontagne and Rasmussen 1993). Juvenile collection occurred concurrent with adult crayfish collection. Juvenile crayfish samples were collected by an underwater forced-air vacuum similar to the method of Wahle and Steneck (1991) for collecting juvenile American lobsters (*Homarus americanus*). We determined the effect of fish predation on crayfish by comparing consumption estimates from fish bioenergetics models (see Assessing *Lepomis* consumption of crayfish, below) against the population of crayfish in each lake. The total crayfish population in each lake was estimated by multiplying the mean

Table 1. Biological, Chemical, and Physical Parameters in Case-Study Lakes

	Arrowhead	Big	Trout	Wild rice
Area (ha)	40	344	1,608	153
Max depth (m)	13.1	18.6	35.6	7.9
Shoreline length (km)	3.3	15.3	16.2	5.9
% Shoreline cobble	6.6	18.7	53.4	33.1
% Shoreline macrophyte	75.1	32.7	9.6	58.1
Littoral area (ha)	14.8	126.4	305.9	140.3
Cobble area (ha)	1.2	42.8	65.1	23.6
Conductivity (µS)	101.5	130.8	93	87
pH	8.1	8.2	7.6	7.5
Total N (µg l^{-1})	353.5	316.75	235	Na
Total P (µg l^{-1})	10	10.25	16.9	Na

crayfish density (adults and juveniles) by the area of the littoral zone covered by cobble (Table 1). The vast majority of juvenile and adult crayfish live in cobble (Lorman 1980; Hobbs and Jass 1988; Lodge and Hill 1994), so sampling these areas during daylight when crayfish seek shelter should yield a close approximation of the total population size. Cobble was defined as fist-size or larger rocks that cover more than 50% of the lake bottom at the 1 m depth contour along shore. We defined the littoral zone as all area less than 5 m in depth, following Lorman (1980), although Wild Rice Lake cobble beds occur only in wave-washed areas and did not occur at this depth. Thus, the effect of consumption by predators on the crayfish population will be more conservative in this lake than the others. The total area of cobble was calculated from GIS data, using georeferenced bathymetric maps of all four lakes.

Assessing *Lepomis* Consumption of Crayfish

We collected bluegill, pumpkinseed, and rock bass (*Ambloplites rupestris*) for stomach contents and for mark-recapture population estimates with fyke nets and electrofishing. Collecting rock bass allowed us to compare *Lepomis* crayfish consumption to an abundant species that is traditionally considered a crayfish predator (Rabeni 1992; Roell and Orth 1993). Fyke nets were used to mark fish throughout summer. We used electrofishing to recapture fish and to integrate local marking effects across the entire lake. Further information on fish collection is available in the Appendix (see http://www.springerlink.com).

Whole-lake crayfish consumption was estimated using the Bioenergetics 3.0 software (Hanson and others 1997) for the period of June 24–August 20.

Consequently, our estimates of crayfish predation could exceed our crayfish population estimates given that diet collection began 2–3 weeks prior to the crayfish surveys and the fact that we limited our crayfish population survey to cobble substrate. We used the mean population estimate of each fish species (Table 2) for each lake. To more accurately quantify the contribution of all predator sizes to crayfish consumption, the population estimate was divided into cohorts according to the abundance of each age-class in each lake. Growth rates (length-at-age) for each species in each lake were determined from scales. In addition to growth rates, Bioenergetics 3.0 requires inputs of diet composition, prey energy density, and temperature (Hanson and others 1997). Diet composition was quantified as the percent diet dry mass on each sampling date; diets collected on consecutive days were counted as a single sample. Further information on diet analyses and the inputs to the bioenergetics models are available in the Appendix (see http://www.springerlink.com).

The model calculates the biomass of crayfish consumed by each species. From this information and a length–weight regression from Sparkling Lake in Vilas County (Hein and others 2006), we calculated the number of crayfish consumed by each predator species:

$$N_{\text{Tot}} = B \cdot \sum_{l=0} \frac{n_l}{N_{\text{measured}}} \cdot b_l \qquad (1)$$

where N_{Tot} is the total number of crayfish consumed, B is the total crayfish biomass consumed (from bioenergetics), n_l is the number of crayfish of length l in each predator species, N_{measured} is the total number of crayfish measured from each predator species, and b_l is the mass of an individual crayfish at length l. This quantity is summed over

Table 2. Summary of Predator and Crayfish Populations in Case-Study Lakes

	Arrowhead	Wild rice	Trout	Big
Bluegill population estimate (high 95% CI–low 95% CI)	40,600 (67,600–29,000)	16,400 (22,100–13,000)	200 (2,600–100)	23,700 (31,900–15,700)
Pumpkinseed population estimate (high 95% CI–low 95% CI)	8,800 (15,700–6,200)	2,400 (4,300–1,000)	126 (6,300–64)	900(1,500–500)
Mean total *Lepomis* density (no. km of shoreline^{-1})	15,400	3,200	35	1,800
Rock bass population estimate (high 95% CI–low 95% CI)	2,900 (3,300–1,600)	900 (3,500–500)	1,340 (na–na)	2,300 (2,900–1,400)
Mean rock bass density (no. km of shoreline^{-1})	200	160	50	160
Total crayfish population (high 95% CI–low 95% CI)	58,400 (66,400–50,400)	4,900,000 (5,400,000–4,400,000)	49,400,000 (51,500,000–47,000,000)	24,000,000 (25,000,000–23,000,000)
Mean crayfish density (no. km of shoreline^{-1})	17,700	620,900	3,046,700	1,569,600

all $l \geq 0$. If the crayfish was partially digested and the carapace could not be measured, we measured the crayfish chelae, then calculated the carapace length via the regression equation used in Roth and Kitchell (2005). We combined the length distribution of crayfish consumed by each predator species across lakes because each species consumed crayfish of similar size in all lakes (unpublished data).

RESULTS

Long-term Study

The long-term data set from Trout Lake clearly displayed trends of a littoral ecosystem shift following the invasion and increase in abundance of rusty crayfish. Total macrophyte dry mass declined at all four sites after rusty crayfish were found (Figure 1), and three sites experienced statistically significant declines (sites 7, 31, 50: all $F > 16$, all $P < 0.005$; site 56: $F = 1.38$, $P > 0.15$). Lakewide, mean rusty crayfish trap catches increased from minimal levels in 1981 to over 35 crayfish per trap from 2000 through 2004 (Figure 2). *Lepomis* catches in beach seines and fyke nets significantly declined over this same period (Figure 2).

Comparative Study Across Lakes

Rusty crayfish, macrophytes, and *Lepomis* species had abundance relationships that were unique among all other predator and crayfish species we investigated. Crayfish trap catches and *Lepomis* electrofishing catches were inversely related across lakes (Figure 3). This pattern was largely driven along the *x*-axis by high trap catches of rusty crayfish. This relationship was significant with a log–log transformation ($F = 7.26$, $df = 55$, $P = 0.009$, $R^2 = 0.117$). No other species showed a negative relationship with crayfish trap catches (Figure 4), although rock bass and walleye illustrated a significant positive relationship with the data log-transformed (for rock bass, ln (rock bass + 1) = 0.15 (ln (crayfish CPUE + 1)) + 0.53; $F_{55} = 4.82$, $P = 0.03$, $R^2 = 0.08$. For walleye, ln (walleye + 1) = 0.44 (ln (crayfish CPUE + 1)) + 0.36; $F_{55} = 24.4$, $P < 0.001$, $R^2 = 0.307$). *Lepomis* catch rates also illustrated a significant positive relationship with macrophyte cover (Figure 5). No other species (alone or together) showed such a strong relationship, although largemouth bass catches were also significant (Figure 6).

Abundant rusty crayfish had a negative effect on site-specific macrophyte cover. The proportion of sites with no macrophyte cover increased from
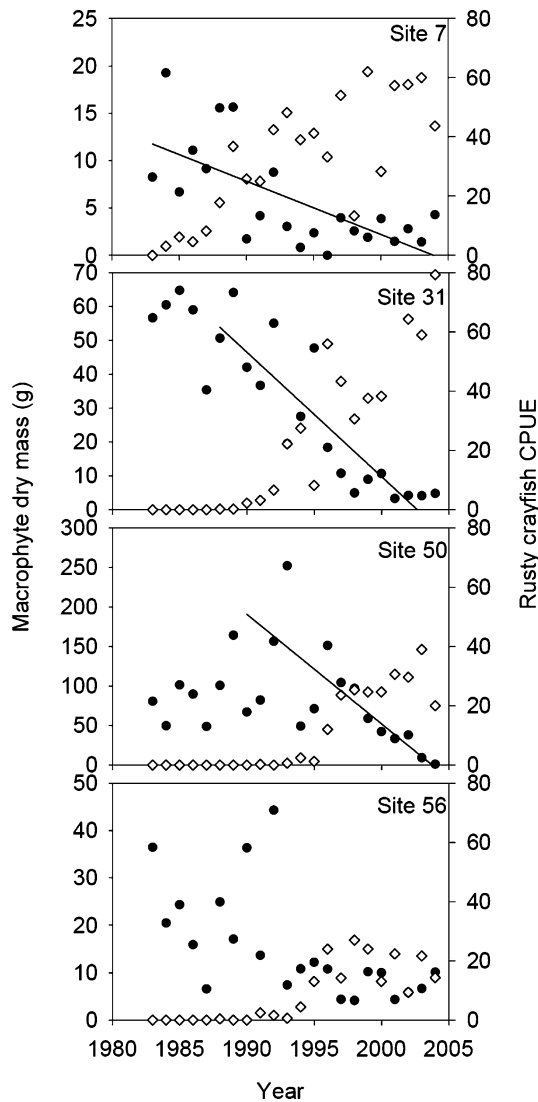
Figure 1. Temporal trends in site-specific macrophyte (*filled circle*) and rusty crayfish (*diamond*) abundance in Trout Lake. Site 7: Macrophyte abundance = 999−0.5 (year), $R^2 = 0.46$, $P < 0.001$. Site 31: Macrophyte abundance = 7,355 − 3.67 (year), $R^2 = 0.74$, $P < 0.001$. Site 50: Macrophyte abundance = 27,772 − 13.86 (year), $R^2 = 0.60$, $P = 0.002$. Site 56: Macrophyte abundance = 847 − 0.42 (year), $R^2 = 0.09$, $P > 0.1$. Note: Regressions start the first year rusty crayfish were found at each site.

Figure 2. Rusty crayfish (*open square*) and *Lepomis* catches in beach seine tows (*filled circle*) and fyke nets (*open circle*) through time in Trout Lake. For beach seine catches (*broken line*), ln (beach seine + 1) = 57.0 − 0.029 (year), $R^2 = 0.36$, $P = 0.002$. For fyke net catches (*solid line*), ln (fyke net) = 248.5 − 0.128 (year), $R^2 = 0.31$, $P = 0.005$.
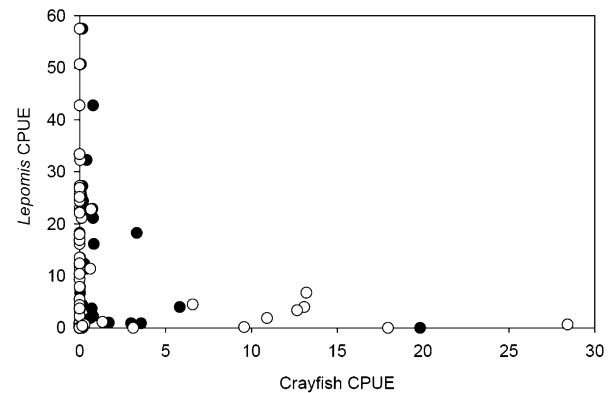

Figure 3. Rusty crayfish (*open circle*) and *O. virilis* and *O. propinquus* (*filled circle*) catches versus *Lepomis* catches from the comparative study.

around 40 to 73% with increasing rusty crayfish trap catches (Figure 7). In contrast, the proportion of sites without macrophytes varied substantially as *O. propinquus* and *O. virilis* catches increased.

Lepomis Consumption of Crayfish

Model estimates of crayfish consumption by *Lepomis* indicated that abundant *Lepomis* can have

strong effects on the abundance of juvenile rusty crayfish. *Lepomis* consumed crayfish smaller than 15 mm (carapace length) in all four lakes we studied, indicating that *Lepomis* only consumed juvenile crayfish (Figure 8). In contrast, most crayfish consumed by rock bass were larger than 15 mm (Figure 8). Nearly all *Lepomis* predation on crayfish occurred in late June, prior to our crayfish surveys. *Lepomis* alone consumed more than 300% of the crayfish population estimate in Arrowhead, and 23% in Wild Rice (Figure 9). Over this same time period, *Lepomis* only consumed 1 and 5% of the crayfish population in Trout and Big lakes, respectively.
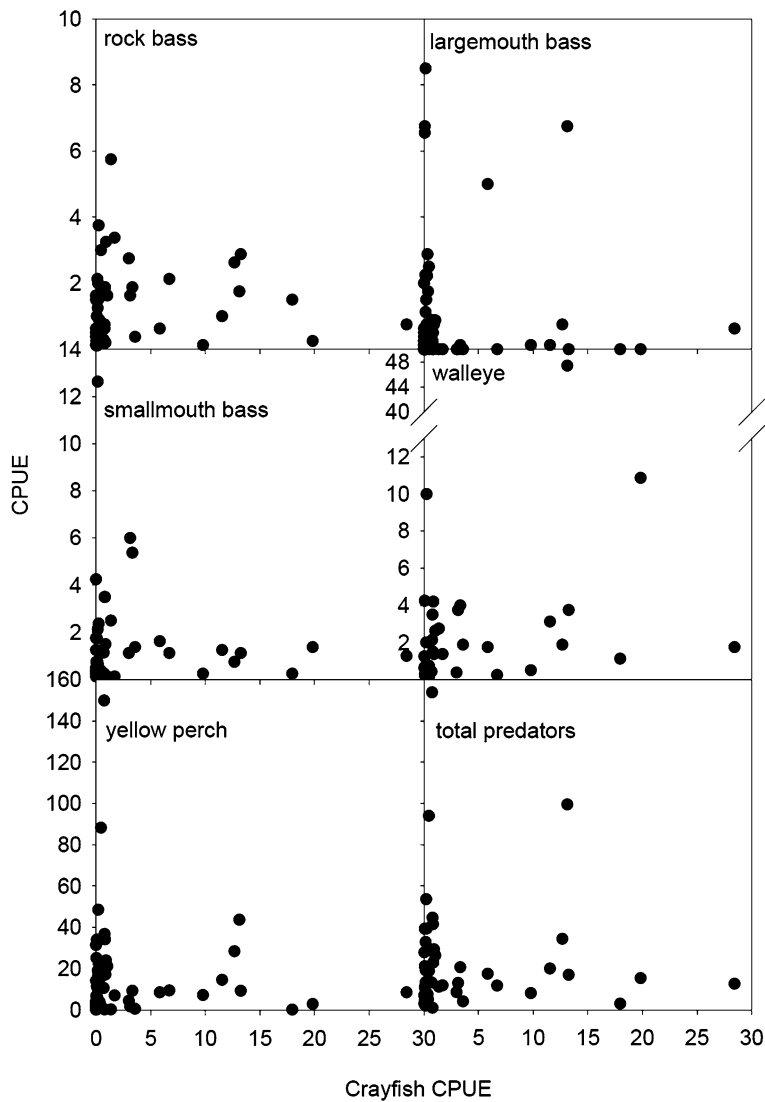
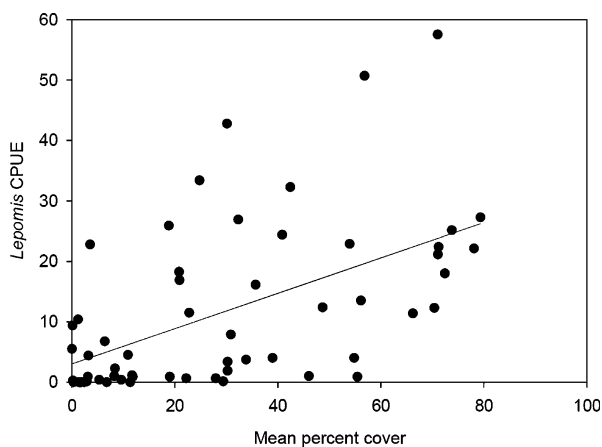**Figure 4.** Crayfish catches versus predator abundance in the comparative study.

Figure 5. *Lepomis* electrofishing catches versus macrophyte cover in the comparative study. Catch = 3.0 + 0.29 (Percent cover); $F_{55} = 22.7$, $P < 0.001$, $R^2 = 0.29$.

In all lakes, *Lepomis* consumed several times more crayfish than rock bass. Rock bass consumed 13 and 2% of the crayfish population estimate in Arrowhead and Wild Rice lakes, respectively, and 0.02 and 0.03% in Trout and Big lakes, respectively (Figure 9). Thus, *Lepomis* consumed 22X, 12X, 8X, and 143X more individual crayfish than rock bass in Arrowhead, Wild Rice, Big, and Trout lakes, respectively.

DISCUSSION

Researchers have wondered why rusty crayfish become very abundant in some lake ecosystems and not others (Capelli and Munjal 1982; Capelli and Magnuson 1983). There are hypotheses offered about this dichotomy, but definitive evidence is lacking (Lodge and Hill 1994; Garvey and others
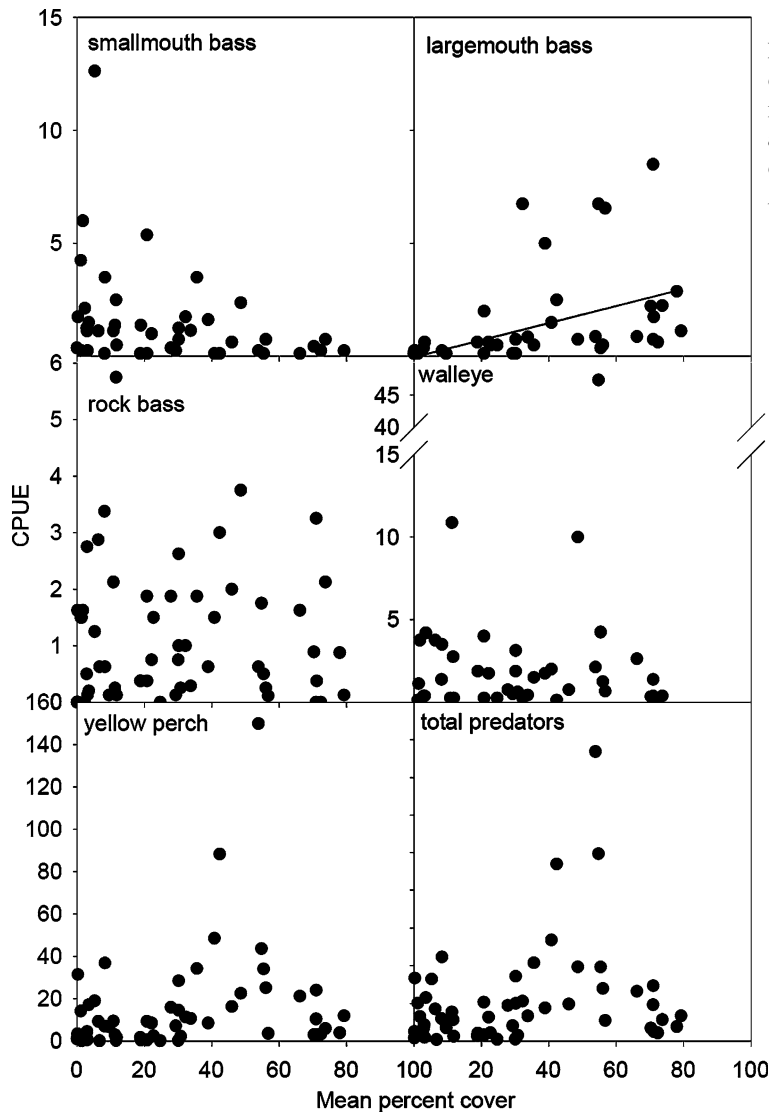
Figure 6. Predator abundance versus macrophyte cover in the comparative study. Statistically significant ($P \leq 0.05$) relationships are plotted with a straight line. For largemouth bass, catch = 0.0378 (macrophyte cover) − 0.0415; $F = 17.7$, $df = 55$, $P < 0.001$, $R^2 = 0.24$.

2003). This study offers some evidence for one hypothesis by demonstrating interrelationships among rusty crayfish, *Lepomis*, and macrophytes that could reciprocally regulate the abundance of all three groups in lake ecosystems.

Across a number of lakes, rusty crayfish and *Lepomis* abundance was inversely related. *Lepomis* abundance was positively related to macrophyte abundance, yet most lake sites that contained abundant rusty crayfish had little or no macrophyte cover. Other studies have demonstrated a negative relationship between rusty crayfish and other potential crayfish predators (Lodge and Hill 1994; Garvey and others 2003). We found no such relationship, and the long-term dataset from Trout Lake did not reveal a negative effect of rusty crayfish on any predator except *Lepomis* species (Wilson and others 2004). Presented alone, the comparative

study can be criticized with regards to sampling each lake only once and using percent cover, which may not fully describe macrophyte abundance. However, the long-term record from Trout Lake revealed an identical pattern through time.

An endogenous feedback associated with rusty crayfish offers a plausible explanation for our findings. Our datasets illustrate patterns that are consistent with feedbacks that lead to either a littoral zone persistently dominated by abundant rusty crayfish and few predatory *Lepomis* (Figure 10, top) or a littoral zone where adult *Lepomis* control crayfish populations and prevent destruction of macrophyte habitat essential to juvenile *Lepomis* survival (Figure 10, bottom).

This latter configuration appeared to be present in two of our case study lakes. These lakes were characterized by abundant macrophytes (Table 1)
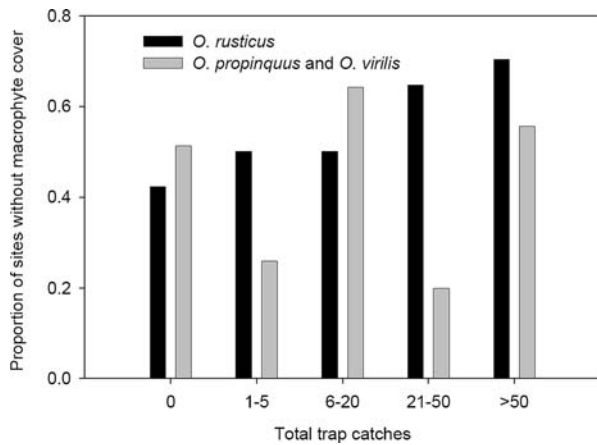
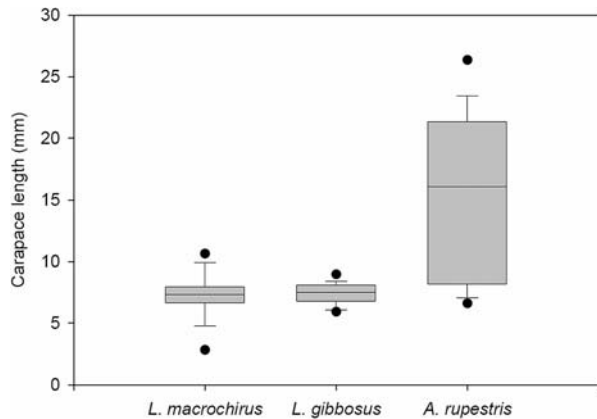Figure 7. Site specific crayfish abundance versus macrophyte cover in the comparative study.

Figure 8. Box-plot of crayfish carapace lengths in predator diets. *Lines within boxes* are the median lengths. Box boundaries mark the 25th and 75th percentiles. *Whiskers below and above the box* indicate the 10th and 90th percentiles, respectively. *Dots* mark the 5th and 95th percentiles.

and a dense population of *Lepomis* (Table 2). Bioenergetics modeling revealed that in Arrowhead Lake, the crayfish population in late June (when bioenergetics simulations commenced) would have to be three times larger than our population estimate in the second week of July to sustain such intense predation. Abundant *Lepomis* populations are likely to have a strong negative effect on juvenile crayfish abundance even where crayfish habitat occupies much of the shoreline, such as in Wild Rice Lake (Table 1). *Lepomis* may also have a stronger effect on the crayfish population growth rate than other predators (such as rock bass) by consuming many immature crayfish over a brief period instead of a few mature individuals over a
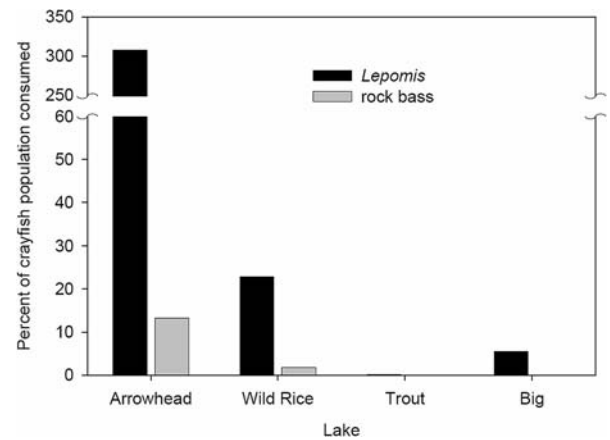

Figure 9. Percent of the crayfish population consumed by *Lepomis* and rock bass in case study lakes. Lakes are listed left to right in order of increasing density.

protracted period (Hein and others 2006). Short-term predation windows can regulate prey populations, even if the predator does not substantially benefit (Claessen and others 2000; De Roos and others 2003; Persson and others 2003). Together, this evidence may help to explain why lakes in the comparative study with abundant *Lepomis* generally had low crayfish trap catches (Figure 3). Further study is necessary to determine the effect of predation on crayfish population growth rates in these lakes.

Alternative Hypotheses for the *Lepomis* Decline After Rusty Crayfish Invasion

We hypothesized that rusty crayfish destroy habitat for juvenile *Lepomis* based on previous literature. This hypothesis utilizes the established premise that sparse macrophytes increase juvenile *Lepomis* mortality, either through starvation or predation (Mittelbach 1981; Werner and others 1983; Werner and Hall 1983). Others have hypothesized that rusty crayfish could impact fish recruitment through macrophyte destruction (Lodge and others 1998; Dorn and Mittelbach 1999; Wilson and others 2004).

Alternative links between crayfish and *Lepomis* could also lead to *Lepomis* decline in the face of rusty crayfish invasions. For instance, others have attributed severe attrition of *Lepomis* recruitment in experimental ponds to predation by *O. virilis* (Dorn and Mittelbach 2004; Dorn and Wojdak 2004). Similarly, rusty crayfish may affect *Lepomis* reproduction indirectly by decreasing suitable spawning substrate (Dorn and Mittelbach 2004). This would occur through the erosion of preferred nesting
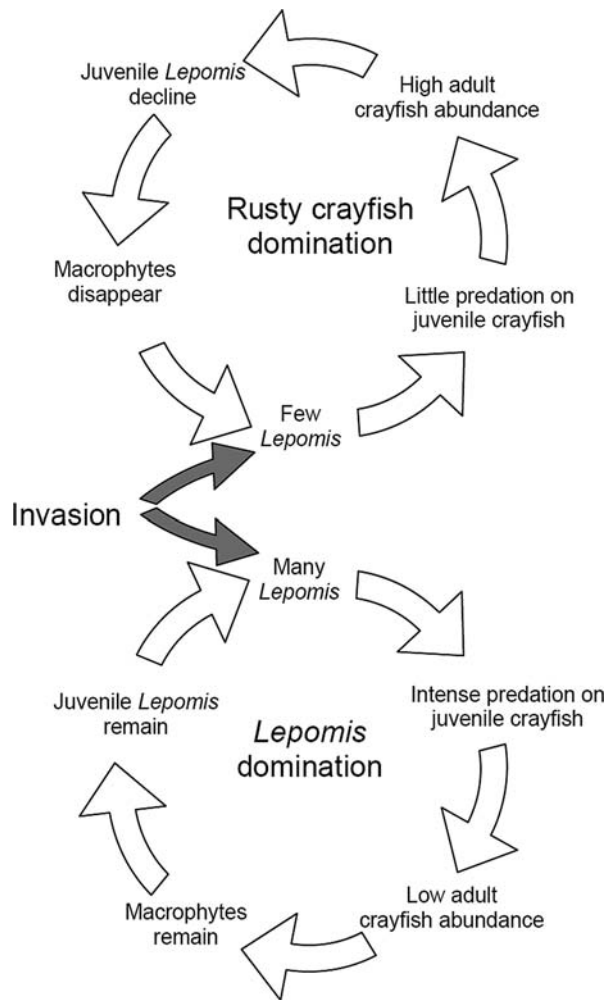
Figure 10. Proposed endogenous feedback loops.

substrate following macrophyte destruction (Jeppesen and others 1990; Carpenter 2003). As evidence in support of these prospects, Wilson (2002) reported that pumpkinseeds nested inside experimental crayfish exclosures with substantial macrophyte growth in Trout Lake, but not outside where macrophytes were absent. Both hypotheses are plausible and probably additive, but difficult to address in field studies because *Lepomis* has probably declined in many of these systems and none of the detailed information that is needed to test each hypothesis is available. These alternate hypotheses may be tested in the future by documenting a decrease in *Lepomis* nests or nesting success following rusty crayfish establishment.

Conditions that promote rusty crayfish or *Lepomis* dominance following a rusty crayfish invasion are unknown. Specifically, rusty crayfish became abundant in the first place because too few *Lepomis* were present during the initial stages of the inva-

sion to keep the lake in its original configuration (Figure 10). There is no direct evidence about factors that control *Lepomis* abundance prior to rusty crayfish invasions, although system productivity, predator abundance, and macrophyte abundance are correlates elsewhere (Olson and others 1998; Tomcko and Pierce 2005). Several lakes in the comparative survey had both few *Lepomis* and few crayfish but it is unclear if those combinations represent the initial stages of crayfish invasion or other unknown constraints. Similarly, lakes in other areas with an alternative set of physical, chemical, and habitat conditions may behave differently. Thus, experimentation at an appropriate scale is necessary to determine if, and under what conditions, a lake can shift from rusty crayfish domination to domination by macrophytes and *Lepomis* (Roth 2005; Hein and others 2006). Experimentation such as that conducted in mesocosms (Wilson 2002) and comparative studies such as those reported herein may help to reveal mechanisms, but definitive tests should be conducted at a whole-lake scale (Carpenter 2003).

CONCLUSIONS

Many studies have documented endogenous feedbacks among predators, macrophyte habitat, and grazers that lead to alternative ecological regimes. For instance, sea otters and other predators that prey heavily on sea urchins maintain a regime with abundant macroalgae (Simenstad and others 1978; Steneck 1998; Konar and Estes 2003). Over fishing herbivorous fishes can lead to a regime of abundant macroalgae in tropical near-shore ecosystems that normally have coral reefs (Hughes 1994, 2003; McCook 1999; Bellwood and others 2004). In freshwater systems, fish predators suppress grazers that would otherwise deplete dominant periphytic algae (Power 1990; Liboriussen and others 2005).

Introductions of exotic species can lead to shifts between regimes, but examples are rare. The few examples that exist offer evidence for dramatic changes in ecosystem configuration and energy flow, for example, the Black Sea and northern temperate lakes (Bax and others 2001; Carpenter 2003). This paper fits within the analytical framework proposed by Scheffer and Carpenter (2003) and Carpenter (2003) to detect alternative regimes with field data by integrating datasets that cover multiple temporal and spatial scales. Our results indicate that predation by *Lepomis* can constrain the ecosystem-scale changes potentially wrought by rusty crayfish invasion. Further experimentation and focus on the endogenous feedback

mechanisms is needed to determine the thresholds and conditions where a lake could move to an alternative domain of attraction (Petraitis and Latham 1999; Carpenter 2003; Scheffer and Carpenter 2003). Similar investigations based on polythetic approaches may help to determine why other exotic species become abundant in some ecosystems but not others.

ACKNOWLEDGEMENTS

REFERENCES

Alexander ML. 2005. Lake ecosystem variation across landscape position and human development gradients in Vilas County, Wisconsin. PhD Thesis. University of Wisconsin-Madison.

Bax N, Carlton JT, Mathews-Amos A, Haedrich RL, Howarth FG, Purcell JE, Rieser A, Gray A. 2001. The control of biological invasions in the world's oceans. Conserv Biol 15:1234–46.

Bellwood DR, Hughes TP, Folke C, Nystrom M. 2004. Confronting the coral reef crisis. Nature 429:827–33.

Capelli GM. 1982. Displacement of northern Wisconsin crayfish by *Orconectes rusticus* (Girard). Limnol Oceanogr 27:741–5.

Capelli GM, Magnuson JJ. 1983. Morphoedaphic and biogeographic analysis of crayfish distribution in northern Wisconsin. J Crust Biol 3:548–64.

Capelli GM, Munjal BL. 1982. Aggressive interactions and resource competition in relation to species displacement among crayfish of the genus *Orconectes*. J Crust Biol 2:486–92.

Carlton JT. 1996. Pattern, process, and prediction in marine invasion ecology. Biol Conserv 78:97–106.

Carpenter SR. 2003. Regime shifts in lake ecosystems: patterns and variation. Oldendorf/Luhe: International Ecology Institute.

Claessen D, de Roos AM, Persson L. 2000. Dwarfs and giants: cannibalism and competition in size-structured populations. Am Nat 155:219–37.

Cohen AN, Carlton JT. 1998. Accelerating invasion rate in a highly invaded estuary. Science 279:555–8.

De Roos AM, Persson L, McCauley E. 2003. The influence of size-dependent life-history traits on the structure and dynamics of populations and communities. Ecol Lett 6:473–87.

Dorn NJ, Mittelbach GG. 1999. More than predator and prey: a review of interactions between fish and crayfish. Vie Et Milieu 49:229–37.

Dorn NJ, Mittelbach GG. 2004. Effects of a native crayfish (*Orconectes virilis*) on the reproductive success and nesting behavior of sunfish (*Lepomis* spp.). Can J Fish Aquat Sci 61:2135–43.

Dorn NJ, Wojdak JM. 2004. The role of omnivorous crayfish in littoral communities. Oecologia 140:150–9.

Forys EA, Allen CR. 1999. Biological invasions and deletions: community change in south Florida. Biol Conserv 87:341–7.

France RL. 1985. Relationship of crayfish (*Orconectes virilis*) growth to population abundance and system productivity in small oligotrophic lakes in the Experimental Lakes Area, Northwestern Ontario. Can J Fish Aquat Sci 42:1096–102.

Garvey JE, Rettig JE, Stein RA, Lodge DM, Klosiewski SP. 2003. Scale-dependent associations among fish predation, littoral habitat, and distributions of crayfish species. Ecology 84:3339–48.

Hanson PC, Johnson TB, Schindler DE, Kitchell JF. 1997. Fish Bioenergetics 3.0. University of Wisconsin Sea Grant Institute.

Hein CL, Roth BM, Ives AR, Zanden MJV. 2006. Fish predation and trapping for rusty crayfish (*Orconectes rusticus*) control: a whole-lake experiment. Can J Fish Aquat Sci 63:383–93.

Hobbs III HH, Jass JP. 1988. The crayfishes and shrimps of Wisconsin. Milwaukee: Wisconsin Public Museum.

Hughes TP. 1994. Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. Science 265:1547–51.

Hughes TP. 2003. Climate change, human impacts, and the resilience of coral reefs. Science 301:929–33.

Jeppesen E, Sondergaard M, Mortensen E, Kristensen P, Riemann B, Jensen HJ, Muller JP, Sortkjaer O, Jensen JP, Christoffersen K, Bosselmann S, Dall E. 1990. Fish manipulation as a lake restoration tool in shallow, eutrophic temperate lakes 1: cross-analysis of three Danish case-studies. Hydrobiologia 200/201:205–18.

Kolar CS, Lodge DM. 2001. Progress in invasion biology: predicting invaders. TREE 16:199–204.

Kolar CS, Lodge DM. 2002. Ecological predictions and risk assessment for alien fishes in North America. Science 298:1233–6.

Konar B, Estes JA. 2003. The stability of boundary regions between kelp beds and deforested areas. Ecology 84:174–85.

Lamontagne S, Rasmussen JB. 1993. Estimating crayfish density in lakes using quadrats: maximizing precision and efficiency. Can J Fish Aquat Sci 50:623–6.

Liboriussen L, Jeppesen E, Bramm ME, Lassen MF. 2005. Periphyton-macroinvertebrate interactions in light and fish manipulated enclosures in a clear and a turbid shallow lake. Aquat Ecol 39:23–39.

Lodge DM. 1993. Species invasions and deletions: community effects and responses to climate and habitat change. In: Kareiva PM, Kingsolver JG, Huey RB, Biotic interactions and global change. Sunderland, MA: Sinaur Associates. p 367–87.

Lodge DM, Hill AM. 1994. Factors governing species composition, population size, and productivity of cool-water crayfishes. Nordic J Freshw Res 69:111–36.

Lodge DM, Lorman JG. 1987. Reductions in submersed macrophyte biomass and species richness by the crayfish *Orconectes rusticus*. Can J Fish Aquat Sci 44:591–7.

Lodge DM, Beckel AL, Magnuson JJ. 1985. Lake-bottom tyrant. Nat History 1985:33–7.

Lodge DM, Kershner MW, Aloi JE, Covich AP. 1994. Effects of an omnivorous crayfish (*Orconectes rusticus*) on a freshwater littoral food web. Ecology 75:1265–81.

Lodge DM, Stein RA, Brown KM, Covich AP, Bronmark C, Garvey JE, Klosiewski SP. 1998. Predicting impact of freshwater exotic species on native biodiversity: challenges in spatial scaling. Aust J Ecol 23:53–67.

Lorman JG. 1980. Ecology of the crayfish *Orconectes rusticus* in northern Wisconsin. PhD Thesis. University of Wisconsin-Madison.

Luttenton MR, Horgan MJ, Lodge DM. 1998. Effects of three *Orconectes* crayfishes on epilithic microalgae: a laboratory experiment. Crustaceana 71:845–55.

Mason JC. 1974. Crayfish production in a small woodland stream. In: Avault JW Jr., Ed. Freshwater Crayfish 2. Baton Rouge, Louisiana. pp. 449–479.

McCook LJ. 1999. Macroalgae, nutrients and phase shifts on coral reefs: scientific issues and management consequences for the Great Barrier Reef. Coral Reefs 18:357–67.

Mittelbach GG. 1981. Foraging efficiency and body size: a study of optimal diet and habitat use by bluegills. Ecology 62:1370–86.

Momot WT. 1995. Redefining the role of crayfish in aquatic ecosystems. Rev Fish Sci 3:33–63.

Olsen TM, Lodge DM, Capelli GM, Houlihan RJ. 1991. Mechanisms of impact of an introduced crayfish (*Orconectes rusticus*) on littoral congeners, snails, and macrophytes. Can J Fish Aquat Sci 48:1853–61.

Olson MH, Carpenter SR, Cunningham P, Gafny S, Herwig BR, Nibbelink NP, Pellett T, Storlie C, Trebitz AS, Wilson KA. 1998. Managing macrophytes to improve fish growth: a multi-lake experiment. Fisheries 23:6–12.

Persson L, de Roos AM, Claessen D, Bystrom P, Lovgren J, Sjogren S, Svanback R, Wahlstrom E, Westman E. 2003. Gigantic cannibals driving a whole-lake trophic cascade. Proc Natl Acad Sci USA 100:4035–39.

Petraitis PS, Latham RE. 1999. The importance of scale in testing the origins of alternative community states. Ecology 80:429–42.

Power ME. 1990. Effects of fish in river food webs. Science 250:811–4.

Rabeni CF. 1992. Trophic linkage between stream centrarchids and their crayfish prey. Can J Fish Aquat Sci 49:1714–21.

Ricciardi A, Rasmussen JB. 1998. Predicting the identity and impact of future biological invaders: a priority for aquatic resource management. Can J Fish Aquat Sci 55:1759–65.

Roell MJ, Orth DJ. 1993. Trophic basis of production of stream-dwelling smallmouth bass, rock bass, and flathead catfish in relation to invertebrate bait harvest. Trans Am Fish Soc 122:46–62.

Roth BM. 2005. An investigation of exotic rusty crayfish (*Orconectes rusticus*) and rainbow smelt (*Osmerus mordax*) interactions in lake food webs: the Sparkling Lake biomanipulation. PhD Thesis. University of Wisconsin-Madison.

Roth BM, Kitchell JF. 2005. The role of size-selective predation in the displacement of *Orconectes* crayfishes following rusty crayfish invasion. Crustaceana 78:299–312.

Scheffer M, Carpenter SR. 2003. Catastrophic regime shifts in ecosystems: linking theory to observation. TREE 18:648–56.

Simenstad CA, Estes JA, Kenyon KW. 1978. Aleuts, sea otters, and alternate stable-state communities. Science 200:403–11.

Steneck RS. 1998. Human influences on coastal ecosystems: does overfishing create trophic cascades? Trends Ecol Evol 13:429–30.

Tomcko CM, Pierce RB. 2005. Bluegill recruitment, growth, population size structure, and associated factors in Minnesota lakes. N Am J Fish Manage 25:171–9.

Wahle RA, Steneck RS. 1991. Recruitment habitats and nursery grounds of the American lobster *Homarus americanus*: a demographic bottleneck? Mar Ecol Prog Ser 69:231–43.

Werner EE, Hall DJ. 1983. Ontogenetic habitat shifts in bluegill: the foraging rate-predation risk trade-off. Ecology 69:1352–66.

Werner EE, Gilliam JF, Hall DJ, Mittelbach GG. 1983. An experimental test of the effects of predation risk on habitat use in fish. Ecology 64:1540–8.

Wilson KA. 2002. Impacts of rusty crayfish (*Orconectes rusticus*) in northern Wisconsin lakes. PhD Thesis. University of Wisconsin-Madison.

Wilson KA, Magnuson JJ, Lodge DM, Hill AM, Kratz TK, Perry WM, Willis TV. 2004. A long-term rusty crayfish (*Orconectes rusticus*) invasion: dispersal patterns and community change in a north temperate lake. Can J Fish Aquat Sci 61:2255–66.