

Size-selective predation on zebra mussels (*Dreissena polymorpha*) by crayfish (*Orconectes propinquus*)

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Abstract. Zebra mussels (*Dreissena polymorpha*) are now a common component of benthic communities in the lower Great Lakes, but information regarding North American predators remains scant. I measured predation by crayfish (*Orconectes propinquus*) on different size classes of zebra mussels in aquarium experiments. Crayfish showed a strong preference for small (3–5 mm) mussels, although larger individuals (8–10 mm, 12–14 mm) were also eaten when presented simultaneously. Feeding rates on different mussel size classes were affected by crayfish size and sex, although results varied between experiments. Survival of zebra mussels was enhanced between 3 and 30% when crayfish were offered alternative macrophyte foods (*Potamogeton*, *Vallisneria*); however, size selective predation patterns on mussels remained virtually unchanged in the presence of alternative foods. Time-lapse videographic studies revealed that both rejection rate and handling time increased with mussel size. Despite high predation rates on small mussels, crayfish attacked medium and large mussels more often than small individuals. Results of this study indicate that predation by *O. propinquus* on *D. polymorpha* will be limited primarily to small- and medium-sized mussels.

Key words: *Dreissena polymorpha*, *Orconectes propinquus*, size selective predation, exotic species.

The Great Lakes currently support at least 53 animal species introduced from other regions of the world (Mills et al. 1993). The zebra mussel (*Dreissena polymorpha*), a native of the Caspian and Black Sea region of Europe, is among the most recent and conspicuous species to invade the Great Lakes. Zebra mussels were first detected in Lake St. Clair and western Lake Erie in 1988, but probably first invaded these systems in 1986 (Hebert et al. 1989, 1991). The distribution of zebra mussels in North America has expanded very rapidly to include, by January 1993, the Illinois, Ohio, Mississippi, Arkansas, Tennessee, Hudson, Susquehanna, Ottawa and St. Lawrence systems, and inland lakes in Ontario, Ohio, and Michigan (Zebra Mussel Information Clearinghouse 1993).

Adult and larval (veliger) mussels are now dominant members of the benthos and plankton in Lake Erie and Lake St. Clair (Leach 1992, Mackie 1991, Hunter and Bailey 1992). Adult mussel densities as high as 342,000 individuals/m² in Lake Erie and 200,000 individuals/m² in Lake St. Clair have been reported (Leach 1992, Mackie 1991). These densities greatly exceed those typically observed in European lakes (e.g., Bij de Vaate 1991, Stańczykowska and Lewandowski 1992) and have resulted in dramatic transformations of the western Lake Erie and Lake St. Clair ecosystems. For example, densi-

ties of native unionid mollusks have declined severely in both systems owing, in part, to infestations of attached zebra mussels on exposed shell surfaces. Unionids fouled in this manner may suffer from both exploitative competition for food and interference in opening and closing their valves (Hebert et al. 1989, Mackie 1991, Hunter and Bailey 1992). *Dreissena* filter-feeding has been implicated in declines of microzooplankton abundance and phytoplankton biomass in western Lake Erie (MacIsaac et al. 1991, 1992, Leach 1992, Bunt et al. 1993, Holland 1993). Water clarity has improved in both Lake St. Clair and Lake Erie since establishment of *Dreissena* (Hebert et al. 1991, Leach 1992, Holland 1993).

Despite the abundance and importance of zebra mussels in some Great Lakes, information regarding predation on settled mussels is limited. Four species of waterfowl (Lesser Scaup *Aythya affinis*, Greater Scaup *A. marila*, Bufflehead *Bucephala albeola*, and Common Goldeneye *B. clangula*) from the Point Pelee, Ontario, area were found to contain *Dreissena* remains in their gizzards, and large flocks of these and other diving ducks have congregated in the Point Pelee region during fall migration since mussels have become common in Lake Erie (Hamilton 1992, Wormington and Leach 1993). Enclosure experiments in Lake Erie near Point Pelee re-

vealed that diving waterfowl could severely deplete *Dreissena* density (Hamilton et al. 1994). Sessile *Dreissena* are also eaten by freshwater drum (*Aplodinotus grunniens*) in the Great Lakes (French and Bur 1992). European workers have observed high rates of predation on zebra mussels by the crayfish *Orconectes limosus*, and have suggested that crayfish predation can greatly reduce the abundance of *Dreissena* populations (Piesik 1974, 1983, Szlauer 1974, Kornobis 1977). Piesik (1974) observed that *O. limosus* tended to prey selectively on small (1–7 mm) zebra mussels, and that predation rates by female crayfish were higher than those of males.

Crayfish are common inhabitants of Lake St. Clair and western Lake Erie at depths of 0.5–5 m (personal observations). In addition to animal prey, crayfish consume detritus (Crocker and Barr 1968) and a variety of aquatic plants (Capelli 1980, Feminella and Resh 1989, Hanson et al. 1990, Chambers et al. 1990, 1991, Olsen et al. 1991, Hart 1992, Hill et al. 1993). The impact of crayfish predation on zebra mussel populations in nature will depend on relative preferences for zebra mussels, other invertebrates, aquatic plants and detritus. To date no studies have addressed predation on zebra mussels by crayfish in the Great Lakes.

The purpose of this study was to assess whether the crayfish *Orconectes propinquus* feeds selectively on different size classes of *D. polymorpha*, and whether feeding rates are affected by crayfish size or sex. Additional experiments were conducted to assess whether feeding rates are affected by the presence of alternative macrophyte foods (*Vallisneria*, *Potamogeton*). Finally, behavioural observations were made to determine *Orconectes* handling times and rejection rates for different size classes of *Dreissena*.

Methods

Mussel-size preference experiment

Crayfish, zebra mussels and water were collected from Lake St. Clair at a site east of Peche Isle, Ontario (42°37'N, 82°28'W), during July and August 1992. *Orconectes propinquus* individuals were hand-collected by divers by overturning small rocks. Crayfish were taken to the laboratory, maintained in 810-L aquaria equipped with a gravel bed, clay pot refuges and aerated,

glass-fibre-filtered (Whatman, retention to 1.5 μ m) lake water, and fed small pieces of beef liver ad libitum. Crayfish were acclimated individually in 38-L aquaria with opaque walls two days before experimental trials. Crayfish hunger level was standardized by adding 250 ± 10 mg of beef liver per aquarium per day during the acclimation period. Only non-berry female and form-1 male crayfish were used in experiments.

Rocks encrusted with zebra mussels were collected from the lake and transferred to 38-L aquaria containing filtered lake water. Cultured mussels were provided with a maintenance ration of a *Cryptomonas* suspension ($\sim 3 \times 10^5$ cells/mL final density) every second day. Fifteen healthy (valves gaped, siphons extended) mussels from each of three shell length categories: small, 3–5 mm (1.9–8.0 mg), medium, 8–10 mm (30.2–56.8 mg), and large, 12–14 mm (95.1–147.2 mg) were collected from the aquaria one day before experimental trials by cutting byssus threads. Individuals were placed on a 250-cm² coarse (1.4 mm) nylon-mesh netting which was subsequently folded over and sealed, and placed in an aquarium with filtered lake water but lacking mussels. Most mussels attached byssal threads to the netting or to other mussels during the acclimation period. Size distributions of settled *Dreissena* in Lakes St. Clair and Erie include mussels both smaller and larger than those used here, but are biased toward mussels <12 mm (Mackie 1991, Leach 1992, MacIsaac et al. 1992). Experimental mussel densities on netting were more than two orders of magnitude lower than maximum densities observed in Lake Erie and Lake St. Clair.

Experimental aquaria (38 L) contained 12.5 L (~ 10 cm) of aerated, glass-fibre-filtered water and a clay pot refuge. The pot rested on a bed of gravel that covered one half of the aquarium. Feeding trials were conducted under conditions (19–20°C, 9:15 light:dark regime) that approximated natural conditions in the lake at that time. At the outset of a feeding trial, a piece of netting containing *Dreissena* was unfolded, placed on the bottom of a crayfish aquarium at the end lacking gravel, and held in place by small rocks at each corner. Identical procedures were followed in control aquaria lacking crayfish. Feeding trials were conducted on four separate dates; between two and five control replicates (lacking crayfish) were conducted on each date (Table

TABLE 1. Design of experiments exploring crayfish predation on different mussel size classes, and macrophyte foods (*Vallisneria*, *Potamogeton*) vs. mussels.

Experiment	Trial	Replicates per treatment				
		Controls	<i>Orconectes</i>		Length range (cm)	
			Male	Female	Male	Female
Mussel size preference	1	2	7	5	5.5–7.2	4.7–6.1
	2	5	7	4	5.0–5.8	4.6–6.7
	3	3	9	3	5.4–6.8	4.0–6.7
	4	3	5	8	3.9–5.5	4.4–6.0
Macrophytes vs. mussels	1	3	6	6	4.6–6.1	5.1–6.8
	2	3	7	6	4.3–7.5	3.5–4.4
	3	4	6	4	4.9–7.5	3.8–5.8
	4	3	3	5	4.7–5.2	5.1–6.6

1). All feeding trials lasted 48 h, after which crayfish were removed and narcotized in carbonated water. Crayfish wet mass was determined to the nearest 0.1 g, and body length (cephalothorax + abdomen) was measured to the nearest 1 mm. Although this study employed body length as a measure of crayfish size, it could be substituted by body mass which is highly related to body length by the equation $\text{dry mass} = 0.108 \times \text{body length}^{2.74}$, $r^2 = 0.97$. Crayfish species and sex were identified using Crocker and Barr (1968). Survival of different size classes of zebra mussels was assessed at the termination of the experiment, and surviving individuals were checked for evidence of non-lethal damage. Crayfish feeding rates (mussels ingested/day) were calculated based on mussel survival patterns.

Feeding on macrophytes vs. mussels

In a second experiment involving four feeding trials, crayfish were provided with alternative foods (*Potamogeton crispus* and *Vallisneria spiralis*) in addition to *Dreissena* prey. Both species of macrophytes, which were collected at the site described above, are common in Lake St. Clair (Edsall et al. 1988) and both are fed upon by *Orconectes* crayfish (Olsen et al. 1991). Macrophytes collected from the lake were taken to the laboratory and maintained in aquaria containing filtered lake water. One day before the feeding trial, individual *Potamogeton* shoots and *Vallisneria* rosettes were cut transversely with a scalpel into 5-cm lengths. Seven pieces of each species were bunched together at the base with either a paper clip or a rubber band (depending

on trial date). All *Vallisneria* rosettes contained at least one leaf. Individual macrophyte bunches were patted dry and weighed to the nearest 0.01 g before the experiment. One bunch of each macrophyte species was placed in each aquarium on the bare glass bottom between the mussel-laden netting and clay pot refuge. Following the experiment, macrophyte tissues were recovered, patted dry and weighed. Differences in plant biomass between control and crayfish aquaria were analyzed separately for *Potamogeton* and *Vallisneria* using Bonferroni-adjusted *t*-tests following $\ln(x + 1)$ -transformation of biomass data.

Behavioural observations

Time-lapse videography studies were conducted to determine handling and rejection times, and predation and rejection rates for *Orconectes propinquus* feeding on 3–5 mm, 8–10 mm, and 12–14 mm *Dreissena*. Animal collection and acclimation procedures followed those outlined above, except that crayfish were fed a daily ration of 160 ± 3 mg ($\bar{x} \pm 1$ SE) of Wardsley® Shrimp Pellets. Procedures were similar to those described for the food preference experiments except that aquaria lacked gravel and macrophytes, trials lasted 24 h, and only one *Dreissena* size class was presented as prey at a time. Fifteen mussels were spaced 1.5 cm apart in a 3×5 array 3-cm away from the clay pot. Trials with other size classes were conducted over the following two days. The order of trials involving different *Dreissena* size classes was determined haphazardly for each of four male and four female crayfish. Crayfish predation behaviour was

recorded over a 24-h period (10:14 h, L:D) using an infrared-sensitive Panasonic camera (model WV-1854) fitted with a 12.5-mm Cosmicar lens and a Panasonic time-lapse video cassette recorder (model AG-6050). Recording was conducted at 5 frames/s. The camera was positioned 21 cm below the test aquarium, providing a field of view of $\sim 14 \times 17$ cm. To enhance images recorded during periods of low natural light, additional illumination was provided by a 250-W General Electric spotlight equipped with a infra-red transmitting filter (Kodak 11). Crayfish behaviour was not affected by the spotlight. I recorded numbers of unsuccessful predation attempts and numbers of mussels eaten. Information on the number of mussels surviving the trial was used rather than the number of recorded successful predation events in calculating predation rates because not all such events occurred within the field of view. Handling time was determined as the difference between time of ingestion and time of initial contact for recorded observations. Rejection time was determined as the difference between time of rejection and that of initial contact.

Statistical analyses

Differences between control and experimental *Dreissena* survival rates for each size class were explored using Bonferroni-adjusted *t*-tests and \sin^{-1} (proportion survival rate)^{0.5} data. Differences in crayfish feeding rate on mussels in the presence and absence of alternative macrophyte food were tested for each mussel size class using $\ln(\text{feeding rate} + 1)$ data and *t*-tests. Feeding-rate data were not corrected for mussel mortality in control containers because this mortality was always $\leq 1.5\%$ and did not vary significantly between experiments with and without macrophytes (*t*-tests, $p > 0.10$). Observations for four crayfish that molted during experimental trials were deleted from analyses.

The effects of crayfish sex and length on feeding rate on mussels was assessed separately for each mussel size class using analysis of covariance, with crayfish length entered as a covariate and sex as a categorical variable. Because preliminary analyses indicated no significant ($p > 0.05$) interactions between independent variables, models presented here lack interaction terms.

Selectivity coefficients were calculated for each *Orconectes* for each *Dreissena* size class us-

ing Chesson's (1983) preference index, α , with corrections for prey depletion. Selectivity coefficients for small *Dreissena* ranged between 0 (only medium and large *Dreissena* eaten) and 1 (only small *Dreissena* ingested), with a value of 0.33 indicating non-selective feeding. Calculated α values for small *Dreissena* are conservative because 10 and 7 observations were omitted from the analysis for experiments 1 and 2, respectively, because of 100% mortality of small-sized *Dreissena*. The significance of differential feeding by *Orconectes* on different *Dreissena* size classes was tested using Yao's (1965) multivariate method (see Manly 1993). This method contrasts differences in survival patterns of different mussel size classes exposed to crayfish with those of comparable control populations. The method is superior to other tests of feeding preference because all control and experimental data may be used and because problems resulting from random pairing of experimental and control values are avoided (Peterson and Renaud 1989, Manly 1993).

Median handling times were computed for each *Orconectes* preying on small and medium *Dreissena* for the videotaped observations. Median rejection times were calculated for unsuccessful recorded predation attempts on medium and large mussels. Differences in median handling times for small and medium mussels and in median rejection times for medium and large mussels were analyzed using Mann-Whitney *U*-tests. Handling times for large mussels and rejection times for small mussels were not used in these analyses because of insufficient recorded observations (1 and 3, respectively).

Results

Feeding experiments

All *Dreissena* size classes from both the size-preference and macrophyte experiments experienced significantly lower survival when incubated with *Orconectes* relative to controls lacking crayfish ($p < 0.01$) (Fig. 1). *Orconectes* preyed intensively on small (3–5 mm) *Dreissena*, but ate fewer medium (8–10 mm) and large (12–14 mm) mussels (Fig. 1). Individual crayfish demonstrated significant preference for small mussels in both the size-preference experiment ($F = 99.8$, $df = 2, 54.4$, $p < 0.0005$) and in the macrophyte experiment ($F = 83.4$, $df = 2, 48.2$,

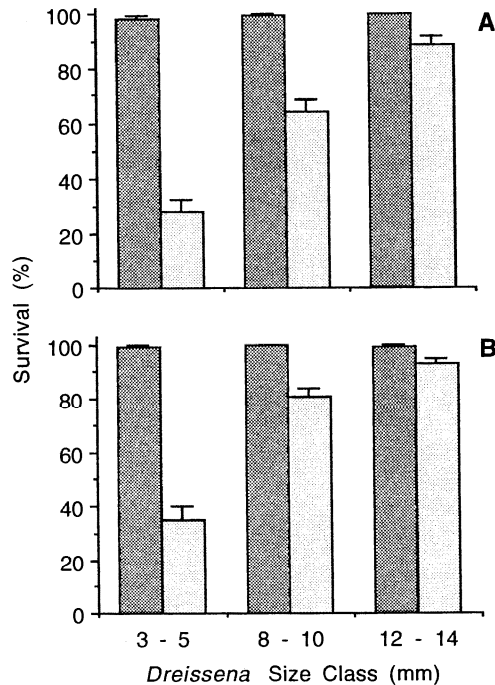


FIG. 1. Mean (+1 SE) survival rate of 3–5-mm (small), 8–10-mm (medium), and 12–14-mm (large) *Dreissena* in aquaria with (light stippling) and without (dark stippling) *Orconectes*. Experiments were conducted with *Dreissena* as the only food (A) or with *Vallisneria* and *Potamogeton* as alternative foods (B).

$p < 0.0005$) (Fig. 2). Crayfish exhibited a slightly stronger preference for small mussels in the presence of macrophytes than in the experiment lacking alternative foods.

Shells of killed and consumed *Dreissena* were typically broken into small fragments and scattered on the netting, although fragments were occasionally found in or adjacent to clay pots on the gravel bed. Visual inspections of large mussels in both experiments revealed no evidence for non-lethal damage by crayfish.

Both crayfish length (Fig. 3) and sex (Fig. 4) affected feeding rate on mussels, although effects varied between experiments with and without macrophytes (Table 2). In a regression analysis of feeding rates on large mussels on crayfish length, both crayfish size and the intercept were significant (t -tests, $p < 0.05$). Thus, the ability to successfully prey on large *Dreissena* was limited to mussels larger than 4.2 cm body length (Fig. 3C). By contrast, feeding rates on small mussels declined slightly with increas-

ing crayfish length (t -test, $p = 0.06$; Fig. 3A). Crayfish length, however, was a poor predictor of feeding rate on mussels in the macrophyte experiment (Table 2). Female crayfish tended to have higher feeding rates than male crayfish (Fig. 4) in the macrophyte experiment, although differences were significant only for large mussel prey (Table 2).

The presence of macrophytes resulted in increased survival of each size class of *Dreissena* when incubated with crayfish (Fig. 1A, B), although differences were significant ($p = 0.008$) only for medium-sized mussels. Overall *Dreissena* survival, adjusted for survival of mussels in control aquaria, increased by 30%, 27% and 3% in treatments with macrophytes for small, medium, and large mussel size classes, respectively. Crayfish significantly reduced the biomass of *Potamogeton crispus* ($t = 4.56$, $df = 51.7$, $p < 0.0001$) and *Vallisneria americana* ($t = 2.85$,

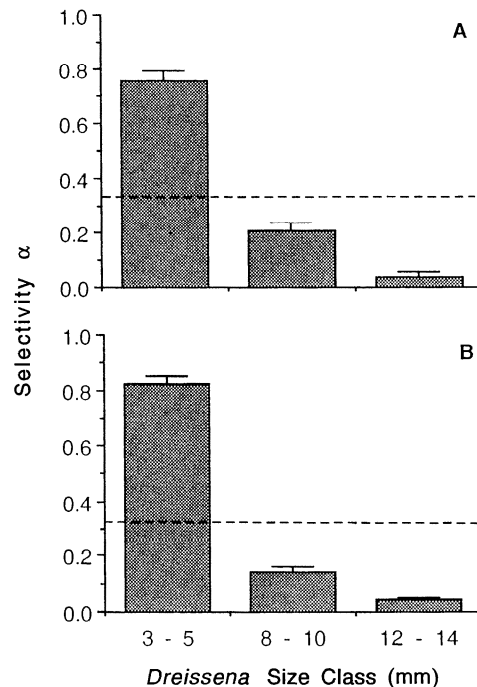


FIG. 2. Mean (+1 SE) selectivity coefficients for *Orconectes* feeding on different size classes of *Dreissena* in experiments without (A) and with (B) macrophyte food. The dotted line depicts non-selective feeding ($\alpha = 0.33$). Points above the line represent positive selection for that food type, and points below represent negative selection.

df = 50.8, $p < 0.01$) relative to control aquaria lacking *Orconectes* (Fig. 5).

Behavioural observations

Orconectes predation patterns on *Dreissena* in the videotaped observations paralleled those in the preference experiments (Fig. 6). High predation rates on small mussels can be explained by the relative ease with which they were handled by crayfish. Small mussels required significantly ($U = 40$, $p = 0.003$) less manipulation

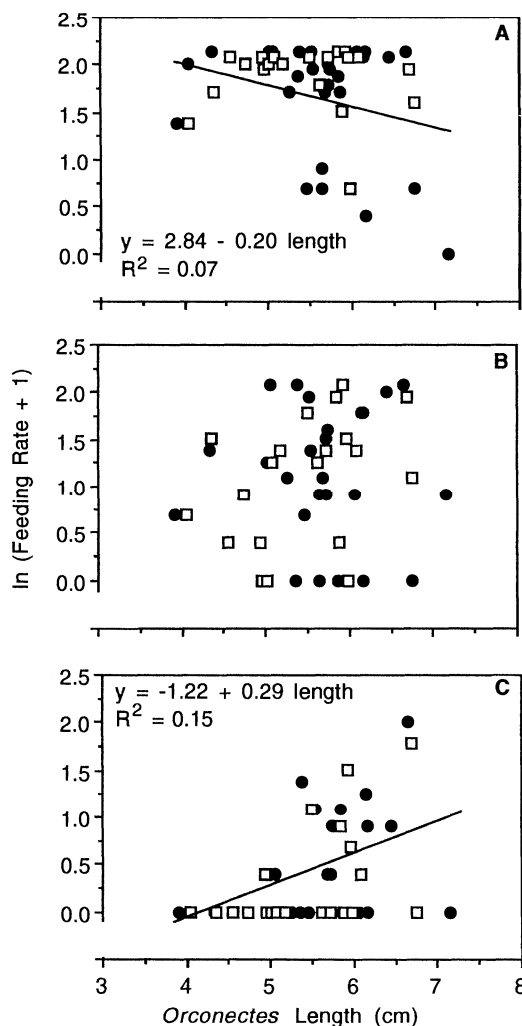


FIG. 3. Relationship between feeding rates of male (solid circle) and female (open box) *Orconectes* on small (A), medium (B), and large (C) *Dreissena* and crayfish length. Data are from the mussel-size preference experiment.

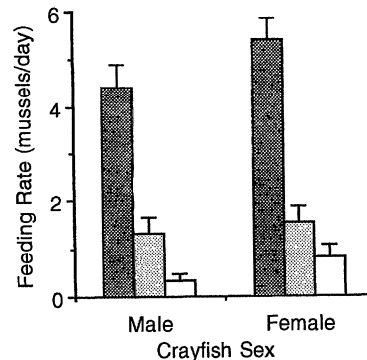


FIG. 4. Mean (+1 SE) feeding rates on small (dark stipple), medium (light stipple) and large (open) *Dreissena* in relation to *Orconectes* sex. Data are from the macrophyte vs. mussels experiment.

time (median = 68 s) than medium mussels (median 456 s) before they were ingested. Low predation rates on large mussels were not the result of avoidance of this prey size by predators. Rather, unsuccessful predation attempts were much more common for large than for medium mussels (Fig. 6). Only one crayfish of eight tested was observed to reject small mussels, whereas all crayfish rejected some medium and large individuals. Despite the high number of unsuccessful predation attempts, rejection times for large mussels (median 16.5 s; $n = 8$) were not significantly higher than those for medium individuals (13.5 s; $n = 8$) ($U = 32.5$, $p = 0.958$).

Discussion

Predation is an important determinant of the abundances and distributions of many animals and plants. Predation by crayfish may affect macroalgae and macrophyte distributions and abundances in both lentic systems and streams (Feminella and Resh 1989, Coffey and Clayton 1988, Hart 1992). Decapods may also affect animal abundances, either directly, by preying on vulnerable species or prey size classes (Robles 1987), or indirectly, by reducing the abundance of aquatic plants used by other animals for shelter or food (Hart 1992). In Europe, predation by crayfish (*Orconectes limosus*) may account for large declines in the seasonal abundance of *Dreissena* (Piesik 1974, 1983, Kornobis 1977). The results reported here suggest that the crayfish *O. propinquus* may be expected to prey on small- and medium-sized zebra mussels in North

TABLE 2. Results of analysis of covariance tests explaining variation in transformed survival data for small (3–5 mm), medium (8–10 mm) and large (12–14 mm) classes of *Dreissena* in preference experiments lacking or with alternative macrophyte foods. Probabilities: * $p < 0.10$; ** $p < 0.05$; *** $p < 0.01$; NS $p > 0.10$.

Experiment	<i>Dreissena</i> size class	<i>Orconectes</i> predictors			
		Body length		Sex	
		F	df	F	df
Mussel size preference	small	3.1*	1,45	1.2 ^{NS}	1,45
	medium	1.9 ^{NS}	1,45	<0.1 ^{NS}	1,45
	large	7.5***	1,45	0.2 ^{NS}	1,45
Macrophytes vs. mussels	small	<0.1 ^{NS}	1,40	1.6 ^{NS}	1,40
	medium	1.8 ^{NS}	1,40	0.7 ^{NS}	1,40
	large	2.0 ^{NS}	1,40	4.2**	1,40

America. Other predators, including roach (*Rutilus rutilus*) and tufted duck (*Aythya fuligula*), prey selectively on small *Dreissena* (Draulans 1984, Prejs et al. 1990, DeLeeuw and van Eerden 1992).

Orconectes propinquus predation on *Dreissena* was affected by crayfish size, particularly with respect to small and large mussels when macrophytes were absent (Fig. 3A, C; Table 2). Although all crayfish preyed extensively and preferentially on small *Dreissena*, selectivity coefficients for small mussels tended to decline with increasing crayfish size. Piesik (1974) reported a similar pattern of increased prey size breadth with increasing crayfish size, but only for females. The inclusion of large prey classes in diets of larger crayfish may reflect a tradeoff between increased energy content and in-

creased handling time. The ratio of *Dreissena* energy content to shell crushing resistance, measured using a vertical press, increased with increasing mussel size (Prejs et al. 1990). This relationship suggests that predators should eat the largest prey possible (Prejs et al. 1990). Difficulty in manipulating, prying open, or crushing large mussels, however, may restrict small crayfish to only small prey, and large crayfish to a combination of small, easily-handled prey with a high cost:benefit ratio and large prey with a lower cost:benefit ratio (Fig. 2). Behavioural observations are consistent with these predictions. In virtually all cases, crayfish seized small mussels using the 2nd or 3rd pereopods, transferred the mussels to the maxillipeds, then crushed or pulled the animals apart using the 2nd pereopods and maxillipeds. Some small mussels were apparently crushed and eaten whole. Piesik (1974) reported that *O. limosus* preyed on small *Dreissena* by tearing them from attached substrates using chelipeds of the 2nd and 3rd walking legs. My observations showed that handling of medium and especially large *Dreissena* was much more laborious and often resulted in rejection (Fig. 6). These mussels were grasped with either the 2nd or 3rd pereopods or by the chelipeds. During manipulation, the chelipeds were often folded and used as supports to minimize mussel movement during manipulation by the maxillipeds and 2nd and 3rd pereopods. Unsuccessful attempts to pry open mussel shells were frequently followed by a reorientation of the mussel and additional predation attempts. This attack behaviour differs from that reported by Piesik (1974). He ob-

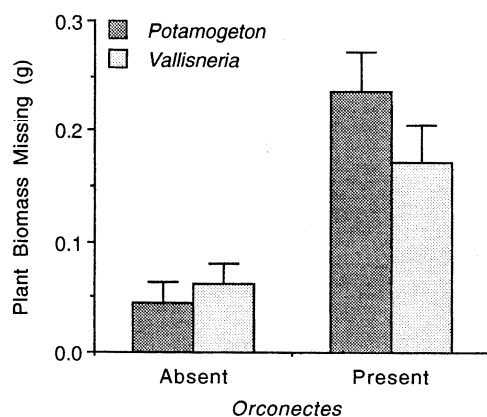


FIG. 5. Loss of macrophyte biomass in aquaria with and without *Orconectes*.

served that large mussels or those more firmly attached to substrates were seized in the mandibles and torn free as the crayfish rose up on its legs from a sitting position (Piesik 1974). Most *Dreissena* were eaten where they were encountered (on the netting), although individuals were occasionally moved to the pot refuge where they were killed and eaten. Covich et al. (1981) observed that some *Cambarus bartonii* and *Procambarus clarkii* individuals retreated to refuges before feeding on the clam *Corbicula*.

Juanes (1992) reported that preference for small-sized molluscan prey is common among decapod predators. Results from my feeding preference trials (Fig. 1) appeared consistent with this pattern. Data for median handling time (68 and 456 s) and median dry mass (4.8 and 44.2 mg) for small and medium mussels suggested that predation on small individuals (14.1 s/mg) was less efficient energetically than that on medium mussels (10.3 s/mg). Juanes and Hartwick (1990) proposed that decapod predators may prefer prey size classes smaller than those predicted to maximize the net rate of energy acquisition if predation on large prey is accompanied by enhanced claw-tooth wear or chelae breakage, either of which would impair subsequent feeding. Videotaped observations, however, contrast predictions of the energy efficiency model with those of the claw breakage model. Although crayfish experienced much higher predation success on small mussels than on larger individuals, and thus appeared to prefer small prey, large mussels are attacked preferentially to small individuals (Fig. 6). When presented with equal numbers of small, medium and large mussels arranged in a regular distribution, crayfish launched an average of 53% of the first ten attacks against large mussels and only 11% against small individuals (unpublished data). Thus the differences in size preference patterns of crayfish observed in this study represent post-contact behaviour and not pre-contact avoidance of large prey. The higher attack rate on large mussels may simply reflect enhanced encounter rates with predators, although the close proximity (1.5 cm) of neighbouring small- and medium-sized mussels suggests that encounter rates should not have differed strongly for different mussel size classes (Fig. 6). Preference studies that rely solely on differences in abundances of different prey classes in predator vs. predator-free arenas may

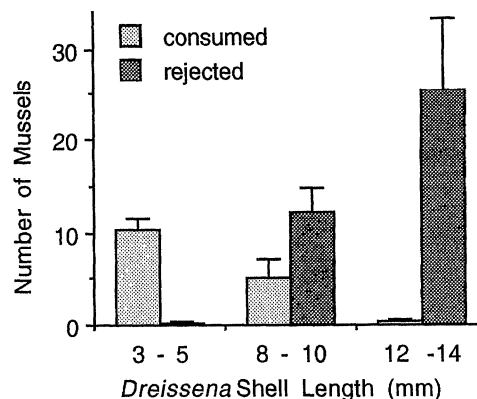


FIG. 6. Mean (± 1 SE) number of consumed and recorded rejections of *Dreissena* by *Orconectes* in relation to mussel size in videotaped observations.

not provide an accurate reflection of total predation costs because unsuccessful, and perhaps costly, attempts to kill larger prey will not be apparent from simple assessments of changes in prey abundances in control vs. predator arenas.

Piesik (1974) observed broad differences in male and female crayfish predation rates on *Dreissena*. I observed a similar difference in preference experiments with macrophytes, particularly for large mussels (Fig. 4; Table 2). Piesik attributed higher female predation rates to the unusual physiological (reproductive) state of male crayfish in his study.

Average predation rates in the mussel preference experiment (8.9 mussels/crayfish/day) and macrophyte experiment (6.8 mussels/crayfish/day) are lower than those reported by Piesik (1974) for *Orconectes limosus* preying on *Dreissena* (36 small mussels/crayfish/day). It is difficult to interpret differences in *O. propinquus* and *O. limosus* predation rates because of differences in experimental procedures used in the two studies. To minimize crayfish disturbance during my short experiments, consumed prey were not replaced. Predation rates would have been higher had consumed mussels been replaced, considering that small mussels were entirely depleted in some aquaria. In addition, the experiments reported here used mussels that had only recently attached to mesh or other mussels. Because the number of byssal threads increases with time since mussel attachment (Eckrodt et al. 1992), naturally attached mussels

might be more difficult to dislodge than those used here. It is also not clear whether predation rates, selectivity patterns and handling times would be affected had naturally attached mussels been used. Large mussels are often encrusted with younger, smaller mussels which may be more accessible to crayfish predators.

Zebra mussels currently represent a very significant component of benthic biomass in Lake Erie and Lake St. Clair (Mackie 1991). The impact of predation from all sources on these populations is not known, but is probably similar to or lower than in Europe where predators are more attuned to *Dreissena* as a food source (e.g., Suter 1982). The relative predation impact on *Dreissena* populations of crayfish, waterfowl, and fish will depend on numerical, functional and developmental responses of predators, seasonal activity patterns of predators, and depth of prey populations in lakes. For example, although the numerical response of waterfowl to increasing *Dreissena* populations in both Lakes Erie and Ontario is impressive (Wormington and Leach 1993), as is the importance of *Dreissena* in the diet of some waterfowl (E. Mazak, University of Windsor, personal communication), feeding on *Dreissena* is generally confined to littoral waters during ice-free periods (e.g., Suter 1982, Bij de Vaate 1991). Predation on *Dreissena* by crayfish could occur at greater depths than predation on *Dreissena* by waterfowl, but it would also be constrained by low water temperatures (Piesik 1974). It is also possible that predation incurred by zebra mussel populations during the non-winter period may be largely inconsequential to overall population dynamics since mussel mortality is most intense between the settling postveliger and settled juvenile stage (Stańczykowska 1977). Mortality of both juvenile and adult mussels is often highest during winter (Stańczykowska 1977, Suter 1982, Cleven and Frenzel 1993). Although winter mortality of zebra mussels has not been closely studied, it is generally attributed to low temperature (Stańczykowska 1977) or to predation (Suter 1982, Suter and van Eerden 1992).

Exploitation of zebra mussels by crayfish represents a novel pathway for energy flow through Great Lakes' ecosystems. The results of this study suggest that *Dreissena polymorpha* may be a common food of *Orconectes propinquus* in the Great Lakes. Depending on their density, crayfish may

have the potential to affect local size distributions and population densities of zebra mussels.

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