

Benthic Invertebrate Community Responses to Round Goby (*Neogobius melanostomus*) and Zebra Mussel (*Dreissena polymorpha*) Invasion in Southern Lake Michigan

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ABSTRACT. The round goby (*Neogobius melanostomus* Pallas), a fish native to eastern Europe, recently has become established in southwestern Lake Michigan. Because round gobies prey on zebra mussels (*Dreissena polymorpha* Pallas) and other benthic invertebrates, the effects of round gobies on invertebrates within zebra mussel colonies was investigated. Using a 2 × 3 factorial design, the effects of round gobies (present or absent) and zebra mussel densities (zero, low, and high) on non-mussel invertebrates was examined. Ten ceramic tiles of each mussel density were colonized in the laboratory and then anchored in Calumet Harbor, IL for 10 weeks. Round gobies had access to half the tiles while half were covered with coarse mesh screening that excluded round gobies, but allowed invertebrates to move into and out of the enclosures. Low and high zebra mussel density tiles supported significantly greater numbers of non-mussel invertebrates ($p < 0.001$) than zero density tiles, particularly amphipods ($p < 0.001$), hydroptilid caddisflies ($p < 0.05$), isopods ($p < 0.05$), and chironomids ($p < 0.001$). Chlorophyll a concentrations were highest ($p < 0.001$) at low zebra mussel densities. The presence of round gobies significantly reduced densities of total non-mussel invertebrates ($p < 0.01$) and leptocerid caddisflies ($p < 0.05$), resulting in a significant increase in chlorophyll a ($p < 0.01$) concentrations. A significant zebra mussel density × round goby interaction showed that total invertebrate biomass responded positively to the combined effect of high zebra mussel density and round goby absence. These results demonstrate that round gobies and zebra mussels are altering benthic invertebrate community structure and algal resources in nearshore rocky areas of southwestern Lake Michigan.

INDEX WORDS: Lake Michigan, benthic invertebrates, round goby, *Neogobius melanostomus*, zebra mussel, *Dreissena polymorpha*.

INTRODUCTION

The repeated introduction and spread of exotic organisms in the Laurentian Great Lakes can have profound impacts on benthic physical structure and energy flow in aquatic ecosystems (Stewart and Haynes 1994). Two recent invaders into the Great Lakes that are impacting southern Lake Michigan are the zebra mussel (*Dreissena polymorpha* Pallas) and the round goby (*Neogobius melanostomus* Pallas), both of which are indigenous to the Black, Azov, and Caspian seas.

Zebra mussels were introduced into Lake St. Clair in 1986 and have spread rapidly across the Laurentian

Great Lakes. Densities as high as 342,000/m² have been reported from areas with suitable substrates (MacIsaac 1994). The establishment of zebra mussels in the Great Lakes has coincided with increases in depth of light penetration and benthic algal biovolume and decreases in phytoplankton populations (Lowe and Pillsbury 1995, MacIsaac 1996). These changes in energy flow from primarily pelagic to benthic may influence benthic algal food resources and benthic invertebrate community structure (Stewart and Haynes 1994, Karatayev *et al.* 1997, Ricciardi *et al.* 1997, Stewart *et al.* 1998).

Round gobies were first discovered in the St. Clair River in 1990 (Jude *et al.* 1992) and have been reported from all five of the Laurentian Great Lakes (Charlebois *et al.* 1997). Mollusks represent a major component of round goby diets in both their North

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American and native habitats (Jude *et al.* 1992, Kovtun *et al.* 1974). In the Great Lakes, zebra mussels comprise up to 82% of the diet of round gobies 80 to 90 mm TL (Jude *et al.* 1995). Although gut analysis studies have provided information on round goby diets in the Great Lakes (Ghedotti *et al.* 1995, Jude *et al.* 1995), few data are available on how round goby predation impacts benthic communities. Round goby predation on zebra mussels may have important implications for other benthic invertebrates living in association with zebra mussel colonies. To determine the impacts of round gobies and zebra mussels on nearshore invertebrate communities in Lake Michigan, responses of benthic invertebrates to zebra mussel colonies of differing sizes and round goby presence or absence were examined.

The overall objective of this study was to examine the effects of zebra mussel density and round goby predation on invertebrates associated with zebra mussel colonies. Specifically, the goals were to determine 1) the effects of zebra mussel colony density on invertebrates within the colony, 2) the effects of round goby predation on non-mussel benthic invertebrates, and 3) whether the effects of zebra mussel density altered the response of benthic invertebrates to round goby predation.

STUDY AREA

This study was conducted in Calumet Harbor, Illinois, U.S.A. (latitude = 41°43'37"N; longitude = 87°31'48"W) in southwestern Lake Michigan on the Illinois/Indiana border. The study site was approximately 4 m from shore in a depth 3 m. This area of Calumet Harbor is characterized by large cobble and boulder substrata with dense zebra mussel (40,000/m²) and round goby (15/m²) populations.

MATERIALS AND METHODS

Experimental Design

Zebra Mussel Density Effects

To determine the effect of zebra mussel density on benthic invertebrates, three densities of zebra mussels (zero = 0/100 cm²; low = 100/100 cm²; high = 1,000/100 cm²) corresponding to 0, 10,000, and 100,000/m² were colonized in the laboratory on 10 × 10 cm unglazed ceramic tiles attached to bricks with silicone caulk. A square piece of plastic mesh (mesh opening = 5 × 8 mm) was attached to each tile to facilitate zebra mussel attachment. Prior to zebra mussel colonization, a wire support frame for cages

was attached to each tile with silicone caulk. Zebra mussels were collected from Calumet Harbor and sorted into three size classes. Each tile was colonized with 50% small mussels (3.0 to 7.9 mm), 45% medium-sized mussels (8.0 to 10.9 mm), and 5% large mussels (11.0 to 15.0 mm). These ratios reflected the size structure of zebra mussels in Calumet Harbor at the time of the experiment. Treatment densities were achieved in the laboratory by placing tiles in tanks with recirculating water and inoculating the tiles with the appropriate number of zebra mussels. Tiles remained in the tanks for three weeks to allow zebra mussels to attach. During the 3-week period, zebra mussels that had migrated off the tiles were replaced with mussels of the appropriate size. Zebra mussels were fed a mixed algal assemblage from a laboratory culture three times weekly during the colonization period.

Round Goby Predation Effects

After the third week of colonization in the laboratory, cages were constructed around the sides of the experimental tiles to either exclude round gobies or allow for round goby predation. Round goby exclusion cages enclosed all four sides of the tile, whereas one side of round goby predation cages was left open to allow round gobies access to the tiles. Cages were constructed from plastic mesh screening (mesh opening = 5 × 8 mm) in the shape of a four-sided pyramid and were added to each tile immediately before placement in the lake. The mesh size allowed free movement of non-mussel invertebrates into and out of the cages.

Five replicates of each treatment (5 replicates × 3 zebra mussel densities × 2 round goby treatments = 30 tiles) were placed randomly along a transect line parallel to the shore. In addition, the open side of each round goby predation cage was oriented randomly. The experiment was conducted for 10 weeks in 1995 (11 July to 18 September). Divers using SCUBA observed round gobies feeding in predation cages on several occasions during day and night, but no other fish were seen in the cages. Crayfish (*Orconectes rusticus* Girard) were abundant in the cobble at the study site, but were not observed using the cages. Cages were examined twice weekly to remove algae that could have interfered with water flow and to check for disturbance. All tiles remained intact during the experiment. At the completion of the experiment, tiles were collected by divers using SCUBA and placed into individual plastic Ziploc[®]

bags. Bags were brought to the surface and placed in coolers for transport to the laboratory.

In the laboratory chlorophyll *a* samples were collected by scraping 25% of the surface area of each tile, including any zebra mussels or other invertebrates. Chlorophyll *a* concentrations were determined spectrophotometrically using methanol extraction and phaeophytin corrections according to Standard Methods (APHA 1985). Invertebrates were removed from the remaining surface area of each tile and preserved in 80% ethanol for later identification and enumeration. All invertebrates collected were identified to genus using Merritt and Cummins (1996) or Thorp and Covich (1991). Dry weight of each taxon, excluding chironomids, was obtained by air-drying at room temperature for 24 hours. Biomass of chironomids was estimated at the subfamily level using the regression equations of Smock (1980). Total invertebrate density and chlorophyll *a* data were analyzed using a two-way ANOVA with replication (2×3 factorial design: 2 levels of round goby predation \times 3 levels of zebra mussel density). Significant zebra mussel density effects were analyzed using Tukey's multiple comparison tests. Responses of individual taxa to zebra mussel densities were analyzed using a one-way ANOVA and Tukey's multiple comparison tests. Chlorophyll *a* and invertebrate density data, excluding total chironomid density, were log transformed to meet homoscedasticity and normality assumptions. Total chironomid density data required no transformation. A test significance level of $p < 0.05$ was used in all analyses.

RESULTS

To determine if differences in zebra mussel densities were maintained on experimental tiles during the experiment, the number of live zebra mussels remaining in round goby enclosures at the completion of the experiment was analyzed using a one-way ANOVA on log-transformed densities. All three zebra mussel density treatments remained significantly different after the 10 week experiment ($F = 203.8; 2, 12$ df, $p < 0.001$).

Zebra Mussel Effects

A total of 20 genera of non-mussel invertebrates were collected from the experimental tiles (Table 1). All invertebrate densities are expressed as mean/100 cm² (\pm SE). Density of total non-mussel invertebrates was 3 to 4 times greater on high and low

zebra mussel density tiles than on zero density tiles (Table 2). The total number of Chironomidae (Diptera) also was significantly greater in the presence of zebra mussels than when zebra mussels were absent (Table 2).

The response of total invertebrate densities among zebra mussel density treatments, especially between low and high treatments, may have been masked by the high contribution of chironomids (54% of total non-mussel invertebrates) to densities of total non-mussel invertebrates. Thus, data on total non-mussel invertebrates exclusive of chironomids also were analyzed. Excluding chironomids revealed a significant positive response of total non-mussel invertebrates to zebra mussel densities (Table 2). Non-mussel invertebrate densities were greater on high density treatments than on low and zero density tiles. Invertebrate densities on low zebra mussel density treatments also were significantly greater than in the absence of zebra mussels (Table 2).

Of the 20 genera collected in this study, 16 responded positively to higher zebra mussel densities (Table 1), although responses of only six taxa were statistically significant. Densities of *Caecidotea* sp. (Isopoda) on high zebra mussel density treatments were significantly greater than on zero zebra mussel tiles, although high and low zebra mussel density treatments did not differ (Table 2). The hydroptilid caddisfly *Agraylea* sp. (Trichoptera) had significantly greater densities in the presence of zebra mussels than on zero zebra mussel density treatments (Table 2). Densities of *Gammarus* sp. on high zebra mussel density tiles were significantly greater than on low or zero zebra mussel treatments (Table 2).

Densities of the most common chironomid genera, *Cricotopus* sp., *Paratanytarsus* sp., and *Psectrocladius* sp., also responded to zebra mussel densities. Densities of *Cricotopus* sp. were significantly greater on low zebra mussel density tiles than on zero density tiles (Table 2). Densities on high density tiles, however, did not differ from those on either low or zero zebra mussel treatments. *Paratanytarsus* sp. and *Psectrocladius* sp. responded similarly with increased densities in the presence of zebra mussels. *Paratanytarsus* sp. densities were significantly greater on high and low zebra mussel tiles than on zero zebra mussel treatments (Table 2). Similarly, *Psectrocladius* sp. densities were significantly greater in the presence of zebra mussels than on zero zebra mussel treatments (Table 2).

TABLE 1. Benthic invertebrate taxa colonizing experimental tiles in Calumet Harbor, IL. General trends in benthic invertebrate densities in response to increasing zebra mussel densities and the presence of round gobies are indicated as + (positive), - (negative), or 0 (no trend). Tables 2 and 3 present taxa with significant effects. Functional feeding groups (FFG) are as follows: C-G = collector-gatherer, SCR = scraper, SHR = shredder, and PRED = predator (from Thorp and Covich 1991, Merritt and Cummins 1996).

TAXA			Zebra Mussel Effects	Round Goby Effects	FFG
Gastropoda	Valvatidae	<i>Valvata</i>	-	-	C-G
Trichoptera	Hydroptilidae	<i>Agraylea</i>	+	+	SHR
	Leptoceridae	<i>Oecetis</i>	+	-	PRED
Diptera	Empididae	<i>Hemerodromia</i>	+	-	PRED
	Chironomidae	<i>Procladius</i>	-	-	PRED
		<i>Krenopelopia</i>	0	0	PRED
		<i>Cricotopus</i>	+	-	SHR, C-G
		<i>Psectrocladius</i>	+	-	SHR, PRED
		<i>Chironomus</i>	+	-	C-G, SCR
		<i>Cryptochironomus</i>	+	+	PRED
		<i>Dicrotendipes</i>	+	0	C-G
		<i>Endochironomus</i>	+	+	SHR
		<i>Parachironomus</i>	+	-	C-G, PRED
		<i>Polypedilum</i>	+	-	SHR, C-G
		<i>Paratanytarsus</i>	+	-	C-G, SCR
		<i>Rheotanytarsus</i>	0	-	C-G
<i>Tanytarsus</i>	+	0	C-G		
Amphipoda	Gammaridae	<i>Gammarus</i>	+	-	C-G
	Talitridae	<i>Hyallela</i>	+	-	C-G
Isopoda	Asellidae	<i>Caecidotea</i>	+	-	C-G

Round Goby Effects

Zebra mussel densities on high density tiles were significantly reduced in the presence of round gobies compared to round goby enclosure tiles ($F = 14.6$; 1, 24 df, $p < 0.01$). Round gobies had no effect, however, on zebra mussel densities in low or zero density treatments ($p > 0.05$).

Total non-mussel invertebrate densities were 44% higher on round goby enclosure tiles than on tiles allowing round goby access (Table 3). Removing chironomids from the analysis revealed a 92% increase in non-mussel invertebrate densities on round goby enclosure tiles (Table 3). Round gobies had no effect on total chironomid densities (Table 3).

The only individual taxon significantly affected by round goby presence was the predatory caddisfly, *Oecetis* (Trichoptera). Densities of *Oecetis* were six times greater in round goby enclosures compared to treatments allowing round gobies access (Table 3). Densities of most taxa also were lower in the presence of round gobies, although differences were not statistically significant (Table 1).

Zebra Mussel and Round Goby Effects on Invertebrate Biomass

The influence of each main effect, zebra mussel density and round goby presence, on total non-mussel invertebrate biomass could not be determined because of a significant statistical interaction ($F = 7.5$; 2, 24 df, $p < 0.01$). Total non-mussel invertebrate biomass, however, exhibited a positive response to the combined effects of high zebra mussel density and round goby absence (Fig. 1).

Zebra Mussel and Round Goby Effects on Algae

Chlorophyll *a* concentrations ($\text{mg}/100 \text{ cm}^2 \pm \text{SE}$) on tiles were quantified to examine possible indirect effects of zebra mussels or round gobies on food availability for algivorous benthic invertebrates. It should be noted that chlorophyll *a* values reflect concentrations on both experimental tiles and zebra mussel shells.

Chlorophyll *a* was influenced by both zebra mussel density and round goby presence. Chlorophyll *a*

TABLE 2. Densities (mean/100cm² ± SE) of benthic invertebrate taxa at zero (0/100cm²), low (100/100cm²), and high (1,000/100cm²) zebra mussel densities. Means with different superscripts are significantly different (*p* < 0.05).

Taxa	Zebra Mussel Density			ANOVA (F; df; P)
	Zero	Low	High	
Chironomidae				
<i>Cricotopus</i> sp.	6.7 ± 1.2 ^a	16.1 ± 3.5 ^b	12.3 ± 2.6 ^{ab}	3.8; 2, 24; < 0.05
<i>Paratanytarsus</i> sp.	2.8 ± 1.3 ^a	7.9 ± 1.5 ^b	13.5 ± 1.7 ^b	15.1; 2, 24; < 0.001
<i>Psectrocladius</i> sp.	1.3 ± 0.3 ^a	4.3 ± 0.8 ^b	4.5 ± 0.6 ^b	11.2; 2, 24; < 0.001
Total	12.9 ± 2.6 ^a	34.7 ± 3.9 ^b	35.1 ± 2.9 ^b	15.9; 2, 24; < 0.001
All Other Invertebrates				
<i>Caecidotea</i> sp.	0.3 ± 0.2 ^a	1.5 ± 0.6 ^{ab}	2.9 ± 1.0 ^b	4.5; 2, 24; < 0.05
<i>Agraylea</i> sp.	0.4 ± 0.3 ^a	2.7 ± 0.7 ^b	2.3 ± 0.5 ^b	7.6; 2, 24; < 0.01
<i>Gammarus</i> sp.	4.4 ± 1.2 ^a	13.9 ± 2.5 ^b	37.8 ± 7.8 ^c	26.7; 2, 24; < 0.001
Total	5.3 ± 1.4 ^a	18.8 ± 3.0 ^b	43.2 ± 8.0 ^c	30.9; 2, 24; < 0.001
Grand Total	18.8 ± 3.2 ^a	54.0 ± 3.2 ^b	78.8 ± 9.1 ^b	48.4; 2, 24; < 0.001

TABLE 3. Densities (mean/100 cm² ± SE) of benthic invertebrate taxa in the presence and absence of round gobies.

Taxa	Gobies Present	Gobies Absent	ANOVA (F; df; P)
Chironomidae	25.6 ± 4.0	29.5 ± 3.4	1.1, 1, 24; ns
All Other Invertebrates			
<i>Oecetis</i> sp.	0.2 ± 0.1	1.2 ± 0.4	5.7; 1, 24; < 0.05
Total	15.4 ± 3.1	29.5 ± 7.1	5.2; 1, 24; < 0.05
Grand Total	41.5 ± 6.2	59.5 ± 9.0	11.4; 1, 24; < 0.01

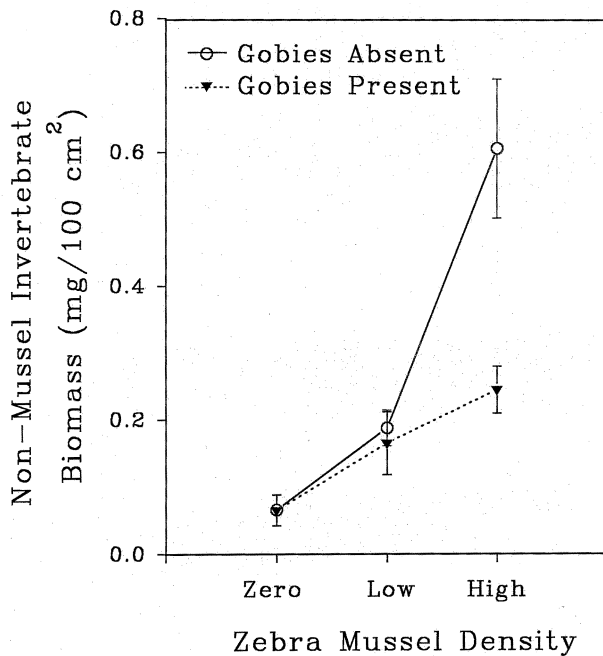


FIG. 1. Relationship between zebra mussel density and round goby presence/absence on total invertebrate biomass (mean ± SE).

concentrations were two-fold greater at low zebra mussel densities (19.6 ± 1.4) than on the zero (9.0 ± 1.7) and high (9.5 ± 1.5) zebra mussel density treatments (F = 20.9; 2, 24 df, *p* < 0.001, Fig. 2a). Chlorophyll *a* concentrations in the presence of round gobies (15.4 ± 1.8) were 50% greater than in round goby enclosures (10.1 ± 1.5) (F = 11.9; 1, 24 df, *p* < 0.01, Fig. 2b).

DISCUSSION

Zebra Mussel Density Effects

Results from the present study on experimental tiles in rocky areas of nearshore Lake Michigan show that densities of most non-mussel benthic invertebrates had a positive response to zebra mussels. In contrast, Dermott and Kerec (1997) and Nalepa *et al.* (1998) reported reductions of some benthic invertebrates in soft sediments of Lake Erie and Lake Michigan, respectively, since the invasion of zebra mussels. The results from this study are consistent with previous studies that have reported increases in non-mussel invertebrate abundance in the presence

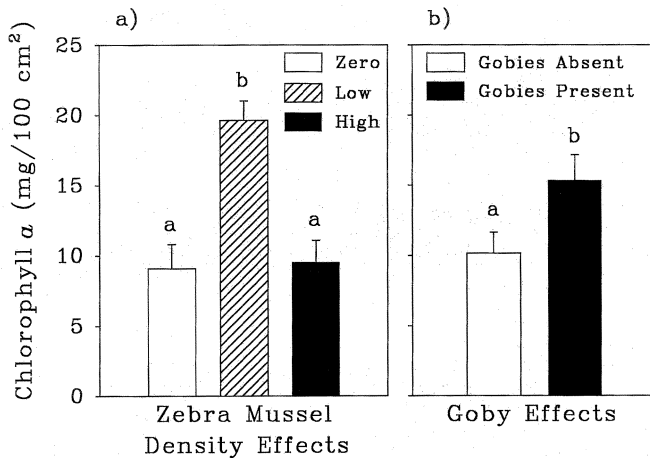


FIG. 2. Benthic chlorophyll *a* concentration in response to (a) zebra mussel density and (b) round goby presence/absence. Bars with different letters are significantly different.

of zebra mussels (Dermott *et al.* 1993, Griffiths 1993, Stewart and Haynes 1994, Wisenden and Bailey 1995, Botts *et al.* 1996, Stewart *et al.* 1998). The mechanism responsible for these increases varies among taxa and may result from additional substrate complexity caused by zebra mussel shells and colony formation, and/or an elevation in the rate of organic matter deposition to the benthos from fecal and pseudofecal production of zebra mussels (Izvekova and Lvova-Katchanova 1992, Botts *et al.* 1996, Ricciardi *et al.* 1997, Thayer *et al.* 1997, Stewart *et al.* 1998).

Round Goby Effects

Round goby diets have been examined in both laboratory and field studies (Ghedotti *et al.* 1995, Jude *et al.* 1995, Ray and Corkum 1997). Although differences in prey species composition exist between the native habitat of the round goby and in the Great Lakes, diet composition of round gobies in both habitats has been reported to be similar (Jude *et al.* 1992, Kovtun *et al.* 1974). Jude *et al.* (1995) reported that diets of small round gobies (< 67 mm) were composed primarily of amphipods, isopods, chironomids, and benthic cladocerans. At sizes > 67 mm, however, round gobies had a more specialized diet ingesting primarily zebra mussels. Ray and Corkum (1997) reported similar ontogenetic diet differences where small round gobies (< 70 mm) ate few zebra mussels and larger round gobies (≥ 70 mm) relied heavily on zebra mussels. Stomach con-

tent analyses of round gobies from the study site support the results from these previous studies. These observations are consistent with a laboratory feeding study of large gobies (60 to 100 mm) that reported a strong preference for zebra mussels over native clams or snails (Ghedotti *et al.* 1995). Despite field and laboratory studies on round goby diets and food preferences, no studies have addressed how the presence of the round goby will affect benthic invertebrate community structure in the Great Lakes.

In the present study, total invertebrate densities in zebra mussel colonies significantly decreased in the presence of round gobies. The most likely explanation for this reduction is round goby predation, although indirect effects of round gobies altering zebra mussel colonies can not be discounted. Many studies have shown decreases in benthic invertebrate density either through direct or indirect effects of fish predation (Gilinsky 1984, Harvey and Hill 1991, Hershey 1985). In the present study, round gobies significantly reduced zebra mussels in high density treatments, suggesting that indirect predation effects may play a role in determining invertebrate densities. Although crayfish (*Orconectes rusticus*) were present at the study site and have been reported to feed on zebra mussels (Martin and Corkum 1994, Perry *et al.* 1997), they were never observed on the round goby access tiles. Similarly, smallmouth bass (*Micropterus dolomieu* Lacépède) also were present at the study site, but were not observed feeding in or around the experimental tiles.

Although cageless controls were not used in this study, these results accurately reflect the effects of round gobies on nearshore benthic invertebrates. Cageless controls would have allowed examination of possible cage effects on round goby feeding behavior and invertebrate colonization and densities. Lower invertebrate densities on round goby access tiles did not result from higher densities of round gobies than in the surrounding area because natural rock shelter areas and zebra mussels were abundant at the study site. In addition, if the plastic mesh surrounding round goby exclusion cages had hampered invertebrate colonization, invertebrate densities would be expected to be lower in those treatments. On the contrary, total invertebrate densities were significantly higher on round goby exclusion tiles. A possible cage effect could have resulted in reduced zebra mussel densities in round goby access cages by wave action dislodging and removing zebra mussels. Because no dislodged zebra mussels were observed in round goby exclusion cages, it is unlikely

that dislodgment in round goby access cages could account for reduced zebra mussel densities.

Community Responses

Zebra mussel colonization adds structural complexity to benthic substrata and channels nutrients to benthic invertebrates via fecal and pseudofecal production (Stańczykowska and Lewandowski 1993, Lowe and Pillsbury 1995, Botts *et al.* 1996, Stewart *et al.* 1998). When zebra mussel densities are high, increased structural complexity and nutrient inputs provide refugia and food resources for invertebrates, respectively. Many of the invertebrates identified in this study are classified as shredders, scrapers, and collector-gatherers (Table 1) (Thorp and Covich 1991, Merritt and Cummins 1996). These invertebrates are all potentially algivorous, and likely reduced chlorophyll *a* in high zebra mussel density treatments. The net result is that chlorophyll *a* levels in high zebra mussel density colonies and concomitant high grazer densities are similar to those without zebra mussels and hence no nutrient enrichment from mussel feces and pseudofeces. Thus, the low zebra mussel density treatments exhibited the highest chlorophyll *a* concentrations.

Chlorophyll *a* on experimental tiles was significantly higher in the presence of round gobies. This is likely because of round goby predation on grazing invertebrates, thereby releasing algae from grazing pressure. When round gobies were excluded, however, invertebrate numbers were significantly higher (50%), resulting in lower chlorophyll *a* concentrations. These results are consistent with previous studies that have reported indirect effects of predators on algal communities by altering herbivore assemblages (McCormick 1990, Bechara *et al.* 1992, Brönmark *et al.* 1992, Power 1992, Wootton, 1992, McCollum *et al.* 1998).

The invasion of round gobies and zebra mussels into Lake Michigan has the potential to change food web dynamics of benthic communities in nearshore rocky areas. Although the design of this study did not allow distinguishing between direct and indirect effects, these results can be used to develop a conceptual model of littoral zone interactions in southern Lake Michigan that illustrates possible direct and indirect effects of round gobies and zebra mussels on benthic communities. A series of complex interactions between round gobies, zebra mussels, and benthic invertebrates can directly and indirectly affect food resources and energy flow, thereby altering the structure and function of littoral zone communities

in nearshore areas of Lake Michigan and other Laurentian Great Lakes.

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