

# Impact of crayfish predation on exotic zebra mussels and native invertebrates in a lake-outlet stream

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**Abstract:** To test the hypothesis that *Orconectes* spp. crayfishes could be a significant source of zebra mussel (*Dreissena polymorpha*) mortality in streams, we conducted a laboratory experiment and a field experiment. In the laboratory experiment, maximum zebra mussel size consumed increased with increasing crayfish size for *Orconectes rusticus*, *Orconectes propinquus*, and *Orconectes virilis*. Slopes differed among crayfish species but not between *O. rusticus* sexes. To quantify crayfish impacts on seminatural zebra mussel populations, we placed 16 enclosures (0.2 m<sup>2</sup>) lined with artificial cobble substrata in a midwestern lake-outlet stream (mean width 17 m). Zebra mussels were stocked in each cage (20 000 individuals/m<sup>2</sup>) 14 days before male *O. rusticus* (20 individuals/m<sup>2</sup>) were stocked in each of eight enclosures. Densities of all sizes of zebra mussels were reduced in enclosures, with a total density reduction of 31% over the 28 days of the experiment, relative to the enclosures. Crayfish also reduced gastropod densities by 54%, but did not significantly affect other invertebrates. Laboratory and field results suggest that predation by *Orconectes* crayfishes may significantly reduce zebra mussel populations in streams.

**Résumé :** Pour vérifier l'hypothèse que les écrevisses appartenant au genre *Orconectes* pouvaient être une cause importante de mortalité des moules zébrées (*Dreissena polymorpha*) dans les cours d'eau, nous avons réalisé une expérience de laboratoire et une expérience sur le terrain. Dans l'expérience en laboratoire, la taille maximale des moules zébrées consommées a augmenté en fonction de la taille des écrevisses *Orconectes rusticus*, *Orconectes propinquus* et *Orconectes virilis*. Les pentes variaient en fonction de l'espèce d'écrevisse, mais non en fonction du sexe d'*O. rusticus*. Pour quantifier les effets des écrevisses sur des populations semi-naturelles de moules zébrées, nous avons délimité 16 enclos (0,2 m<sup>2</sup>) délimités par des substrats de cailloux artificiels dans un émissaire dans le Midwest (largeur moyenne de 17 m). Des moules zébrées ont été placées dans chacun des enclos (20 000 individus/m<sup>2</sup>) 14 jours avant que l'on ajoute, dans huit de ces enclos, des écrevisses mâles de l'espèce *O. rusticus* (20 individus/m<sup>2</sup>). Les densités de moules zébrées de toutes tailles ont été réduites dans les enclos, la réduction totale de la densité étant de 31% au cours des 28 jours qu'a duré l'expérience, par rapport aux enclos témoins. Les écrevisses ont également réduit la densité des gastéropodes de 54%, mais n'ont pas influé de manière statistiquement significative sur les autres invertébrés. Les résultats obtenus en laboratoire et sur le terrain donnent à entendre que la prédation par les écrevisses du genre *Orconectes* peut réduire de manière substantielle les populations de moules zébrées dans les cours d'eau.

[Traduit par la Rédaction]

## Introduction

The rate of introductions of exotic species is increasing and threatens the biodiversity of many regions (Lodge 1993). Limiting the spread of established exotic species is often impossible. Thus, the challenge is to focus management efforts on threatened or endangered species inhabiting systems that are the most susceptible to colonization by harmful exotics. The invasion of North America by zebra mussels (*Dreissena polymorpha*) poses a serious threat to native unionid molluscs (Gillis and Mackie 1994; Schlosser and Nalepa 1994). The ability to predict systems that are at high risk of being colonized by

large numbers of zebra mussels will be important for natural resource managers.

The colonization of the Laurentian Great Lakes by zebra mussels has been associated with a change in the planktonic (Leach 1993) and benthic flora (Pillsbury and Lowe 1995) and fauna (Griffiths 1993; Ludyanskiy et al. 1993; Hebert et al. 1991). In heavily colonized lakes St. Clair and Erie and in Green Bay of Lake Michigan, water transparency has increased (Leach 1993) with a corresponding increase in benthic primary and perhaps secondary productivity (Griffiths 1993; Pillsbury and Lowe 1995). Reductions in phosphorous inputs over the past 20 years may be in part responsible for some of these changes, although zebra mussels have clearly had a significant impact.

The rapid range expansion of zebra mussels in North America and the high densities achieved in many lakes (Hebert et al. 1991) leave the impression that zebra mussels have been unconstrained by predators. However, few quantitative studies have examined the impact of North American predators in lakes (French and Burr 1993; Hamilton et al. 1994), and no studies have examined the role of predation in streams. It is possible that, relative to lakes, predation may be more important

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in streams where zebra mussel recruitment may already be constrained by water velocity or other lotic factors (Jenner and Janssen-Mommen 1993; Horvath et al. 1996).

Estimates of zebra mussel predation by commonly studied European fauna suggest that waterfowl consume between 14 and 63% of the annual zebra mussel production whereas fish consume from 1 to 2% (Smit et al. 1993; Stempniewicz 1974). In North America, several species of diving ducks prey extensively on large zebra mussels (11-21 mm shell length) and significantly reduce zebra mussel populations, but such predation may be largely compensatory (Hamilton et al. 1994). Fish predation on North American zebra mussel populations may also be important to their population dynamics (French 1993; French and Burr 1993). Crayfish have received little attention as natural predators even though they consume large numbers of zebra mussels in laboratory tanks (Piesik 1974; MacIsaac 1994; Martin and Corkum 1994).

Three crayfish species examined to date readily consume large numbers of zebra mussels, at least in the absence of alternative food: *Orconectes limosus* (Piesik 1974), *Orconectes virilis* (Love and Savino 1993) and *Orconectes propinquus* (MacIsaac 1994; Martin and Corkum 1994). Predation rates on mussels decrease, however, in the presence of alternative prey (Love and Savino 1993; MacIsaac 1994). These studies suggest that crayfish have the potential to be important predators on zebra mussels, particularly on zebra mussels 512 mm (Piesik 1974; MacIsaac 1994; Martin and Corkum 1994). Related studies also suggest that crayfish may be important predators on zebra mussels because of the following: (i) crayfish reduce native gastropod populations (Lodge et al. 1994); (ii) crayfish are common in many lakes and streams susceptible to invasion by zebra mussels (Strayer 1991) and commonly occur at densities from 1-8 to 18 individuals/m<sup>2</sup> in the streams and lakes in northern Indiana and eastern North America (Mather and Stein 1993; Charlebois 1994; Lodge and Hill 1994; W.L. Perry, D.M. Lodge, and G.A. Lamberti, unpublished data); (iii) crayfishes (Lodge and Hill 1994) and zebra mussels (Dorgelo 1993) both preferentially inhabit hard substrata; (iv) unlike migratory waterfowl, crayfishes are present year-round; and (v) crayfishes inhabit depths greater than those reached by diving ducks (Love and Savino 1993; MacIsaac 1994). However, no previous study has directly tested the impact of any crayfish on zebra mussels in a natural community of other invertebrates.

The first objective of this study was to determine in laboratory choice experiments if zebra mussels had a size refuge from predation by three common crayfishes of the midwestern United States and southern Canada: *Orconectes rusticus*, *O. propinquus*, and *O. virilis*. The second objective was to determine how *O. rusticus* affected the population density and size structure of zebra mussels and the abundance of associated invertebrates in a lake-outflow stream using a cage experiment.

## Materials and methods

### Laboratory feeding experiments

To determine the potential effect of zebra mussel size on its prey potential to a wide size range of three species of *Orconectes*, we conducted laboratory feeding trials in which individual crayfish of each species were offered zebra mussels ranging from 3 to 31 mm

shell length. Among-species comparisons were conducted with female crayfish. Comparisons between male and female crayfish were conducted with only *O. rusticus* (using form II males). Naive crayfish (never exposed to zebra mussels) were collected from streams in the St. Joseph River basin (northwestern Indiana and southwestern Michigan) as follows: *O. propinquus*, Little Elkhart River and Rock Run Creek, Elkhart County, Indiana; *O. rusticus*, Stony Creek, Elkhart County, Indiana; and *O. virilis*, Rock Run Creek, Elkhart County, Indiana. Crayfish were maintained individually in the laboratory on flake fish food for 2 days prior to experiments. Feeding trials were conducted in Nalgene pans (26 x 20 cm) tilled to a depth of 7 cm with 2.5 L of aged tap water, which was changed daily and aerated. Water temperature was maintained at 24°C and a 12 h light: 12 h dark regime was used. Zebra mussels were collected from Eagle Lake (Cass County, Michigan) 1 day prior to the trials and sorted into 15 1-mm size-classes ranging from 3 mm (3.0-3.9 mm shell length), 5 mm (5.0-5.9 mm), etc., to 31 mm (31.0-31.9 mm) and maintained overnight in 1-L beakers filled with aerated fresh lake water.

One zebra mussel from each of the 15 size-classes was placed into each experimental pan (identical to crayfish holding tanks) and a crayfish added within 1 h. Trials were run on 5 July, 17 July, and 5 August 1994 using at least four crayfish of different sizes from each species. A total of 12 *O. propinquus* females, 13 *O. virilis* females, 17 *O. rusticus* females, and 17 *O. rusticus* form II males were tested over the three trial dates. The largest crayfish individuals used were representative of the largest size commonly encountered for each species. Feeding trials typically lasted for about 72 h and were ended when no zebra mussels had been consumed for 48 h. The maximum size zebra mussel consumed was plotted against crayfish carapace length.

Regression coefficients and  $R^2$  values for the relationships between maximum zebra mussel size eaten and crayfish carapace length for each species-sex were calculated using SYSTAT (Wilkinson 1990). Regressions were compared among species (for females) and between sexes (for *O. rusticus*) using analysis of covariance (ANCOVA) with a Bonferonni corrected post  $F$  test (Wilkinson 1990).

### Field cage experiment

To determine the impact of crayfish on the density and size-frequency distribution of zebra mussels and on the density of cooccurring invertebrates, we conducted a replicated (N= 8) enclosure-exclosure experiment in Christiana Creek (Cass County, Michigan), a lake-outlet stream. Wetted channel width of the experimental reach was 16-22 m, and depth was 4245 cm. Stream substratum was a sand-gravel mixture covered with a dense growth of *Chara* spp. Current velocity averaged 0.18 m/s, and the water temperature ranged from 25°C in June to 29°C in July. The experimental reach had contained a resident zebra mussel population since about 1993 (Horvath et al. 1996). Ambient zebra mussel population density was about 190 individuals/m<sup>2</sup> (Horvath et al. 1996). Ambient crayfish density was about 1 crayfish/m<sup>2</sup> (*O. propinquus*) (W.L. Perry, unpublished data).

Cages were constructed from laboratory rat cages (50 L x 40 W x 20 H cm), modified by replacing tops and upstream and downstream walls with silicon mesh (6 x 9 mm openings). Artificial cobbles (sand-filled, unglazed ceramic "eggs"), 7.5 cm long with a surface area of 130 cm<sup>2</sup>, were arranged in a 5 x 5 matrix on a sand base in each cage. A row of natural cobble surrounded the matrix of artificial cobble substrata.

Eight pairs (enclosure and exclosure) of cages were placed in the stream. Current velocity in the cages was approximately half the ambient flow rate. To estimate initial stocking densities, we used the mean wet weight of 1000 zebra mussels (267 ± 12.5 g (mean ± SE), N = 6) collected randomly from a lake upstream (Eagle Lake, Cass County, Michigan). We used zebra mussels collected at the same time to stock the cages using 1080 g of zebra mussels of all sizes (equivalent to an estimated abundance of 20 225 individuals/m<sup>2</sup>) on 7 June 1994.

This density is in the midrange of zebra mussel densities in North American lakes (Dermott et al. 1993). All cages were then left without crayfish for 14 days to allow attachment of zebra mussels to the artificial cobble and colonization by other invertebrates.

Samples of zebra mussels and associated invertebrates were taken immediately prior to adding crayfish by removing three artificial cobbles from each cage. As each cobble was removed, a cylinder with a 250- $\mu\text{m}$  mesh was held on the downstream side to catch any invertebrates that detached or washed off the substrata. All organisms scraped from each artificial cobble were preserved in 75% ethanol and identified to order under a dissecting microscope. Sampled cobbles were replaced with ones that had been preincubated in the stream for 14 days. Replacement cobbles did not have zebra mussels attached to them and were not sampled. Although restocking cobbles without zebra mussels could have affected stocking densities, no zebra mussels migrated onto the replacement cobble substrata, and thus sampling nearby cobbles accurately represented zebra mussel stocking densities.

Four form II male *O. rusticus* ranging from 33 to 35 mm carapace length (the average size of non young of the year observed in northern Indiana streams) were added to each of the eight enclosures (equivalent to an area abundance of 20 individuals/ $\text{m}^2$ ) on 20 June. We used this stocking density because it represented the upper range of crayfish densities seen in streams in northern Indiana and would represent the maximal impact of crayfish on zebra mussel populations. Cages were resampled for mussels and invertebrates on 30 June and 18 July. Crayfish viability was monitored via snorkeling every 2nd day throughout the experiment. Seven crayfish died and were replaced within 1 day with male *O. rusticus* of the same size. Cage screens were cleaned in situ every 2nd day with a stiff bristled brush to prevent fouling by drifting macrophytes and other debris.

To test the effect crayfish had on the density of zebra mussels and cooccurring invertebrates, a repeated measures analysis of variance (rmANOVA) was used to compare the density of each of six dominant taxa between the enclosure and exclosure cages. To normalize variances, data were transformed ( $\ln(x+1)$ ). For these and subsequent rmANOVAs, the treatment effect of interest was the time  $\times$  crayfish interaction ( $T \times C$ ), which tested whether the temporal trend in prey abundance differed in enclosures versus exclosures. We also report the crayfish main effect ( $C$ ), but do not report the time effect (which was almost always significant) because it was not relevant to our analysis.

To examine the potentially different impact of crayfish on different sizes of zebra mussels, we conducted three additional rmANOVAs, comparing density ( $\ln(\text{density} + 1)$ ) of zebra mussels in three specific size-classes between enclosures and exclosures: 0-17 mm (on the basis of day-0 sizes), which we deemed to be high predation risk on the basis of results of the laboratory feeding trials for male *O. rusticus*; 18-32 mm, which laboratory results suggested were at low predation risk; and zebra mussels that recruited from the plankton into our cages (first detectable on day 10). To correct for growth of the two larger size-classes during the experiment, growth rate was estimated from the change over time in median size of the exclosure population (estimated from samples from the artificial cobbles) and applied to both larger size-classes in the enclosures.

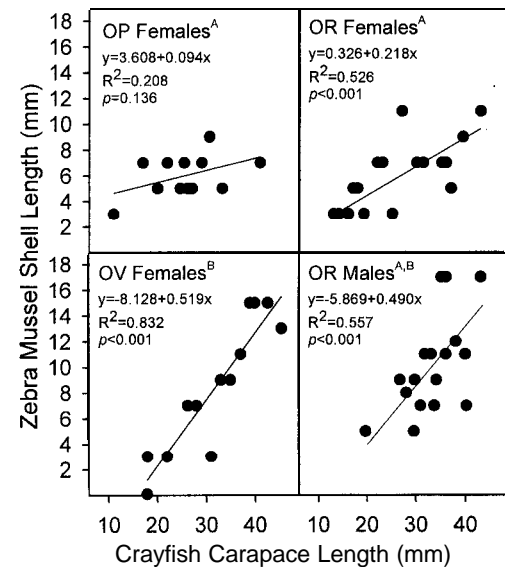
## Results

### Laboratory feeding experiments

Crayfish typically attacked a zebra mussel by using the first and second pairs of walking legs to orient the sharp edge of the shell so that it could be chewed with the mandibles. Smaller zebra mussels (5.5 mm) were commonly ingested whole, but larger shells were cracked open.

With the exception of *O. propinquus* females, a significant

**Fig. 1.** Relationships between the maximum zebra mussel shell length consumed versus crayfish carapace length for *O. propinquus* (OP) females, *O. virilis* (OV) females, and *O. rusticus* (OR) females and form II males. The  $p$  values indicate whether the slopes are different from zero; superscript letters on species represent species groupings that were not significantly different on the basis of a Bonferroni post  $F$  test comparing slopes across species and sexes ( $p < 0.05$ ).



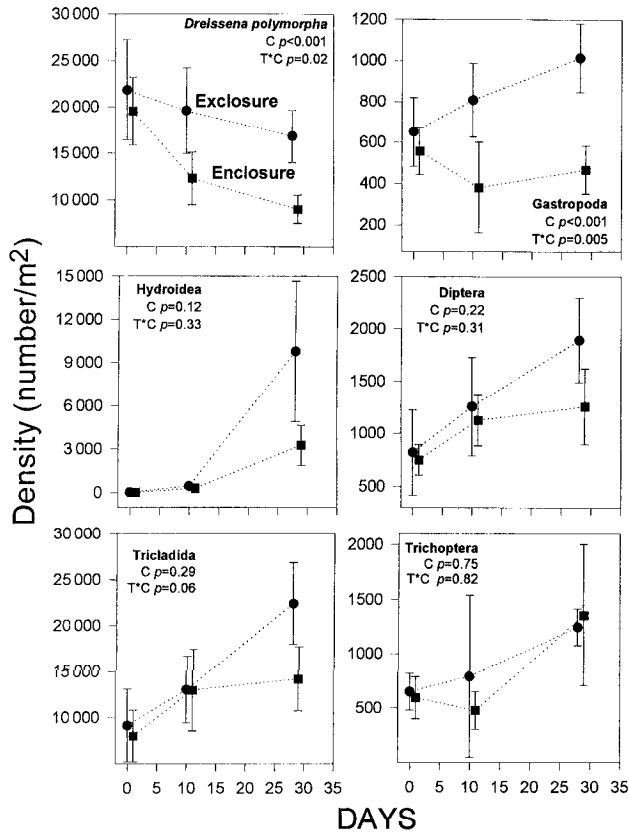
positive relationship existed between the maximum size of zebra mussel consumed and crayfish carapace length (Fig. 1). The slopes of the regressions were significantly different among the four predator categories ( $F_{[3,62]} = 5.22, p = 0.003$ ). Of all the females tested, large *O. virilis* were able to prey upon the largest sizes of zebra mussels. The slope of the relationship for *O. rusticus* form II males did not differ significantly from that for *O. rusticus* females, *O. propinquus* females, or *O. virilis* females ( $p > 0.05$ ) but the slope of the relationship for *O. virilis* females differed significantly from the slopes for *O. rusticus* and *O. propinquus* females ( $p < 0.05$ ). The maximum size of zebra mussel consumed by the largest crayfish (on the basis of actual data, not the regression line) was 9 mm for female *O. propinquus*, 11 mm for female *O. rusticus*, 15 mm for female *O. virilis*, and 17 mm for male *O. rusticus* (Fig. 1).

### Field enclosure-exclosure experiments

Abundances of zebra mussels ( $T \times C; F_{[2,13]} = 5.35, p = 0.02$ ) and gastropods ( $T \times C; F_{[2,13]} = 8.03, p = 0.005$ ) in crayfish enclosures declined significantly over the course of the experiment relative to those in the exclosures (Fig. 2). Apparent reductions by crayfish in the densities of hydra (Hydroidea) ( $F_{[2,13]} = 1.22, p = 0.32$ ), Diptera (primarily chironomids) ( $F_{[2,13]} = 1.28, p = 0.31$ ), and flatworms (Tricladida) ( $T \times C; F_{[2,13]} = 3.43, p = 0.06$ ) were not statistically significant (Fig. 2). Trichoptera, primarily net-spinning forms (Hydropsychidae), were clearly not reduced by crayfish ( $F_{[2,13]} = 0.20, p = 0.82$ ) (Fig. 2).

From the median sizes of the exclosure zebra mussel population on day 0 (9 mm), day 10 (10 mm), and day 28 (12 mm) (Fig. 3), growth was estimated to be 0.1 mm/day; enclosure

**Fig. 2.** Density (mean  $\pm$  95% CI) over time of six potential prey groups in enclosures and exclosures. Crayfish were introduced into enclosures on day 0 (20 June), immediately after prey taxa were sampled. C, repeated measure ANOVA treatment effect of crayfish; T\*C, repeated measure ANOVA treatment effect of time x crayfish).



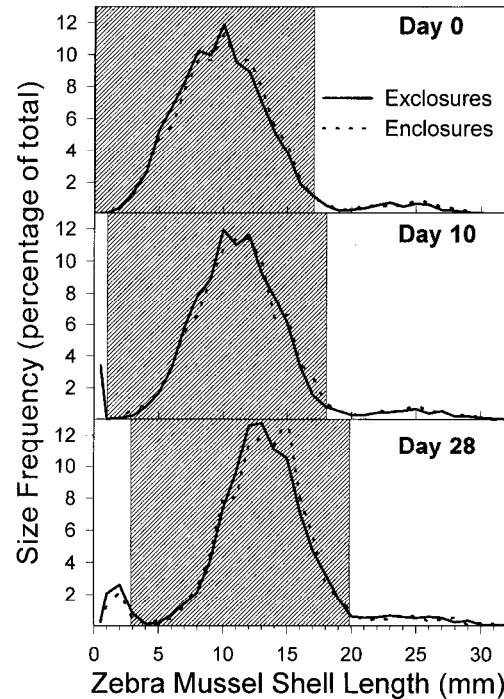
median sizes were the same as in exclosures. Thus, the size category at high risk was estimated to be 0-17 mm on day 0 (from data for *O. rusticus* males in Fig. 1), 1-18 mm on day 10, and 3-21 mm on day 28 (Fig. 3).

As predicted, the density of this high-risk size-class was reduced in crayfish enclosures relative to exclosures (T x C;  $F_{[2,13]} = 4.5, p = 0.03$ ) (Fig. 4B). Contrary to expectation, zebra mussels 217 mm (presumed lower risk) were also significantly reduced by crayfish in the enclosures relative to the exclosures, as indicated by a significant crayfish effect (Fig. 4C, C;  $F_{[1,14]} = 4.678, p = 0.048$ ), although the T x C effect was not significant. Recruitment of zebra mussels into the enclosures was detectable on day 10 (shell lengths 0.5 and 1 mm in Fig. 3) and day 28 (shell lengths 0.5-3 mm in Fig. 3) and was also significantly reduced relative to the exclosures over time (Fig. 4A, T x C;  $F_{[2,13]} = 5.6, p = 0.017$ ). Overall, crayfish reduced all size-classes of zebra mussels in the enclosures relative to the exclosures, including the largest size-class that laboratory results suggested were not eaten.

### Discussion

In our field experiment, *O. rusticus* significantly reduced the density of stocked zebra mussels by 31%, reduced recruitment of zebra mussels, and also reduced snail abundance by about

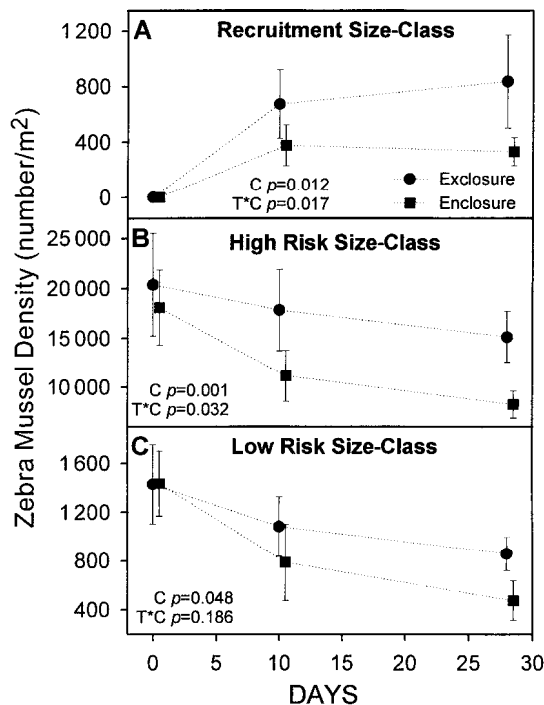
**Fig. 3.** Size-frequency distribution (percentage of total) of zebra mussels in enclosures and exclosures. Hatched area represents the size-class susceptible to predation by crayfish as predicted from laboratory feeding trials. Zebra mussels less than 0.5 mm were not included in the laboratory feeding trials.



54%. Before crayfish were added, the zebra mussels appeared to be uniformly distributed on the artificial cobble. Ten days after crayfish addition, zebra mussels were no longer present on the tops of the artificial substrata in the enclosures. We did not see zebra mussels on the walls of the cages, on the mesh, or on the outside of the cages, suggesting that they had not emigrated. The remaining zebra mussels occupied the inter-cobble spaces, and this pattern persisted on the last sampling date. In exclosures, mussels were present on both the tops and sides of artificial cobble throughout the experiment. These observations suggest that the initial sharp decline in zebra mussel densities in the enclosures resulted when exposed mussels were consumed during the first 10 days of the experiment, presumably because the intercobble spaces provided a spatial refuge from crayfish predation during the following 18 days. We also began to see an increasing reduction of macroinvertebrates in enclosures relative to exclosures from day 10 to day 28, but this reduction could have resulted from a decrease in structural complexity (as mussel populations declined) as well as from crayfish predation. The smaller decline in enclosure zebra mussel densities apparently resulted from nonpredatory mortality and not from emigration from the cages.

Our laboratory results for the maximum size of zebra mussels consumed by each crayfish species were comparable with published values (Love and Savino 1993; MacIsaac 1994; Martin and Corkum 1994; Piesik 1974). The laboratory experiments, however, were not consistent with the effects of crayfish observed in the field experiment with *O. rusticus* males. Our finding that *O. propinquus* would eat zebra mussels 29 mm was roughly consistent with previous results suggesting

**Fig. 4.** Densities (mean  $\pm$  95% CI) of three size-classes of zebra mussels in enclosures and exclosures over the course of the experiment. C, repeated measure ANOVA treatment effect of crayfish; T\*C, repeated measure ANOVA treatment effect of time  $\times$  crayfish.



a preference for 3- to 5-mm zebra mussels and a maximum shell length consumed of 14 mm (MacIsaac 1994) or consumption primarily of zebra mussels 28 mm with a maximum size consumed of 12 mm (Martin and Corkum 1994). Similar to Martin and Corkum (1994), we also found that there was no significant relationship between the maximum size of zebra mussel consumed and the carapace length of *O. propinquus*. While MacIsaac (1994) found differential rates of consumption of zebra mussels by male and female *O. propinquus*, Martin and Corkum (1994) did not. For *O. rusticus*, we found no difference in the maximum size of zebra mussel consumed by males and females.

Most importantly, we found that our laboratory results underestimated the range of zebra mussel sizes consumed in our field cages. On the basis of laboratory feeding trials, we expected consumption of only those zebra mussels less than 17 mm, which should have shifted the size-frequency distribution from one dominated by smaller zebra mussels to one dominated by larger zebra mussels. However, the apparent consumption of all size-classes in the enclosures resulted in no change in the size-frequency distribution of zebra mussels in the enclosures relative to the exclosures. It is possible that large zebra mussels that were attached to substratum (such as in the field cages) were easier for the crayfish to consume than nonattached mussels (such as those in the laboratory experiment).

Charlebois (1994) found that *O. rusticus* significantly reduced the abundance of several macroinvertebrate taxa and altered community structure in a northern Michigan stream that lacked zebra mussels. This disparity of results between Charlebois (1994) and this study suggests that the presence of

zebra mussels may reduce the impact of crayfish on other invertebrates, possibly because of (i) the large food resource provided by zebra mussels, or (ii) the spatial refugia offered by mussel shells. In our field experiment, flatworms, hydra, Trichoptera, and Diptera were not significantly reduced as observed in similar experiments using lower densities of *O. rusticus* (5510 crayfish/m<sup>2</sup>) in the experiment by Charlebois (1994).

In general, our field experiment suggests that lakes and streams containing *O. rusticus* populations may experience slower colonization and lower overall densities of zebra mussels than systems lacking crayfish. Consumption of zebra mussels by *O. propinquus* and *O. virilis* in our laboratory experiments suggests that natural populations of those species would also reduce natural zebra mussel populations. If smaller crayfish had been used in the field experiment, they would most likely not have consumed the larger mussels. However, smaller crayfish may be capable of exploiting intercobble spaces inaccessible to adult crayfish. Densities of juvenile crayfish are often higher than those of adults (Lodge and Hill 1994), and this higher density may result in an even larger impact on small zebra mussels than revealed by our field experiment. Certainly, while crayfish may act to reduce populations of zebra mussels and while the presence of large populations of zebra mussels may provide a novel food resource for crayfish, it is unlikely that crayfish can reduce zebra mussel populations below densities that are ecologically important.

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