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REPLACEMENT OF RESIDENT CRAYFISHES BY AN EXOTIC CRAYFISH: THE ROLES OF COMPETITION AND PREDATION

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Abstract. Exotic species are often a threat to native biodiversity. In northern Wisconsin lakes, the invading crayfish *Orconectes rusticus* is replacing *O. virilis*, the native, and *O. propinquus*, a previous invader. We tested the impacts of interspecific competition for food and of nonconsumptive effects of predation by largemouth bass, *Micropterus salmoides*, on growth and mortality of these three species. In competition experiments, *O. virilis* grew less, and *O. propinquus* suffered increased mortality in the presence of *O. rusticus* relative to single-species treatments. *Orconectes rusticus* was unaffected by the presence of congeners. In experiments testing nonconsumptive effects of predation, *O. virilis* growth declined substantially in the presence of largemouth bass, *O. rusticus* growth declined slightly, and *O. propinquus* growth was unaffected. Mortality of all three crayfishes increased in the presence of largemouth bass, with *O. virilis* experiencing the greatest and *O. rusticus* the least mortality.

To explore how competition, predation, and their interaction influence species replacements, we compared a fitness index (mortality/growth = μ/g) among species across biotic interaction domains: no interaction, intraspecific competition, interspecific competition, predation by fish, fish predation with competition, and predation risk with competition. In three of six domains, *O. virilis* and *O. propinquus* had somewhat similar μ/g , but reversals in μ/g rank between *O. virilis* and *O. propinquus* among domains occurred. These reversals are consistent with lack of unidirectionality of species replacements observed where *O. virilis* and *O. propinquus* distributions overlap. In all four interspecific interaction domains, *O. rusticus* had the lowest μ/g (indicating greatest fitness), which is consistent with observed unidirectional replacement of *O. propinquus* and *O. virilis* by *O. rusticus*. Whereas some fish management strategies might reverse the replacement of *O. virilis* by *O. propinquus*, no realistic interaction domain is likely to reverse replacement of the native species by *O. rusticus*.

Key words: competition; crayfish; exotic; fitness; growth; invasion; mortality; nonconsumptive effects; *Orconectes*; predation risk; predation; survival.

INTRODUCTION

Exotic species are a major threat to native biodiversity worldwide (Pimm 1991, Lodge 1993a, b, Ruesink et al. 1995, Vitousek et al. 1996, Williamson and Fitter 1996). Both intentional and accidental vectors of introductions of aquatic species (e.g. ships' ballast, fish-bait trade, aquarium trade, aquaculture, fisheries management) often deposit into freshwater ecosystems many individuals of many exotic species (Lodge et al. 1998). Indeed, exotic species are implicated in the extinction or endangerment of a high proportion of the North American fishes (Miller et al. 1989) and are clearly responsible for the demise of many other fishes worldwide (e.g., Pitcher and Hart 1995). More recently, conservationists have drawn attention to the precarious conservation status of many North American freshwater invertebrates (Master 1990, Dobson et al. 1997),

especially molluscan bivalves and crayfishes, many of which have small natural ranges (Lodge et al. 1998). Worldwide, one of the predominant threats to native crayfish biodiversity is exotic species; in Europe and Scandinavia, several species have been driven to local extinction through interactions with exotic crayfishes and/or their diseases (Abrahamsson 1971, Smith and Söderhäll 1986, Cerenius et al. 1988, Holdich 1988, Söderbäck 1991, Alderman 1993, Nylund et al. 1993, Lodge and Hill 1994). Such case studies of crayfishes are important to conservation, and they also provide a valuable opportunity to test the interactions of various biotic interactions in freshwater community structure.

The importance of the interaction of competition and predation in community structure is well documented (e.g., Morin 1986, Mittelbach 1988, Kohler and McPeck 1989, Wissinger 1989). However, few generalizations exist, in part because the interactions may be complex and, therefore, hard to predict. Such complex interactions might include diffuse interactions (e.g., Fox 1981, Wissinger 1992, Bock et al. 1992), nonadditive effects (e.g., Sredl and Collins 1992), and

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responses to risk (e.g., Kohler and McPeck 1989, Stamp and Bowers 1991, Werner 1991). In addition, few quantitative methods of comparison exist across experiments or across case studies. In this paper, we synthesize measurements of mortality and growth of crayfishes, using the mortality/growth ratio μ/g (Werner and Gilliam 1984) as a tool to compare success of congeneric species experiencing predation, competition, and their interaction.

In light of an ongoing biotic invasion, we compare μ/g of three congeneric crayfish species as they experience several domains of biotic interactions (e.g., interspecific competition, predation). *Orconectes rusticus* (Girard), native to the lower Midwest (USA), is invading northern Wisconsin lakes and streams where it is replacing two congeneric crayfishes, *Orconectes virilis* (Hagen), a northern Wisconsin native, and *Orconectes propinquus* (Girard), another nonnative species (Capelli 1982, Hobbs and Jass 1988, Olsen et al. 1991). *O. rusticus* also is invading lakes and streams in southern Canada and other parts of the upper midwest and New England states (Hobbs and Jass 1988, Taylor and Redmer 1996). In northern Wisconsin aquatic systems, *O. rusticus* is moving into an occupied niche with apparent ease (Hill et al. 1993, Hill and Lodge 1994) and has been implicated in the reduction of macrophyte, benthic invertebrate, and fish populations (Lodge and Lorman 1987, Weber and Lodge 1990, Lodge et al. 1994). Interspecific differences in survival and growth (Hill et al. 1993), olfaction ability (Willman et al. 1994), interspecific competition (Capelli and Munjal 1982, Hill and Lodge 1994), selective predation (DiDonato and Lodge 1993, Garvey et al. 1994), and reproductive interference (Capelli and Capelli 1980, Berrill 1985) are all possible mechanisms of this crayfish species invasion. In this paper, we focus on the potential importance of competition, predation, and their interaction as mechanisms of species replacement.

Over the long term, replacement of *O. virilis* and *O. propinquus* by *O. rusticus* seems inevitable in every system in which *O. rusticus* has become established (Olsen et al. 1991), but the pattern of replacement between *O. virilis* and *O. propinquus* is not always unidirectional (Lodge et al. 1986). Early in this century, *O. virilis* was the only common crayfish in Trout Lake (Vilas County, Wisconsin, USA) (Creaser 1932). After its introduction, *O. propinquus* displaced *O. virilis* in many areas of the lake. Along the lake's east shore, *O. propinquus* comprised >99% of the crayfish population between 1971 and 1981 (Lodge et al. 1986). In 1983 *O. virilis* had regained ground, making up 25–50% of the crayfish population. After its introduction (between 1973 and 1979), *O. rusticus* steadily increased in abundance and now constitutes nearly 100% of crayfish along that shoreline (Lodge et al., unpublished data). Shifting species composition along invasion fronts suggests that year-to-year or system-to-system variability in biotic interactions may alter the rates of species re-

placement, allowing *O. propinquus* or *O. virilis* to temporarily "reclaim" territory from each other (but not from *O. rusticus*). Variations in biotic interactions may include changes in intensity of interspecific competition or predation effects, which may differentially affect the relative success of these three species.

Here, we describe laboratory experiments that quantify the relative effects of intra- and interspecific competition for food and outdoor pool experiments that quantify nonconsumptive effects of predation risk on growth and mortality of the three crayfishes. We also tested the influence of species, size, and sex on the outcome of one-on-one competitive interactions for limited food. These one-on-one experiments shed light on how individual crayfish may contribute to observed population responses to competition and predation.

Using our data as well as previously published data, we compare μ/g for the three crayfishes over a range of biotic interaction domains (e.g., interspecific competition, predation by fish). As a summary of experimental results, μ/g allows easy comparison of species across biotic interaction domains, providing insight for predictions and management decisions. Prediction and management are particularly crucial issues for the increasingly common problem of determining biological effects of invading exotic species (Hengeveld 1989, Lodge 1993a, b, Lodge et al. 1998). Given observed species replacement patterns among the crayfishes we studied (Lodge et al. 1986, Olsen et al. 1991), we expected consistently greater success of *O. rusticus* (lower μ/g) relative to congeners in all biotic domains of interaction, but different relative success of *O. propinquus* and *O. virilis* in different domains.

METHODS

Experimental animals

Crayfish were collected by trapping (Lodge et al. 1986) or by hand (snorkeling) from Trout Lake (*Orconectes rusticus* and *O. propinquus*) (46°2' N, 49°40' W; Township 41N, Range 7E) and White Sand Lake (*O. rusticus* and *O. virilis*) (46°7' N, 89°35' W; T42N, R7E). Until used in experiments, each crayfish species was maintained separately in aerated laboratory aquaria and fed daily with TetraMin fish food (TetraWerke, Melle, Germany).

Largemouth bass (*Micropterus salmoides* [Lacépède]) were collected by electroshocking in Carrol Lake (45°58' N, 89°38' W; T39N, R7E) and maintained in outdoor lake water (epilimnetic) flow-through Frigid Unit tanks 1.8 m in diameter (Frigid Units, Toledo, Ohio, USA). Largemouth bass were fed various minnows (Cyprinidae) and crayfish of all three orconectid species until used in experiments.

Effects of interspecific competition on growth and mortality

Beginning 19 June 1992, we conducted a laboratory experiment in which we compared growth and mor-

tality of *O. rusticus*, *O. propinquus*, and *O. virilis* when competing intraspecifically to when competing interspecifically. Predators were absent from all tanks. Treatments in tanks were (1) *O. rusticus*, (2) *O. propinquus*, (3) *O. virilis*, (4) *O. propinquus* with *O. rusticus*, and (5) *O. virilis* with *O. rusticus* ($n = 10$ crayfish per treatment). Only males were used in this experiment. Females were not used because at the beginning of the experiment, they were berried (carrying extruded eggs), which might have confounded data interpretation because young-of-year would vary in abundance and would both consume resources and be consumed by adult crayfishes.

Over 6 wk, we maintained crayfish in aerated 38-L aquaria containing substrata of half cobble (0.16 m^2) and half sand with macrophytes (0.16 m^2). We used cobble because it was the preferred habitat for all three species (Hill and Lodge 1994). Each aquarium contained four crayfish, equivalent to 25 crayfish/m^2 . We used this substitutive design rather than both additive and substitutive designs (as in Underwood [1986]) because previous studies indicate overall crayfish density does not increase with the invasion of *O. rusticus* (Olsen et al. 1991).

Though densities of 1+ [age ≥ 1 and < 2 yr old] and older crayfish are typically $1\text{--}15 \text{ individuals/m}^2$, they range seasonally up to $82 \text{ individuals/m}^2$ in dense cobble (Lodge and Hill 1994, Lorman 1980, Capelli 1975). Crayfish prefer cobble habitat, though they will use sandy macrophyte habitat. Thus, the range of "effective density" in our experiment's cobble habitat was $25\text{--}50 \text{ individuals/m}^2$, depending on the level of competitive exclusion from preferred habitat and use of the less preferred macrophyte habitat. Thus, crayfish densities used in this experiment were high relative to typical densities, but were well below the highest densities observed in nature.

Timed lights approximated natural Wisconsin summer photoperiod (~ 15 h light). Crayfish were individually marked by clipping uropods.

Orconectes rusticus and *O. virilis* were 26–30 mm carapace length (CL) at the outset while *O. propinquus* were 21–25 mm. We used smaller *O. propinquus* because individually held *O. propinquus* grow more slowly than *O. rusticus* and *O. virilis* (Hill et al. 1993). Thus, the sizes of crayfish we used reflect naturally occurring modal sizes at equal age (2+) as observed in measurements taken from single-species and nearly single-species lake populations (Momot 1967 [*O. virilis*], Capelli 1975 [*O. propinquus*], and Lorman 1980 [*O. rusticus*]).

All tanks were initially supplied with detritus, macrophytes, and invertebrates as food. Our goal was to mimic a natural array and quantity of foods available in low to moderate resource lakes. Detritus collected with sweep nets from a heavy deposit of terrestrial leaf litter in Trout Lake's southeast bay was initially supplied to each tank ($\sim 187 \text{ g wet mass/m}^2$). We collected

macrophytes (*Ceratophyllum demersum* L., *Elodea canadensis* (Michx.) Planchon, *Potamogeton amplifolius* Tuckerm, *Potamogeton richardsonii* (Benn.) Rydb., *Potamogeton robbinsii* Oakes), and associated invertebrates from Trout Lake, sufficient to initially provide 80–100 macrophyte shoots/ m^2 in the sand/macrophyte area.

Invertebrates were collected from the littoral zone of a mesotrophic lake, Plum Lake ($46^{\circ}0' \text{ N}$, $89^{\circ}30' \text{ W}$; T41N, R8E), using a sweep net ($40 \times 20 \text{ cm}$ opening) for ~ 45 min every 2 wk. Plum Lake has abundant snails (*Physella*, *Amnicola*, *Helisoma* sp., and others) and insects (most aquatic orders) (see Lodge et al. 1994). The large littoral area swept had few rocks and abundant low growing macrophytes, allowing for easy, rapid collection of large numbers of invertebrates. Collected animals were evenly distributed among aquaria to provide crayfish with a natural array of invertebrate prey. Snail densities in tanks were $50\text{--}100 \text{ individuals/m}^2$. Densities of other invertebrates were $300\text{--}1000 \text{ individuals/m}^2$. Densities varied from collection to collection because of natural variations in invertebrate populations. Densities of invertebrates provided to tanks were comparable to naturally measured densities in Plum Lake (Lodge et al. 1994).

We measured individual crayfish wet masses on day 0 and again after 6 wk and assessed survival twice each week. We replaced individuals that died with crayfish that matched the dead individual's size within 1 mm CL. Replacement crayfish were excluded from final analyses of mortality and growth given their different histories within the experiment.

For analyses, we used two-way ANOVAs and Tukey's multiple comparisons to test for differences in proportional growth ($[\text{final mass} - \text{initial mass}]/\text{initial mass}$) and proportional mortality (number that died/initial number) among the three crayfish species in single and mixed species treatment. All proportions were arcsine transformed. All *O. rusticus* mixed species replicates were pooled for the ANOVAs because neither *O. rusticus* growth nor mortality differed between *O. rusticus* with *O. propinquus* and *O. rusticus* with *O. virilis* treatments ($F_{1,11} = 0.039$, $P = 0.847$ for growth and $F_{1,18} = 0.648$, $P = 0.431$ for mortality). To test for interspecific competition effects on growth and mortality of each species, we used pairwise *t* tests comparing growth and mortality in single-species treatments to that in mixed-species treatments. We also made pairwise comparisons of growth between species. Thus, for mortality the Bonferroni-adjusted critical value for three nonindependent comparisons was $\alpha = 0.017$. For growth, it was $\alpha = 0.006$ for nine comparisons. The true critical alphas for the *t* tests are somewhere between $\alpha = 0.05$ and the adjusted alphas (Maxwell and Delaney 1990). We provide *P* values for all *t* tests.

Nonconsumptive effects of predation on growth and mortality

During 3 July–21 August 1992, we conducted experiments to assess nonconsumptive effects of predation risk from fish on growth and mortality of the three crayfish species. Each of the 10 experimental tanks (Frigid Units tanks, 1.8 m diameter, ~1 m deep, 2.54 m²) contained all three species of crayfish. For each crayfish species, 11 males and 9 females were individually marked by clipping one to two of their five uropods in various combinations. We were able to use females in this experiment because by this time, they were no longer berried. Each tank contained 60 crayfish (20 individuals per species), a density of 24 crayfish/m².

Five tanks contained fish predators: one largemouth bass for the first 2 wk and two for the remaining 5 wk (because we became concerned that one predator did not provide crayfish with adequate predation risk). Largemouth bass were small (15–20 cm total length [TL]) because our goal was to eliminate the possibility of actual consumption of crayfish. Butler and Stein (1985) found that largemouth bass of 30 cm TL would not consume crayfish ≥ 28 mm CL (crayfish of CL $\geq 9.3\%$ of bass length). In our experiment, the smallest crayfish was 21 mm CL and the largest bass 19.8 cm TL. Thus, CL of all crayfish exceeded 10.6% of bass TL. We believe, but cannot be completely certain, that no crayfish were consumed by bass; we saw no evidence of consumption of crayfish. However, largemouth bass actively foraged, and crayfish did react to bass proximity with chelae displays, shelter-seeking behavior, and inactivity (A. M. Hill, *personal observations*). We fed largemouth bass with small tethered crayfish suspended in the water column and with ~12 minnows per tank every 1.5–2 wk. The largemouth bass were fed enough to allow growth, but they were kept hungry to encourage active foraging.

Experimental *O. rusticus* and *O. virilis* were 26–35 mm CL, and *O. propinquus* were 21–30 mm. These sizes provided results representative of interactions that may be occurring among crayfishes from the same year class and predators. The sizes of the species overlapped as they would in natural populations, with most of the *O. virilis* and *O. rusticus* larger than the largest *O. propinquus* and most of the *O. propinquus* smaller than the smallest *O. virilis* and *O. rusticus*. As in the competition experiment described above, these size classes approximated summer sizes of the 2+ age class for the three species (Lorman 1980, Capelli 1975, Momot 1967), but the classes were broader than in the competition experiment because the greater number of crayfish in this experiment allowed us to represent more of the natural size distributions.

Bottom habitat consisted of 1/3 area (0.85 m²) of cobble on sand and 1/3 area of macrophytes in sand. These two habitats were separated by a band of open

sand, also equivalent to 1/3 of the pool's bottom area. The purpose of this arrangement was to provide the crayfish with a somewhat realistic heterogeneous habitat. Water depth was 40 cm in all tanks, supplied by flow-through epilimnetic water from Trout Lake.

Initially, we added similar amounts of macrophytes and associated invertebrates (collected as described for the competition experiment above) to each tank to provide crayfish with moderate amounts of food within the macrophyte habitat. Macrophytes consisted of a mixture of *C. demersum*, *E. canadensis*, *P. amplifolius*, *P. richardsonii*, *P. robbinsii*, and *Vallisneria americana* Michx. (initial total density of 70–80 shoots/m²). Food probably became limiting in cobble, a habitat preferred by crayfish (Hill and Lodge 1994). Every 1.5–2 wk thereafter, macrophytes and associated invertebrates were added in similar quantities to each tank (~10 similar size shoots/tank). After 2 and 5 wk, we supplemented invertebrate resources. On each occasion, we evenly divided among tanks invertebrates collected by sweep netting for 1.5 h in Plum Lake. Natural leaf fall from trees as well as a single large addition of Trout Lake detritus (~175–195 g wet mass/m²) at the outset of the experiment served as the detritus sources for the summer.

We measured individual crayfish body mass and counted crayfish at the beginning and end of the experimental period (7 wk) to determine proportional growth and proportional mortality for each species within each tank. We used three-level nested ANOVAs (sex within species within predator treatment) and Tukey's multiple comparisons tests to test for nonconsumptive effects of predation on growth and mortality (arcsine transformed) of males and females of the three crayfish species. To test for effects on each species and sex, we used pairwise *t* tests comparing growth and mortality in predator to that in the no-predator treatment. For growth and for mortality, we performed six *t* tests, one for each species and sex. We also compared growth and mortality between species for each sex (12 *t* tests per variable). Thus, the Bonferroni-adjusted critical value for 18 nonindependent comparisons was $\alpha = 0.003$. The true critical value for the *t* tests lies somewhere between $\alpha = 0.05$ and $\alpha = 0.003$ (Maxwell and Delaney 1990). We provide *P* values for all *t* tests.

Possible mechanisms of competition and nonconsumptive effects of predation

During three summers, 1991–1993, in a Competition for Limited Food experiment we tested the success of *O. rusticus*, *O. propinquus*, and *O. virilis* among species and sizes and between sexes when competing for limited food to assess the potential role of each factor in crayfish species replacement mechanisms. (See Table 1 for a summary of specific contest conditions and pairings.) Pairwise contests were performed in plastic pans (30 × 20 × 15 cm) containing ~3 mm of clean

TABLE 1. Effects tested, conditions, and pairings of three crayfish species in the laboratory Competition for Limited Food experiment.

Year	Effects	Conditions	Pairings (all equal-sized except 1993)
1991	species	males only	OR/OP, OR/OV, OP/OV
1992	sex and species	males and females	OR δ /OR φ , OP δ /OP φ , OV δ / OV φ , OR δ /OP φ , OP δ / OR φ
1993	size	males only	OR _l /OV _l , OR _l /OV _m , OR _l /OV _s , OR _l /OP _l , OR _l /OP _m , OR _l /OP _s , OV _l /OR _m , OV _l /OR _s , OP _l / OR _m , OP _l /OR _s

Notes: OV = *Orconectes virilis*, OP = *O. propinquus*, OR = *O. rusticus*. Where the paired individuals are not of the same size (carapace length [CL]), l = large, m = medium, and s = small. Large crayfish were 3 mm CL larger than medium crayfish. Medium crayfish were 3 mm CL larger than small. Results for size-effect trials (1993) are reported in Fig. 4.

sand and 5 cm of lake water. No crayfish was used more than once.

For each trial, crayfish were starved for 24 h. In late afternoon and 1 h before food addition, lights were turned off to simulate post-dusk conditions, a time during which crayfish forage actively, even on open sand, because predation risk is greatly reduced (Hill and Lodge 1994). During this period, fresh night crawlers (*Lumbricus* sp.) were cut into 0.5–1 cm sections. One section of night crawler was placed in the center of each pan. After 20 min, pans were inspected using a red light to determine which of the two crayfish possessed the food fragment. The “winning” individual was recorded for each pan. If neither crayfish had taken the food or if both individuals possessed a fragment of the night crawler, the outcome was recorded as a tie. The food fragments were large enough that the crayfish usually took much longer than the 20 min to consume

most of the night crawler fragment. If a fragment was completely consumed, the replicate was discarded.

Using unreplicated *G* tests, pairwise crayfish interactions were compared against an expected equal number of wins per individual in each pairing scenario. Ties were excluded from the analyses because we had no basis for generating an expected frequency of ties and because the number of ties was very low.

Comparing a fitness index (μ/g) of crayfishes

Using our data and previously published data, we calculated μ/g for *O. rusticus*, *O. virilis*, and *O. propinquus* over a range of biotic interaction domains: no interactions, intraspecific competition, interspecific competition, predation, predation and interspecific competition, and predation risk and interspecific competition. (See Table 2 for data sources and crayfish size/sex used in calculations.) Data were converted to daily

TABLE 2. Summary of growth and mortality data sources used to calculate the fitness index (mortality/growth ratio = μ/g) of three crayfish species in different biotic interaction domains.

Interaction domains	Size and sex of crayfish used†	Data source	
		Growth	Mortality
None	18–20 mm CL, males and females	Hill et al. 1993	Hill et al. 1993
Intraspecific competition	21–30 mm CL, males only	Effects of competition, single-species treatment (this paper)	Effects of competition, single-species treatment (this paper)
Interspecific competition	21–35 mm CL, males and females	Nonconsumptive effects of predation, no-predator treatment (this paper)	Nonconsumptive effects of predation, no-predator treatment (this paper)
Predation	18–20 mm CL, males and females	Hill et al. 1993	Garvey et al. 1994
Predation and interspecific competition	growth: 21–35 mm CL males and females, mortality: 25 mm CL males only	Nonconsumptive effects of predation, no-predator treatment‡ (this paper)	Garvey et al. 1994
Predation risk and interspecific competition	21–35 mm CL males and females	Nonconsumptive effects of predation, predator treatment (this paper)	Nonconsumptive effects of predation, predator treatment (this paper)

† CL = carapace length.

‡ Data from the treatment with no predator were used so that effects of predation risk on growth were absent.

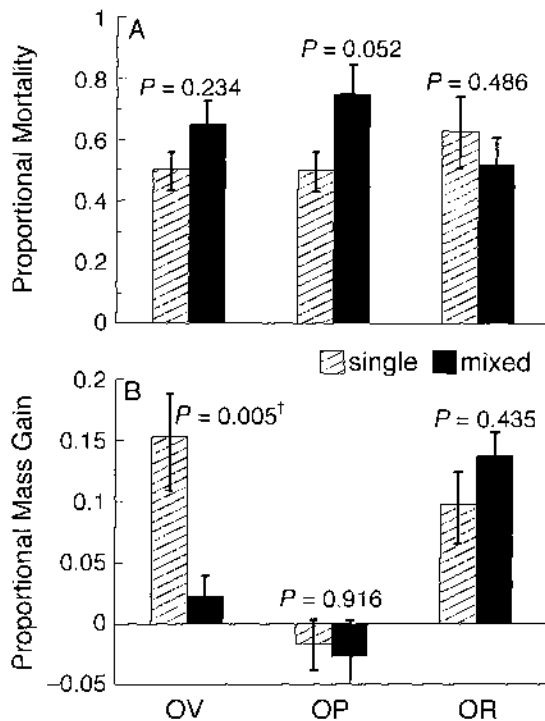


FIG. 1. Crayfish mortality (A) and growth (B) during 6 wk in single- and mixed-species treatments of Effects of Interspecific Competition experiment. OV = *Orconectes virilis*, OP = *O. propinquus*, OR = *O. rusticus*. P values are for species-specific t tests comparing mortality and comparing growth between single- and mixed-species treatments. Bonferroni-adjusted critical value for all t tests performed is $\alpha = 0.017$ for mortality and $\alpha = 0.006$ for growth. Dagger (\dagger) marks P values \leq the adjusted alpha.

proportional growth and daily proportional mortality to allow comparisons across studies. Data from other publications are study means, yielding mean mortality and mean growth for domains of no interactions, predation, and predation and interspecific competition. Because we had no measure of variance for these values, statistical comparisons of μ/g were not possible. Values calculated from our results were mean μ/g with 95% confidence limits. Where growth was negative, crayfish were assigned a negligible positive growth value (0.001) because the model does not consider negative growth.

Fitness index values for the three species were plotted on a logarithmic scale for qualitative comparison of relative μ/g among species across the range of biotic interaction domains. We focus on how the rank of μ/g among species differs across domains. Though the same tanks and similar methods were used in some of the experiments (e.g., *Methods: Nonconsumptive effects ... mortality*, above, and consumptive effects [Garvey et al. 1994] of predation), we do not compare absolute values of μ/g among domains because differences existed among some of the experimental arenas.

The index μ/g was originally designed to compare

populations within a single species. Our use of the index for comparing congeners is valid because the species have similar (though not equal) fecundities at equal size and because their life histories are very similar. At the latitude of this study, females of all three crayfishes produce eggs for the first time during spring of their 2+ year (see Momot 1967, Capelli 1975, Lorman 1980). In the *Discussion*, we elaborate on the possible impact of differences in fecundity on the index.

RESULTS

To determine whether growth and mortality were independent of each other, we examined mortality and its relationship to initial size of crayfish in our Effects of Interspecific Competition and NonConsumptive Effects of Predation experiments. We could not directly test the relationship between growth and mortality because we could not measure growth of dead crayfish. In the competition experiment, mean initial size of crayfish that later died was smaller than mean initial size of surviving crayfish. However, this difference was significant ($P < 0.05$) in only one of six cases (*Orconectes virilis* in mixed-species treatment). In the predation experiment, initially larger crayfish survived better than smaller crayfish in 7 of 12 cases (but only one case was significant [$P < 0.05$]), while in the remaining five cases, the reverse was true (again with only one significant case). In this experiment, our results showed no clear relationship between growth and mortality. Overall, growth rates may have been weakly related to mortality rates, but the magnitude of the effect, if any, was small. We therefore present the mortality and growth results below as if they were independent. In the end, our use of the mortality/growth ratio controls for this potential interaction.

Because the calculation for proportional growth includes initial mass, we also were concerned that proportional growth and initial mass might be systematically related. To test for this relationship, we ran various combinations of regressions (e.g., pooling species and sexes, separating species and sexes) between initial mass and proportional growth. We found no strong relationship between variables (r^2 was never >0.092 , but was generally much lower). In addition, the comparisons of interest were largely within species (between single- and mixed-species treatments or between predator and no-predator treatments). Within species, crayfish were size matched between treatments, reducing the likelihood that initial size differences would contribute to observed results for a particular species. Thus, our use of proportional growth did not introduce any bias to our results.

Effects of interspecific competition

Mortality.—Overall, mortality was similar for the three crayfishes (ANOVA $F_{2,63} = 0.096$, $P = 0.908$), ranging from 50 to 60% in single-species treatments during the 6-wk experiment (Fig. 1). Relative to mor-

tality in single-species treatments, mortality in the presence of interspecific competitors did not differ for *O. virilis* or *O. rusticus*, but appeared to increase from ~50 to 75% for *O. propinquus* ($F_{1,18} = 4.32$, $P = 0.052$).

Growth.—Overall, crayfish growth over 6 wk differed among crayfishes (ANOVA $F_{3,50} = 13.569$, $P < 0.001$) and between single- and mixed-species treatments (ANOVA $F_{1,50} = 6.552$, $P = 0.014$) (Fig. 1). In single-species treatments, *O. virilis* and *O. rusticus* grew similarly (10–15%) (Tukey's $P = 0.550$) and faster than *O. propinquus* (–2–3%) (Tukey's $P = 0.001$ for *O. virilis* vs. *O. propinquus* and $P = 0.019$ for *O. rusticus* vs. *O. propinquus*). Growth of *O. propinquus* and *O. rusticus* in mixed-species treatment did not differ from their respective single-species growth, whereas growth of *O. virilis* declined markedly in the presence of *O. rusticus*, from ~15% to <5% ($t_{1,13} = 11.58$, $P = 0.005$). In mixed-species treatments, *O. rusticus* grew more rapidly than *O. propinquus* (Tukey's $P = 0.002$), whereas *O. virilis* did not (Tukey's $P = 0.154$). *O. propinquus* grew poorly regardless of whether they were competing intra- or interspecifically.

Nonconsumptive effects of predation

Mortality.—Under threat of largemouth bass predation, the three crayfishes experienced different levels of mortality (nested ANOVA $F_{4,48} = 4.39$, $P = 0.055$); females experienced greater mortality than males ($F_{6,48} = 2.11$, $P = 0.055$) (Fig. 2). With largemouth bass, mortality appeared to increase for *O. propinquus* females ($t_{1,8} = 7.06$, $P = 0.029$) and did increase for *O. rusticus* females ($t_{1,8} = 42.86$, $P < 0.001$). All other trends for females and males of the three crayfishes, though nonsignificant, were consistent with increased mortality in the predator relative to no-predator treatment.

O. rusticus females experienced lower mortality than both *O. propinquus* and *O. virilis* females in the no predator treatment (Tukey's $P = 0.002$ for both comparisons) and perhaps marginally lower mortality than congener females in predator treatments (Tukey's $P = 0.085$ and 0.068 , respectively). *O. rusticus* males experienced lower mortality than at least *O. virilis* in the absence of bass (Tukey's $P = 0.003$), but not when predators were present.

Growth.—The three crayfishes grew differently (nested ANOVA $F_{4,45} = 5.18$, $P = 0.035$), and male crayfish gained more body mass than females (nested ANOVA $F_{6,45} = 3.17$, $P = 0.012$) (Fig. 3). *O. rusticus* males gained more body mass than *O. virilis* and *O. propinquus* males in both the presence and absence of predators (Tukey's $P \leq 0.003$ in all but one case where $P = 0.005$ [*O. rusticus* vs. *O. virilis* in predator treatment]). Female *O. rusticus* grew more than female *O. propinquus* whether or not predators were present (Tukey's $P < 0.002$ in both cases), whereas female *O. virilis* appeared to grow more than *O. propinquus* only

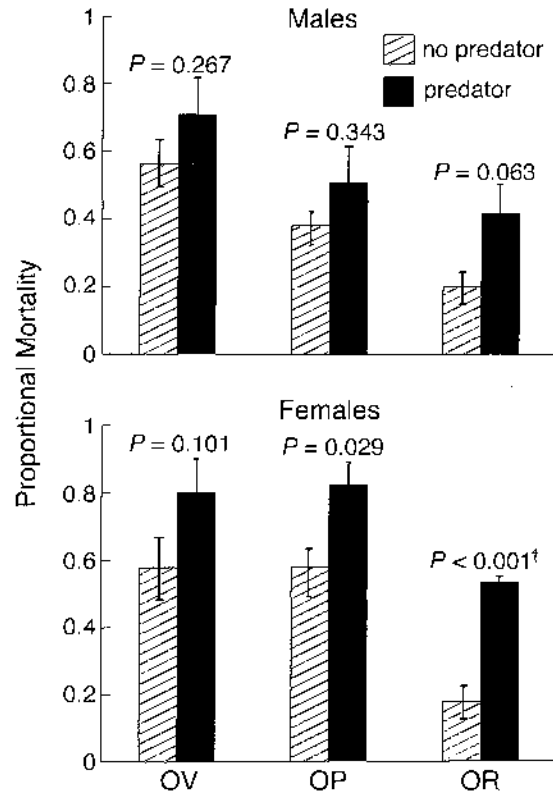


FIG. 2. Mortality of male and female crayfish during 6 wk in predator and no-predator treatments of Nonconsumptive Effects of Predation experiment. OV = *Orconectes virilis*, OP = *O. propinquus*, OR = *O. rusticus*. P values are for species-specific and sex-specific t tests comparing mortality between predator and no-predator treatments. The Bonferroni-adjusted critical value for all t tests performed is $\alpha = 0.003$. The dagger (†) marks P value \leq the adjusted alpha.

in the absence of predators (Tukey's $P = 0.049$ for no-predator treatment). *O. rusticus* and *O. virilis* females grew similarly whether or not predators were present (Tukey's P always > 0.187).

In the presence of predators, *O. rusticus* males exhibited only a moderate decline in mass gain relative to conspecifics in the no-predator treatment, decreasing from ~28% to 23% ($t_{1,8} = 5.16$, $P = 0.053$). *O. virilis* males appeared to experience a large reduction in growth, declining from ~17% to <10% gain of body mass in the predator treatment ($t_{1,8} = 6.65$, $P = 0.037$). Growth did not change for *O. propinquus* males in the presence of predators ($t_{1,8} = 0.001$, $P = 0.974$). Body-mass gain of females of all three crayfishes did not change in the presence of predators relative to the no-predator treatments (Tukey's P always > 0.257).

Possible mechanisms of competition and nonconsumptive effects of predation

When in competition for limited food, size-matched *O. propinquus* and *O. rusticus* males were equally suc-

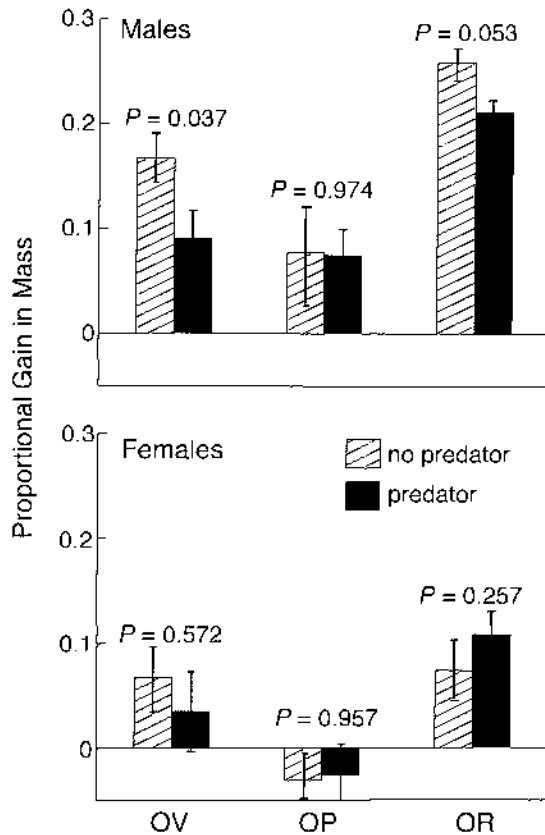


FIG. 3. Growth of male and female crayfish during 6 wk in predator and no-predator treatments of Nonconsumptive Effects of Predation experiment. OV = *Orconectes virilis*, OP = *O. propinquus*, OR = *O. rusticus*. P values are for species-specific and sex-specific *t* tests comparing growth between predator and no-predator treatments. The Bonferroni-adjusted critical value for all *t* tests performed is $\alpha = 0.003$.

successful (Fig. 4). As size of *O. rusticus* declined relative to *O. propinquus* and *O. virilis*, *O. rusticus* success also declined (Fig. 4), but not to levels significantly lower than success of congeners. However, as sizes of *O. propinquus* and *O. virilis* declined relative to *O. rusticus*, success of *O. propinquus* and *O. virilis* declined markedly. *O. rusticus* were generally more successful in encounters with *O. virilis* than with *O. propinquus*, winning 93% of the encounters when matched for size with *O. virilis* vs. only 50% when matched with same size *O. propinquus*. Small *O. rusticus* won 55% of their encounters with large *O. virilis* and only 33% with large *O. propinquus*.

In tests comparing relative success of conspecific males vs. females, we found that *O. rusticus* females and males were equally successful in one-on-one encounters for food, as were male and female *O. virilis* (8:9 and 5:6 win ratios, respectively; *G* test $P > 0.05$ in both cases). However, female *O. propinquus* were very unsuccessful in contests with conspecific males, winning no encounters (0:18 win ratio, *G* test $P < 0.001$).

Other interspecific contests were consistent with trends in previous pairings. Success of *O. rusticus* females did not differ from that of *O. propinquus* females when paired (15:22 win ratio, *G* test $P > 0.05$). *O. rusticus* males won many more encounters than *O. propinquus* females (15:4 win ratio, *G* test $P < 0.001$), while *O. propinquus* males did no better than *O. rusticus* females (12:8 win ratio, *G* test $P > 0.05$).

Comparing a fitness index (μ/g) of crayfishes

Across the range of biotic interaction domains, *O. rusticus* had the lowest μ/g except in intraspecific competition, a domain that is not germane to invasion mechanisms (Fig. 5). *O. propinquus* and *O. virilis* had similar μ/g in three of six interaction domains (no interaction, predation, and predation + interspecific competition) and somewhat similar μ/g in two other domains (interspecific competition and predation risk + interspecific competition). *O. propinquus*, which were smaller than congeners in our experiment, had considerably higher μ/g than *O. virilis* under the interaction domain of intraspecific competition. Overall, *O. rusticus* μ/g was less strongly influenced by competition

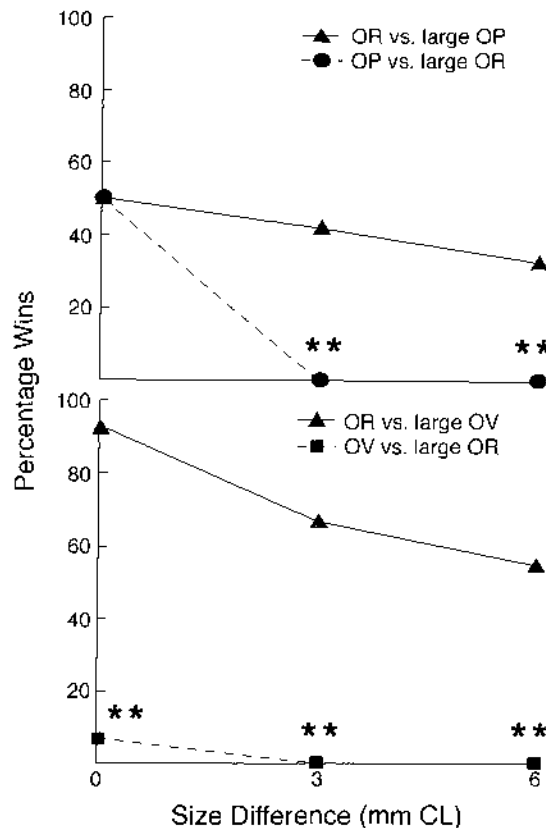


FIG. 4. Percentage of contests won by male crayfish when paired with equal-size and larger male congeners in Competition for Limited Food experiment. Double asterisks (**) indicate that species differed in number of contest won (*G* test, $P < 0.01$).

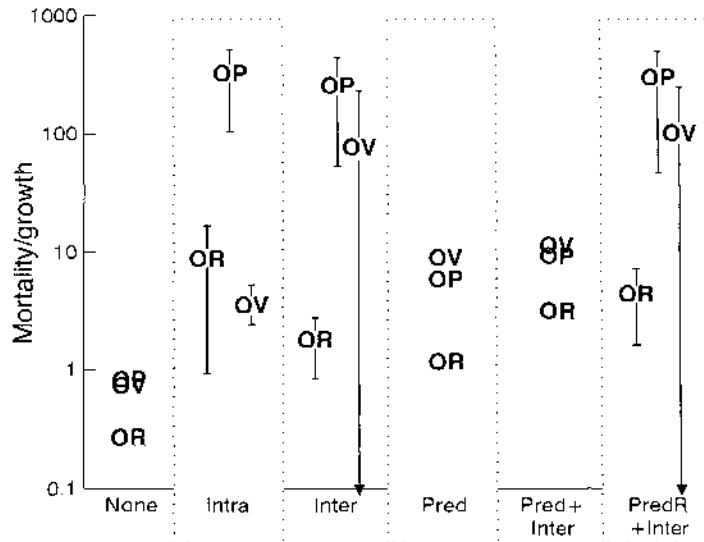


FIG. 5. Index of fitness (mortality/growth ratio) of three crayfish species across biotic interaction domains: None = no interactions, Intra = intraspecific competition, Inter = interspecific competition, Pred = predation (only consumptive effects), PredR = predation risk (only nonconsumptive effects). OV = *Orconectes virilis*, OP = *O. propinquus*, OR = *O. rusticus*; these two-letter species codes in the diagrams indicate the location of that species' ratio in that interaction domain. Note log scale. Ninety-five percent confidence limits are provided where possible.

and predation effects than μ/g of *O. virilis* and *O. propinquus*.

DISCUSSION

Comparing a fitness index (μ/g) of crayfishes

Many researchers have used the μ/g ratio in modeling responses of species in cost/benefit trade-off scenarios. For example, the μ/g ratio has been used to model prey habitat switching (or activity rates) in response to trade-offs between growth (or feeding) and mortality due to predation (Gilliam and Fraser 1987, Werner and Hall 1988, Werner and Anholt 1993). The ratio has also been used to model scenarios for size at metamorphosis to help explain variation in amphibian life histories (Werner 1986). Many other studies have used fitness correlates, such as growth and survival, to measure direct and indirect impact of predation on prey species (e.g., Holomuzki 1986, Dixon and Baker 1988, Ydenberg 1989, Mather and Stein 1993, Peckarsky et al. 1993). This index does not incorporate reproductive value and is therefore most appropriate for juveniles (Werner and Gilliam 1984); however, it is a useful metric for comparisons among species like our crayfishes that have similar reproductive capacities.

By quantifying biotic effects across studies using a fitness index, we were able to generalize about the relative impact of competition, predation, and their interaction on one native and two exotic species. The most recent invader, *Orconectes rusticus*, invariably had the lowest μ/g of the three crayfish species, possibly explaining its consistent success in replacing *O. virilis* and *O. propinquus* (Lodge et al. 1986, Olsen et al. 1991). Though the rate of replacement of congeners by *O. rusticus* varies, consistent with variation in competition and predation intensity as well as abiotic effects, we have not yet seen *O. rusticus* "lose ground" to either *O. propinquus* or *O. virilis* along an invasion

front (Lodge et al. 1986, Olsen et al. 1991; D. M. Lodge and T. M. Kratz, unpublished data). *O. virilis* and *O. propinquus* differed in μ/g rank across interaction domains, consistent with the observation that these two congeners do not always experience unidirectional replacement (Lodge et al. 1986, Olsen et al. 1991). The lack of unidirectionality of these replacements probably reflects variations in type and strength of biotic interactions, especially abundance of predatory fishes, over space and time.

We reiterate that comparisons of the absolute value of μ/g among biotic interaction domains may be inappropriate because of differences among some of the experimental arenas. However, our comparisons among species of relative μ/g are not confounded by experimental differences and thus yield useful insights. In our interaction domains where interspecific competition influenced crayfish fitness, *O. virilis* appeared to have somewhat lower μ/g than *O. propinquus*, whether or not competition was in concert with nonconsumptive (but not consumptive) predation effects. Where interaction domains include fish predation, *O. propinquus* had somewhat lower μ/g than *O. virilis*. Perhaps this advantage for *O. propinquus* was the result of lower susceptibility to predation than equal size *O. virilis*, but that advantage in predator avoidance for *O. propinquus* becomes less apparent when *O. propinquus* decline in size relative to *O. virilis* (DiDonato and Lodge 1993, Garvey et al. 1994). The consistently lower μ/g of *O. rusticus* reflected greater success of *O. rusticus* vs. congeners in competitive interactions, in avoiding predation, and in reducing impact of nonconsumptive effects of predation via adaptive behavior.

We did not have treatments that directly contrasted the relative impact of consumptive effects vs. nonconsumptive effects of predation alone. However, comparing crayfishes' index of fitness in the domain of

predation and interspecific competition with the domain of predation risk and interspecific competition suggests that predation effects may have very strong effects via mortality and that nonconsumptive effects of predation risk may have similarly strong impact via mortality and reduced growth.

Reduced growth, and consequently smaller size at age, reduces fecundity of crayfish (Corey 1987), but we did not incorporate fecundity into our fitness index. We used the ratio μ/g as a conservative estimate of fitness rather than the ratio $([\mu - b]/v)/g$ (where b = birth or hatching rate, and v = reproductive value [Werner and Gilliam 1984]). Same size *O. virilis* and *O. rusticus* produce about the same number of eggs whereas same size *O. propinquus* produce somewhat fewer eggs (Corey 1987). Incorporating reproduction parameters in the equation would lower μ/g for *O. rusticus* more than for its congeners, given its already lower mortality relative to both congeners and higher fecundity relative to *O. propinquus*. Whether the reduction in the measure of fitness would be greater for *O. propinquus* or *O. virilis* would depend on their relative differences in mortality and fecundity and the effect of fecundity in reducing the index numerator $([\mu - b]/v)$. Thus, μ/g is a straightforward and conservative (with respect to *O. rusticus* success) tool for comparing effects of biotic interactions.

Effects of interspecific competition on growth and mortality

O. virilis experienced strongly depressed growth when competing with *O. rusticus* relative to when competing with conspecifics. Reduced growth for *O. virilis* would further reduce its success when competing for food. As the Competition for Limited Food experiments showed, size imparts an advantage in competitive interactions for food among crayfish. This was particularly true for interactions between *O. rusticus* and *O. propinquus*, where same size congeners were equally successful, but somewhat smaller *O. propinquus* were much less successful than larger *O. rusticus* in one-on-one encounters. Additionally, reduced growth for crayfishes increases susceptibility to size-selective predators (Stein 1977, DiDonato and Lodge 1993, Garvey et al. 1994), reduces fecundity (Corey 1987), and reduces success in competition for preferred refuge habitat (Bovbjerg 1956, Rabeni 1985, Hill and Lodge 1994). For the already more predation-susceptible *O. virilis* (DiDonato and Lodge 1993, Garvey et al. 1994), decreased competitive success for food and habitat would further increase susceptibility to predation.

Increased mortality for *O. propinquus* in the presence of *O. rusticus* may have been due to competitive effects, but also may derive from predation by *O. rusticus*. The importance of inter-crayfish predation or cannibalism has not been tested, though we have observed it in both laboratory and field. Regardless of the cause

of increased mortality, costs for the already somewhat less fecund *O. propinquus* (Corey 1987) include fewer individual *O. propinquus* contributing to reproduction within a population. As a result, increased mortality for *O. propinquus* would provide for rapid replacement by the larger invading *O. rusticus*.

Two possible explanations exist for the poor growth of *O. propinquus* in our Effects of Interspecific Competition experiment. First, *O. propinquus* may not grow well under laboratory conditions. However, in earlier laboratory experiments, individually held *O. propinquus* that were fed ad libitum had substantial positive growth, indicating they grow well under laboratory conditions in the absence of competition (Hill et al. 1993). Second and more likely (and consistent with our interpretations), *O. propinquus* may suffer from intense competition effects (whether intraspecific or interspecific) at high densities such as those in our experiment (25 individuals/m²).

In this interspecific competition experiment, we did not test the consequences of competition for female crayfish growth and survival. Results from our Competition for Limited Food experiment suggest that female *O. rusticus* would probably not suffer negative effects from interactions with congeners; they were as successful as male and female *O. propinquus* and male *O. rusticus* in one-on-one encounters. *O. propinquus* females would suffer negative effects when in competition with male *O. rusticus* and with male conspecifics, but not with female *O. rusticus*. However, given our size-effect results and lower growth of *O. propinquus* relative to *O. rusticus* (Hill et al. 1993), *O. propinquus* females would probably suffer from reduced growth and survival when competing with either male or female *O. rusticus* for food. Competition for Limited Food results also suggest *O. virilis* females would suffer as much as *O. virilis* males from interspecific competitive effects. Thus, our conclusions regarding effects of interspecific competition on crayfish growth and mortality would probably not have changed had we included females in the experiment.

The mortality rates we observed in our experiments were consistent with those observed for same aged (2+) *O. rusticus* in Upper Sugarbush Lake, Wisconsin (Lorman 1980). In the only seasonal field survivorship data available for any of our species, Lorman (1980) documented 61% mortality over a 9-wk period (14 June–18 August) that coincided closely with our experiments (6 wk starting 19 June and 7 wk starting 3 July). Assuming a constant mortality rate over the 9-wk period in Lorman (1980), natural mortality rates for our 6-wk and 7-wk experimental durations would have been 40% and 48%, respectively. The 20–60% mortality we observed for *O. rusticus* in our experiments was similar to or only slightly higher than mortality for the field populations. In the absence of any seasonal field data to compare with our mortality results for *O. virilis* (50–80%) or *O. propinquus* (40–80%), there is

no reason to doubt that their natural mortality rates would exceed those of *O. rusticus*.

Nonconsumptive effects of predation on growth and mortality

Nonconsumptive effects of predators on prey species may be more costly to prey populations than consumptive effects because many more individuals may be affected by the costs of predator avoidance than by the costs of being consumed (Zaret 1980, Dill 1987, Sih 1987, Peckarsky et al. 1993). *O. virilis* are most susceptible of the three crayfish species to predation (DiDonato and Lodge 1993, Garvey et al. 1994), and as expected, they exhibited the strongest response to predation risk (Collins et al. 1983, Sih 1987). We observed large reductions in growth of *O. virilis* under predation risk relative to no-predator treatments.

Somewhat surprisingly, *O. propinquus* did not experience reduced growth in the presence of predators although they were smaller and therefore more susceptible to predation than *O. rusticus*. The obvious benefit to *O. propinquus* was no reduction in growth and, therefore, probably no reduction in individual fecundity or competitive success. However, *O. propinquus* (being smaller than congeners and more vulnerable to size-selective predation) would experience greater risk of mortality from predation while foraging than congeners. Regardless of whether largemouth bass predators were present, *O. propinquus* grew more slowly than *O. rusticus*.

The decreased crayfish growth observed in the predator treatment was not the result of differences in crayfish density or differences in food availability. Rather, it was likely due to behavioral differences of crayfish between predator and no-predator treatments. Had the differences in growth between treatments been due to differences in food resource availability, we would have seen growth trends opposite to those we observed. Growth was highest in the no-predator treatment, where crayfish densities were higher and final intact macrophyte and invertebrate abundances were lower relative to predator tanks (Hill and Lodge 1995). Thus, competitive interactions and, therefore, effects would have been most intense in the no-predator treatment. The observed changes in crayfish growth and mortality indicate that predation risk, in conjunction with interspecific competition, increased negative effects.

With nonconsumptive effects of predation, *O. virilis* and *O. propinquus* females suffered the greatest mortality and *O. rusticus* the lowest mortality of the three species. Thus, with fewer females, reproductive success of *O. virilis* and *O. propinquus* populations would be lower than for *O. rusticus*.

In our study, we found that interspecific competition and predation can act in concert to strongly reduce growth and survival of crayfishes. Competition and nonconsumptive effects of predation, by affecting growth of individuals, would affect the success of those

individuals in future encounters with competitors and with predators. The feedback created by the interaction of competition and predation may create far more unfavorable conditions for some species and far more favorable conditions for other species than would be possible with competition or predation alone. Because these biotic interactions may, as we saw, differentially affect the mortality and growth of co-occurring species, they may result in accelerated replacement of one or more species.

Management implications

From our comparisons of μ/g across interaction domains, we gain confidence in our ability to predict shifts in species composition as *O. rusticus* and *O. propinquus* invade northern Wisconsin and other regions. Where *O. virilis* and *O. rusticus* come into contact, *O. virilis* will be replaced under all realistic scenarios. In lakes where *O. virilis* co-occurs only with *O. propinquus*, our results suggest that the native species may be favored in environments with the lowest populations of predatory fishes (*O. virilis* had lower μ/g than *O. propinquus* in domains where predation was absent). Such lakes may include those heavily exploited by humans. Lakes with low predation pressure on crayfishes might provide a refuge for *O. virilis* against *O. propinquus* (but not *O. rusticus*).

We had hoped to identify at least one interaction domain that would both favor *O. virilis* over *O. rusticus* and be achievable through altered lake management or fisheries management practices. However, our results suggest that the only certain way to achieve a management goal of protecting the native *O. virilis* would be to prevent the further spread of *O. rusticus*. If this was a management goal, more state agencies should adopt tighter regulations on the trade in live crayfish as fish bait. Bait buckets, which are effective vectors for many aquatic exotics (Ludwig and Leitch 1996), were probably the major vector for the original introductions of *O. propinquus* and *O. rusticus* in northern Wisconsin. The policy of outlawing the use of live crayfish as fish bait has already been adopted by some states and should be adopted by others if the management goal is protection of native biota.

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