



9-2004

Zebra Mussels Affect Benthic Predator Foraging Success

Mark Beekey

Sacred Heart University, beekeym@sacredheart.edu

D. J. McCabe

Saint Michaels College

I. E. Marsden

University of Vermont

Follow this and additional works at: http://digitalcommons.sacredheart.edu/bio_fac



Part of the [Population Biology Commons](#), and the [Terrestrial and Aquatic Ecology Commons](#)

Recommended Citation

Beekey, M., D. J. McCabe, and I. E. Marsden. "Zebra Mussels Affect Benthic Predator Foraging Success." *Oecologia* (2004) 141: 164-170. DOI 10.1007/s00442-004-1632-1

This Article is brought to you for free and open access by the Biology Department at DigitalCommons@SHU. It has been accepted for inclusion in Biology Faculty Publications by an authorized administrator of DigitalCommons@SHU. For more information, please contact ferribyp@sacredheart.edu.

M. A. Beekey · D. J. McCabe · J. E. Marsden

Zebra mussels affect benthic predator foraging success and habitat choice on soft sediments

Received: 1 October 2003 / Accepted: 20 May 2004 / Published online: 24 July 2004
© Springer-Verlag 2004

Abstract The introduction of zebra mussels (*Dreissena* spp.) to North America has resulted in dramatic changes to the complexity of benthic habitats. Changes in habitat complexity may have profound effects on predator-prey interactions in aquatic communities. Increased habitat complexity may affect prey and predator dynamics by reducing encounter rates and foraging success. Zebra mussels form thick contiguous colonies on both hard and soft substrates. While the colonization of substrata by zebra mussels has generally resulted in an increase in both the abundance and diversity of benthic invertebrate communities, it is not well known how these changes affect the foraging efficiencies of predators that prey on benthic invertebrates. We examined the effect of zebra mussels on the foraging success of four benthic predators with diverse prey-detection modalities that commonly forage in soft substrates: slimy sculpin (*Cottus cognatus*), brown bullhead (*Ameiurus nebulosus*), log perch (*Percina caprodes*), and crayfish (*Orconectes propinquus*). We conducted laboratory experiments to assess the impact of zebra mussels on the foraging success of predators using a variety of prey species. We also examined habitat use by each predator over different time periods. Zebra mussel colonization of soft sediments significantly reduced the foraging efficiencies of all predators. However, the effect was dependent upon prey type. All four predators spent more time in zebra mussel habitat than in either gravel or bare sand. The overall effect of zebra mussels on benthic-

feeding fishes is likely to involve a trade-off between the advantages of increased density of some prey types balanced against the reduction in foraging success resulting from potential refugia offered in the complex habitat created by zebra mussels.

Introduction

Habitat complexity is an important structuring component of biological communities and may stabilize predator-prey interactions (Murdoch and Oaten 1975; Caswell 1978; Holt 1984; Taylor 1984; McNair 1986). Changes in habitat complexity may affect encounter rates between predators and prey, and predator efficiency (Briand and Cohen 1987; Whitehead and Walde 1992). Complex habitats may provide prey refuges by reducing predator efficiency in portions of the habitat (Huffaker 1958). Habitat complexity interacts with predator foraging modes and encounter rates so that the number of prey consumed generally decreases with structural complexity (Savino and Stein 1982, 1989; Eklöv 1997; Eklöv and Diehl 1994; Persson and Eklöv 1995). In a number of fish-prey systems, per capita prey-capture rates declined with habitat complexity as search and pursuit times increased (Glass 1971; Ware 1973; Vince et al. 1976; Stein 1977; Stoner 1982).

In freshwater systems, habitat complexity is most commonly associated with littoral vegetation, large-particle substrates, or depth-gradient diversity. Each has profound effects on species abundance and diversity of prey (Werner et al. 1977; Eadie and Keast 1984). Different forms of habitat complexity provide prey refuges by reducing predation efficiency (Mittelbach 1988; Werner and Hall 1988). For example, the foraging efficiency of pike increased at low vegetation densities and decreased at high vegetation densities (Savino and Stein 1989).

Zebra mussels have been associated with system-wide changes over virtually all trophic levels. The introduction of zebra and quagga mussels (*Dreissena polymorpha* and *D. bugensis*) to North America has significantly altered water clarity (Mellina et al. 1995), chlorophyll *a* levels

M. A. Beekey · J. E. Marsden (✉)
School of Natural Resources, Aiken Center, University of Vermont,
Burlington, VT, 05405, USA
e-mail: Ellen.Marsden@uvm.edu
Tel.: +1-802-6560684
Fax: +1-802-6568683

D. J. McCabe
Department of Biology, St. Michael's College,
Colchester, VT, USA

M. A. Beekey · D. J. McCabe · J. E. Marsden
Rubenstein Ecosystem Science Laboratory,
Burlington, VT, USA

(Caraco et al. 1997), zooplankton communities (Jack and Thorp 2000), and benthic community structure (Ricciardi et al. 1997). In addition to enriching the benthic food web (e.g., Stewart et al. 1998), zebra mussels benefit benthic macro-invertebrates by creating structural complexity on previously simple surfaces. Increased complexity provides benthic invertebrates protection from disturbances such as increased wave action (Bially and MacIssac 2000) and more importantly, potential refugia from predation (Mayer et al. 2001; Cobb and Watzin 2002; Kolar et al. 2002).

Zebra mussel colonies on soft sediments may reduce fish foraging success by blocking access to the benthos or by reducing the ability of fish to find and capture prey. Soft-sediment macroinvertebrates including burrowing mayflies (Ephemeroptera: Ephemeridae: *Hexagenia* spp.) and *Chironomus* (Diptera: Chironomidae) are important dietary components of fish such as suckers (Catostomidae), catfishes (Ictaluridae), cyprinids (Cyprinidae), lake sturgeon (*Acipenser fulvescens*), and commercially important fishes such as walleye (*Stizostedion vitreum*) and yellow perch (*Perca flavescens*; Scott and Crossman 1973; Beamish et al. 1998).

The impact of zebra mussels on fish foraging will likely be related to foraging mode and prey type. Predators such as sculpins (*Cottus* spp.) that utilize lateral line detection of infaunal prey will likely be impeded by zebra mussels on soft substrates and may switch to visually detected crawling and swimming prey. In contrast, surface “pickers” such as logperch (*Percina caprodes*) may benefit from increased invertebrate densities in zebra mussel colonies. Zebra mussels may protect burrowing invertebrate prey, whereas free-swimming and crawling invertebrates may find refugia within zebra mussel colonies. Therefore, in order to understand the impact of zebra mussels on foraging efficiencies of benthic fish species, it is necessary to examine multiple predators with different foraging modes and their interaction with different prey types.

We examined the effect of zebra mussels on foraging efficiency of four benthic predators; slimy sculpins, logperch, brown bullheads, and crayfish (*Orconectes propinquus*). We conducted laboratory experiments to assess foraging success with multiple prey types and different levels of habitat complexity. We also examined the habitat preference of each predator in order to determine how zebra mussels may affect fish and crayfish distributions in addition to foraging success. We discuss our results in relation to foraging modalities, prey type, and habitat complexity.

Materials and methods

Organisms

All predator species were wild-caught in the Lake Champlain drainage and used once for foraging experiments and once for habitat choice before being returned to the wild. The predator species were acclimatized in the laboratory for a minimum of 2 days, placed in experi-

ments, and released within 2 weeks. The predators were fed a diet of frozen blood worms and maintained without food for 24 h before the foraging experiments. Bullheads were collected in minnow traps in the Winooski Reservoirs on Gill Brook in Winooski Township, Vermont, and by electrofishing in Alder Creek in Essex Township, Vermont (total length \bar{x} =97 mm, range 61–140 mm). The crayfish were minnow-trapped and hand picked in the shallows of Lake Champlain (average carapace length from tip of rostrum to the mid-dorsal posterior margin of the carapace=28 mm; range 19–41 mm). We collected log perch in minnow traps and by snorkeling and hand netting in Lake Champlain (TL \bar{x} =84 mm; range 65–120 mm) The sculpins were electrofished in Lake Champlain and Brown’s River in Underhill Vermont (TL \bar{x} = 66 mm; range 48–90 mm).

We reared chironomids in bulk cultures in the laboratory (length range 4–8 mm). Isopods were purchased from Connecticut Valley Biological Supply Company (length range 4–11 mm). Amphipods were collected from springs in Pennsylvania (length range 4–8 mm). We collected zebra mussels from Lake Champlain and washed them free of macroinvertebrates and sediment in a coarse sieve with dechlorinated water prior to their use in the experiments. We used a mixture of live mussels and the shells of dead individuals as is typically encountered in benthic mussel colonies. We added the mussels to the experiments individually and in small clusters. The live mussels laid down byssal threads such that most individual mussels were attached to conspecifics and dead shells before the experiments began.

Foraging success

To test whether zebra mussels affect the foraging success of benthic predators, we conducted a set of separate laboratory experiments with three prey species and four predator species. Each predator-prey combination was evaluated separately for a total of 12 replicated experiments. The number of replicates per experiment depended on predator availability and varied between three and nine (Fig. 1). The selected prey represented three modes of habitat use: burrowing (chironomids—*Chironomus* sp.), crawling (isopods—*Asellus communis*), and swimming (amphipods—*Gammarus minus*). The predator species use distinctly different modes of foraging and habitat use; lateral line system, visual, and strictly benthic (sculpins), barbels and mostly benthic (bullhead); visual and partly pelagic (logperch); chemotactic, strictly benthic and burrowing (crayfish).

All experiments were conducted in 8-l circular microcosms (27 cm diameter, 14 cm depth). Each microcosm was filled with clean, sifted, washed sand to a depth of 2.5 cm. The microcosms were filled with continuously aerated de-chlorinated water. We established a full factorial design with percent zebra mussel coverage and predator presence/absence as the factors in the design and number of prey items remaining after each experiment as

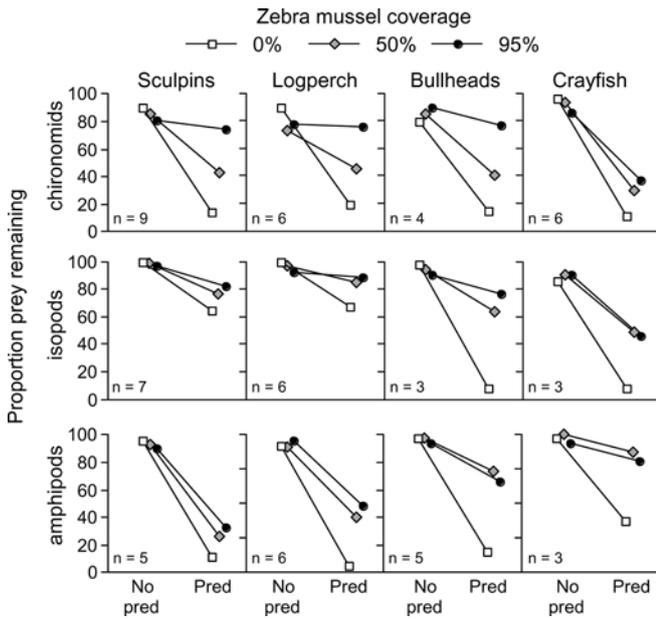


Fig. 1 Consumption of prey by four benthic predators in enclosures with three levels of zebra mussel coverage of substrate (0, 50, and 95%). The proportion of prey (chironomids, isopods, and amphipods) remaining after 48 h (chironomids) or 24 h averaged across replicates are plotted versus the presence and absence of four predators: sculpins, logperch, bullheads, and crayfish. Initial number of prey were 70 for chironomids and 30 for isopods and amphipods for all predators. *n* number of replicate experiments with each predator

the response variable. This design resulted in the following six treatments: (1) bare substrate; (2) bare substrate and predator; (3) 50% zebra mussel coverage; (4) 50% zebra mussel coverage plus predator; (5) 95% zebra mussel coverage; and (6) 95% zebra mussel coverage plus predator. Percent cover of zebra mussels was estimated visually. This design allowed us to measure the main effects and interactions of fish and zebra mussels on the number of prey remaining.

A statistically significant predator effect would simply confirm that the predator in question consumed the prey item offered under the experimental conditions. A significant effect of zebra mussels would clearly imply that zebra mussels were somehow affecting the prey densities. A significant zebra mussel by predator interaction would confirm that the presence of zebra mussels modified the foraging success of the predators.

The duration of the trial and the number of prey added to each microcosm depended on the prey species. We added 70 chironomids (effective density 1,223 individuals per m^2) to each microcosm 24 h prior to the addition of predators to allow the chironomids time to burrow into the substrate. Because amphipods and isopods are substantially larger than chironomids, fewer individuals will likely be consumed to achieve similar predator satiation; we added 30 (effective density 524 individuals per m^2) of either of these species to the microcosms at least 2 h prior to the addition of predators. Predators were allowed to forage on chironomids for 48 h and on isopods or amphipods for 24 h. Upon termination of the experiments,

the predators were removed, measured to the nearest 0.1 mm (standard length for fish, carapace length for crayfish) and weighed (wet weight) to the nearest 0.1 g. Remaining prey were removed from the zebra mussels and sand and counted using sieves and forceps.

Habitat choice

We examined fish preference for habitat type in experimental laboratory microcosms. Bare sand, gravel, and live zebra mussels were arranged in three equal-sized segments in each of six circular 43.2-l tubs (61 cm diameter). Identical depths of all three substrates were used. In contrast to the foraging experiments, the mussels were placed directly on the microcosm floor, as was the gravel. The experimental setups were allowed to sit for 24 h prior to addition of the fish or crayfish. We examined habitat preference of slimy sculpins ($n=12$), brown bullheads ($n=8$), logperch ($n=11$), and crayfish ($n=12$). Individuals were placed in the tubs and allowed to settle for 4–6 h prior to the start of the experiment. Each tub contained a single individual. We recorded the location of each individual at 10-min intervals. The observer was careful to minimize potential disturbance of the predator, and the predators rarely moved when the observer recorded their position. Observations were conducted during three time periods; dawn (5:30–9:30 a.m.), midday (10:30 a.m.–2:30 p.m.), and dusk (6:30–10:30 p.m.), for a total of 72 observations per individual predator.

Statistical analyses

The foraging experiments were analyzed using a factorial ANOVA with forager presence/absence and zebra mussel density (absent, 50% coverage, and 95% coverage) as the two factors in the analysis. In order to satisfy the assumptions of ANOVA, the response variables (number of prey remaining) were arcsine transformed prior to analysis. We used a Tukey's post hoc analysis to ask if the number of prey differed among the three mussel density treatments. Because the question of interest in these experiments was the effect of zebra mussels on fish foraging, non-predator treatments were not compared. Simple inspection suggested that differences in prey recovery were trivial regardless of zebra mussel presence or density.

Habitat choice experiments were analyzed using *G*-tests on each individual fish or crayfish for each daily time period. The number of observations in each substrate type was compared to the distribution that would be expected if a fish or crayfish was unbiased in its habitat choice, i.e., it was found in each habitat type for an equal number of observation periods. Data from each individual fish and crayfish were independent from data for other conspecifics; therefore, for each species at a given time period we summed the *G*-test values and the *df* to achieve a statistic for all replicates combined.

Results

Foraging success

In general, zebra mussels inhibited the ability of predators to forage successfully. However, the degree to which predators were inhibited by zebra mussels was influenced by prey type and percent coverage of zebra mussels. In most cases predators consumed far more prey in the absence of zebra mussels than in treatments containing zebra mussels. Foraging success also varied among predator species.

Predators tended to consume fewer chironomids over 48 h in treatments containing zebra mussels than in the absence of zebra mussels (Fig. 1). Both zebra mussel coverage and predator presence/absence had significant effects on the number of chironomids remaining after the termination of the experiments in all cases ($P < 0.05$, Table 1). There was also an interaction effect between predator species and percent zebra mussel coverage for all predators with the exception of crayfish such that fewer chironomids were consumed in the presence of zebra mussels than in their absence ($P < 0.05$, Table 1). Sculpins consumed more chironomids in the treatment lacking zebra mussels than in either the 50 or 95% zebra mussel coverage treatments (Tukey's, $P < 0.05$). Logperch and bullheads consumed significantly more chironomids in the treatment lacking zebra mussels than in the 95% zebra mussel coverage treatment; however, there was no difference between the bare and 50% treatments (Tukey's, $P < 0.05$). In contrast to fish-foraging results, zebra mussels had no significant effect on the consumption of chironomids by crayfish. Crayfish foraged successfully regardless of percent zebra mussel coverage (Fig. 1).

On average, the consumption of isopods declined as percent zebra mussel coverage increased (Fig. 1). There was a predator effect for all predator species ($P < 0.05$,

Table 1). There was an effect of zebra mussel coverage on isopod consumption for sculpins, bullheads, and crayfish ($P < 0.05$, Table 1), but not for logperch. Sculpins consumed more isopods in the 0% zebra mussel coverage treatment than in the 95% treatments (Tukey's, $P < 0.05$). Bullheads and crayfish consumed more isopods in the absence of zebra mussels than in either the 50 or 95% zebra mussel coverage treatments (Tukey's, $P < 0.05$). Regardless of zebra mussel density, sculpins and logperch consumed fewer isopods than did either of the other predators. Sculpins and logperch consumed more chironomids and amphipods than they did isopods. This pattern was very consistent among individual replicates.

All predators consumed more amphipods in the absence of zebra mussels than in either treatment containing zebra mussels (Fig. 1). In all cases there was a significant effect of predator on the number of amphipods remaining ($P < 0.05$, Table 1). There was an effect of percent zebra mussel coverage on amphipod consumption for bullhead and crayfish ($P < 0.05$, Table 1); both species consumed more amphipods in bare treatments than in either the 50 or 95% zebra mussel coverage treatment (Tukey's, $P < 0.05$). There was no effect of percent zebra mussel coverage on amphipod consumption for sculpins or logperch.

Habitat choice

All four predators were observed more frequently on complex substrates (gravel and zebra mussels) than on sand (Fig. 2). For each species, the number of times a predator was observed in each of the three habitat types was nonrandom ($G = 438.2$ for bullhead, $G = 207.8$ for sculpin, $G = 296.8$ for logperch, $G = 255.4$ for crayfish, $df \geq 16$, $P < 0.001$ for all species). All predators except sculpin were observed more frequently on zebra mussels than on gravel or sand. Sculpin were observed less often on zebra mussels as the day progressed (Fig. 2). Both

Table 1 Results of factorial ANOVAs on the effects of zebra mussels on foraging success of each of four predators. Zebra mussel density (0, 50, or 95% coverage), and predator presence or absence were the two factors in each analysis. A significant effect of zebra mussels indicates that the number of prey items recovered from the experimental microcosm after the foraging period differed among zebra mussel treatments. A significant predator effect simply confirms that the predators consumed the prey in question. A zebra mussel by predator interaction effect indicates that foraging success was influenced by the presence of zebra mussels

	Chironomids			Isopods			Amphipods		
	<i>F</i>	<i>df</i>	<i>P</i>	<i>F</i>	<i>df</i>	<i>P</i>	<i>F</i>	<i>df</i>	<i>P</i>
Sculpin									
Zebra mussel	14.30	2	<0.0001	5.92	2	0.006	0.964	2	0.3957
Predator	113.60	1	<0.0001	170.16	1	<0.0001	219.74	1	<0.0001
Zebra mussel×predator	26.14	2	<0.0001	11.43	2	0.0001	2.70	2	0.0874
Logperch									
Zebra mussel	4.26	2	0.0235	0.82	2	0.4510	2.09	2	0.1409
Predator	24.56	1	<0.0001	9.63	1	0.0041	40.38	1	<0.0001
Zebra mussel×predator	8.97	2	0.0009	2.77	2	0.0787	1.72	2	0.1970
Bullhead									
Zebra mussel	16.63	2	0.0002	18.79	2	0.0002	19.02	2	<0.0001
Predator	64.50	1	<0.0001	103.84	1	<0.0001	131.41	1	<0.0001
Zebra mussel×predator	9.06	2	0.0026	27.75	2	<0.0001	20.45	2	<0.0001
<i>O. propinquus</i>									
Zebra mussel	1.07	2	0.357	5.95	2	0.0158	9.60	2	0.0032
Predator	159.18	1	<0.0001	82.47	1	<0.0001	31.2	1	0.0001
Zebra mussel×predator	3.78	2	0.034	3.81	2	0.0523	9.05	2	0.0040

sculpin and crayfish were frequently observed burrowed among zebra mussels. We did not observe any of the predators actively feeding on zebra mussels during the experiments.

Discussion

The effects of habitat structure on predator-prey interactions has been very well studied in a wide range of ecological systems (e.g. Huffaker 1958; Persson and Eklöv 1995; Dudgeon 1996; Lombardo 1997). In general, increased habitat complexity has been shown to influence the ability of predators to forage successfully (Crowder and Cooper 1982; Gilinsky 1984; Gotceitas and Colgan 1989; Deihl 1992). Zebra mussels increase habitat complexity, and, in an elegantly designed experiment, Botts et al. (1996) convincingly demonstrated that the positive effects of zebra mussels on benthic macroinvertebrate communities are mediated through increased habitat complexity as well as food web enrichment.

As zebra mussels colonize soft sediments, they have the potential to affect the foraging success of a range of species. In particular, juveniles of some species (e.g., yellow perch, walleye, sturgeon) utilize soft sediment zoobenthos for food during critical growth periods (Ritchie and Colby 1988; Scott and Crossman 1973; Beamish et al. 1998). Negative effects on already threatened or endangered species such as the lake sturgeon

may have important implications for conservation and reintroduction programs. Zebra mussels may impede the ability of these species to obtain burrowing prey. Whether this potential negative effect of zebra mussels on fish foraging is offset by zebra-mussel facilitation of the macrozoobenthos would depend on the prey specificity of the fish species in question.

We have demonstrated that zebra mussels impede the foraging of bullheads, sculpins, and logperch on burrowing prey (*Chironomus*). Because crayfish burrow under the mussel colonies, they consume *Chironomus* regardless of zebra mussel coverage. Crawling prey (isopods) were not readily consumed by logperch, regardless of treatment, but all other foragers had reduced foraging success on isopods in the presence of zebra mussels. Amphipods (swimming prey) were consumed by all predators, but there was no effect of zebra mussels on the number consumed by sculpins or log perch. There was a marked reduction in the number of amphipods consumed by bullheads and crayfish in the presence of zebra mussels. It is possible that because crayfish and bullheads are less visual than the other predators, the amphipods stood a better chance of evading capture in the complex environment provided by the zebra mussels.

Other investigators have used a range of techniques to assess the impacts of zebra mussels on fish foraging and habitat selection. Mayer et al. (2001) used videotaped trials and counted yellow perch foraging attacks and captures of amphipods in aquariums with and without zebra mussels, at three different light levels. In addition to videotaping trials of yellow perch foraging on amphipods with zebra mussels and bare sand in the same tanks, Cobb and Watzin (2002) ran foraging trials with and without zebra mussels followed by stomach analysis to quantify the number of amphipods and chironomids consumed on sandy and hard substrates. The video techniques used by Mayer et al. (2001) and Cobb and Watzin (2002) are advantageous because failed foraging attempts can be distinguished from successful captures. González and Downing's (1999) experiments are most directly comparable to our study in that they ran timed foraging trials with yellow perch or bluegill in aquariums with and without zebra mussels on rocky substrates. By adding a known number of amphipods to each aquarium and recovering the remaining prey at the end of the foraging trial, González and Downing (1999) had a measure of foraging success that was similar to ours.

Despite the diversity of techniques employed in previous studies, a strong pattern is emerging. With one exception (yellow perch; González and Downing 1999) zebra mussels reduced the foraging success of fish on macroinvertebrates on hard substrates. In addition, Cobb and Watzin (2002) found that yellow perch were proportionately more successful when foraging on sand versus foraging on zebra mussel colonies. Yellow perch also made more foraging attempts in zebra mussel colonies and fewer attempts in sand than would have been expected based on the area of each substrate type available.

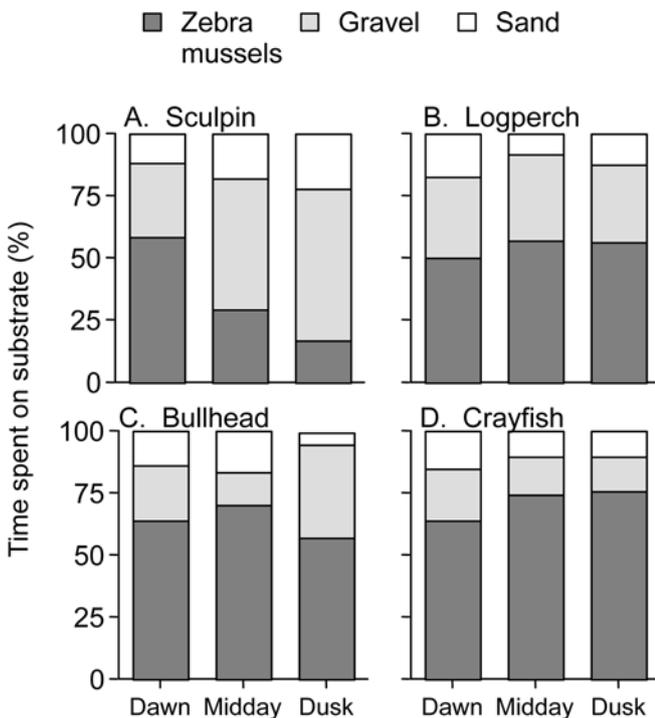


Fig. 2 Habitat use of four benthic species, **a** sculpins, **b** logperch, **c** bullhead, and **d** crayfish, presented as the percentage of time spent in zebra mussels, gravel, and bare sand during three time periods: dawn, midday, and dusk. *Stacked bars* represent the average time spent in each habitat for each time period. $n=12, 11, 8,$ and $11,$ for sculpins, logperch, bullheads, and crayfish, respectively

González and Downing (1999) found no effect of zebra mussels on yellow perch foraging success and suggested that this was because the perch were more adept at capturing macroinvertebrates and thus less affected by zebra mussels. Another possibility is that the larger perch used by González and Downing (1999) had lower affinity for macroinvertebrates. Cobb and Watzin (2002) found in one of their trials that larger perch consumed fewer amphipods, and indeed ontogenetic changes in diet have previously been documented in yellow perch such that their diets shift from zooplankton, to macroinvertebrates, to piscivory as they grow larger (e.g., Wu and Culver 1992). González and Downing (1999) used perch with an average total body length of 130 mm, at the upper extreme of the range of the fish used by Cobb and Watzin (2002; range 59–131 mm; hard substrate, full coverage trial). Similarly, Mayer et al. (2001) used small yellow perch (range 65–126 mm) and found that the presence of zebra mussels reduced foraging success.

Our results compliment the previously existing studies by examining a range of foraging styles and prey uses of the habitat. The absence of an effect of zebra mussels on sculpins and log perch foraging on amphipods suggests that these predators may benefit from the increases in non-burrowing amphipod abundance reported following zebra mussel colonization. In addition, because zebra mussels have different effects on predation depending on the prey species considered, predators may switch prey species in response to zebra mussel colonization. Thus, even though the number of a given prey species consumed may change, there may not be a net total effect of zebra mussels on total biomass consumed by a given predator.

Predator utilization of zebra mussel beds as habitat may result in significant local redistribution of fish, potentially altering access to food and vulnerability to predation. Predators typically associated with rocky substrates may utilize zebra mussels on soft sediments. With the exception of the sculpins in two out of three time periods, the predators in our experiments spent the majority of their time on zebra mussels. Cobb and Watzin (2002) found that yellow perch made a disproportionate number of foraging attempts on zebra mussel colonies relative to surrounding bare substrates, but this response was in part because prey density in the zebra mussel colonies was 300 times greater than in the surrounding substrate. Our results are free from the effects of prey density and demonstrate that there is a strong tendency for benthic predator species to spend more time on zebra mussels than on sand or gravel.

Zebra mussels increase surface area, and add three-dimensional structure to the surfaces to which they attach. The zebra mussel druses (isolated clumps) and layers that form on sandy and silty sediments produce a nook-and-cranny effect unlike anything previously existing on soft or bedrock substrates in newly invaded lakes. Our results convincingly demonstrate that zebra mussels reduce the foraging success of a range of benthic predators, including the first such demonstration for an invertebrate. By testing a range of prey types, we have demonstrated that prey position in the habitat (burrowing, crawling, or swimming)

interacts with the foraging modes of the predators (tactile, visual, lateral line, strictly benthic, burrowing) to produce a range of potential interactions among zebra mussels, macroinvertebrates, and predators. Zebra mussels clearly inhibit predation on burrowing and crawling prey by benthic foraging fish. In contrast, swimming/crawling prey such as amphipods are susceptible to predation even in the presence of zebra mussels, except by bullheads. All predators used in these experiments spent more time among zebra mussels as compared to bare sand or gravel. Clearly, increased habitat complexity created by zebra mussel colonization of substrates has an effect on habitat use. Whether this usage shift is influenced by reduced predation from larger predators remains to be determined.

Acknowledgements We would like to thank Ryan Dubois, Kathleen Coons, Anna Mazloff, Kevin Rice, Eric Carlson, and Aimee Ahari for their help conducting the laboratory experiments, and Douglas Glazier for providing amphipods. This project was funded by an EPSCoR grant from the University of Vermont and by National Sea Grant. Additional funds and materials were provided by St. Michael's College and the Vermont Genetics Network. All experiments conducted during this study conform to laws regarding animal care in the United States.

References

- Beamish FWH, Noakes DLG, Rossiter A (1998) Feeding ecology of juvenile lake sturgeon, *Acipenser fulvescens*, in northern Ontario. *Can Field Nat* 112:59–468
- Bially A, MacIsaac HJ (2000) Fouling mussels (*Dreissena* spp.) colonize soft sediments in Lake Erie and facilitate benthic invertebrates. *Freshwater Biol* 43:85–97
- Botts PS, Patterson BA, Schloesser DW (1996) Zebra mussel effects on benthic invertebrates: Physical or biotic? *J N Am Benth Soc* 15:179–184
- Briand F, Cohen JE (1987) Environmental correlates of food chain length. *Science* 283:956–960
- Caraco NF, Cole JJ, Raymond PA, Strayer DL, Pace ML, Findlay SEG, Fischer DT (1997) Zebra mussel invasion in a large, turbid river: Phytoplankton response to increased grazing. *Ecology* 78:588–602
- Caswell H (1978) Predator mediated coexistence: a non-equilibrium model. *Am Nat* 112:127–154
- Cobb SE, Watzin MC (2002) Zebra mussel colonies and yellow perch foraging: spatial complexity, refuges, and resource enhancement. *J Great Lakes Res* 28:256–263
- Crowder LB, Cooper WE (1982) Habitat structural complexity and the interaction between bluegills and their prey. *Ecology* 65:1802–1813
- Diehl S (1992) Fish predation and benthic community structure: the role of omnivory and habitat complexity. *Ecology* 73:1646–1661
- Dudgeon D (1996) The influence of refugia on predation impacts in a Hong Kong stream. *Arch Hydrobiol* 138:145–159
- Eadie JM, Keast A (1984) Resource heterogeneity and fish species diversity in lakes. *Can J Zool* 62:1689–1695
- Eklöv P (1997) Effects of habitat complexity and prey abundance on the spatial and temporal distributions of perch (*Perca fluviatilis*) and pike (*Esox lucius*). *Can J Fish Aquat Sci* 54:1520–1531
- Eklöv P, Diehl S (1994) Piscivore efficiency and refuging prey: the importance of predator search mode. *Oecologia* 98:344–353
- Gilinski E (1984) The role of fish predation and spatial heterogeneity in determining benthic community structure. *Ecology* 65:455–468

- Glass NR (1971) Computer analysis of predation energetics in the largemouth bass. In: Patten BC (ed) Systems analysis and simulation in ecology, vol 1. Academic, New York, pp 325–363
- González MJ, Downing A (1999) Mechanisms underlying amphipod responses to zebra mussel (*Dreissena polymorpha*) invasion and implications for fish-amphipod interactions. *Can J Fish Aquat Sci* 56:679–685
- Gotceitas V, Colgan P (1989) Predator foraging success and habitat complexity: quantitative test of the threshold hypothesis. *Oecologia* 80:158–166
- Holt RD (1984) Spatial heterogeneity, indirect interactions and the coexistence of prey species. *Am Nat* 124:377–406
- Huffaker CB (1958) Experimental studies on predation: dispersion factors and predator-prey oscillations. *Hilgardia* 27:343–383
- Jack JD, Thorp JH (2000) Effects of the benthic suspension feeder *Dreissena polymorpha* on zooplankton in a large river. *Freshwater Biol* 44:569–579
- Kolar CS, Fullerton AH, Martin KM, Lamberti GA (2002) Interactions among zebra mussel shells, invertebrate prey, and Eurasian ruffe or yellow perch. *J Great Lakes Res* 28:664–673
- Lombardo P (1997) Predation by *Enallagma* nymphs (Odonata, Zygoptera) under different conditions of spatial heterogeneity. *Hydrobiologia* 356:1–9
- Mayer CM, Rudstam LG, Mills EL, Cardiff SG, Bloom CA (2001) Zebra mussels (*Dreissena polymorpha*), habitat alteration, and yellow perch (*Perca flavescens*) foraging: system-wide effects and behavioural mechanisms. *Can J Fish Aquat Sci* 58:2459–2467
- McNair JN (1986) The effects of prey refuges on predator-prey interactions: a reconsideration. *Theor Popul Biol* 29:38–63
- Mellina E, Rasmussen JB, Mills EL (1995) Impact of mussel (*Dreissena polymorpha*) on phosphorus cycling and chlorophyll in lakes. *Can J Fish Aquat Sci* 52:2553–2573
- Mittelbach GG (1988) Competition among refuging sunfishes and effects of fish density on littoral zone invertebrates. *Ecology* 69:614–623
- Murdoch WW, Oaten A (1975) Predation and population stability. *Adv Ecol Res* 9:1–131
- Persson L, Eklöv P (1995) Prey refuges affecting interactions between piscivorous perch (*Perca fluviatilis*) and juvenile perch and roach (*Rutilus rutilus*). *Ecology* 76:70–81
- Ricciardi A, Whoriskey FG, Rasmussen JB (1997) The role of the zebra mussel (*Dreissena polymorpha*) in structuring macroinvertebrate communities on hard substrata. *Can J Fish Aquat Sci* 54:2596–2608
- Ritchie BJ, Colby PJ (1988) Even-odd year differences in walleye year-class strength related to mayfly production. *N Am J Fish Manage* 8(2):210–215
- Savino JF, Stein RA (1982) predator-prey interaction between largemouth bass and bluegills as influenced by simulated submersed vegetation. *Trans Am Fish Soc* 111:255–266
- Savino JF, Stein RA (1989) Behavior of fish predators and their prey: habitat choice between open water and dense vegetation. *Environ Biol Fish* 24:287–293
- Scott WB, Crossman EJ (1973) Freshwater fishes of Canada. *Bull Fish Res Bd Can* 184:966
- Stein RA (1977) Selective predation, optimal foraging, and the predator-prey interaction between fish and crayfish. *Ecology* 58:1237–1253
- Stewart TW, Miner JG, Lowe RL (1998) Quantifying mechanisms for zebra mussel effects on benthic macroinvertebrates: organic matter production and shell generated habitat. *J North Am Benth Soc* 17:81–94
- Stoner AW (1982) The influence of benthic macrophytes on the foraging behavior of pinfish, *Lagodon rhomboides*. *J Exp Mar Biol Ecol* 58:271–284
- Taylor RJ (1984) Predation. Chapman and Hall, London
- Vince SU, Valiela, Backus N, Teal JN (1976) Predation by the salt marsh killifish *Fundulus heteroclitus* in relation to prey size and habitat structure: consequences for prey distribution and abundance. *J Exp Mar Biol Ecol* 23:255–266
- Ware DM (1973) Risk of epibenthic prey to predation by rainbow trout (*Salmo gairdneri*). *J Fish Res Bd Can* 30:787–797
- Werner EE, Hall DJ (1988) Ontogenetic habitat shifts in bluegill: the foraging rate-predation risk trade-off. *Ecology* 69:1352–1366
- Werner EE, Hall DJ, Laughlin DR, Wagner DR, Wilmann LA, Funk FC (1977) Habitat partitioning in a freshwater fish community. *J Fish Res Bd Can* 34:360–370
- Whitehead H, Walde SJ (1992) Habitat dimensionality and mean search distances of top predators: implications for ecosystem structure. *Theor Popul Biol* 42:1–9
- Wu L, Culver DA (1992) Ontogenetic diet shift in Lake Erie age-0 yellow perch (*Perca flavescens*): a size-related response to zooplankton density. *Can J Fish Aquat Sci* 49:1932–1937