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LOYOLA UNIVERSITY CHICAGO

BENTHIC INVERTEBRATE COMMUNITY RESPONSES TO ROUND GOBY  
(NEOGOBIUS MELANOSTOMUS) AND ZEBRA MUSSEL (DREISSENA  
POLYMORPHA) INVASION IN SOUTHERN LAKE MICHIGAN

A THESIS SUBMITTED TO  
THE FACULTY OF THE GRADUATE SCHOOL  
IN CANDIDACY FOR THE DEGREE OF  
MASTER OF SCIENCE  
DEPARTMENT OF BIOLOGY

BY

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## ABSTRACT

The round goby (Neogobius melanostomus Pallas), a fish native to the Black, Azov, and Caspian Seas, recently has become established in southwestern Lake Michigan. Because round gobies prey on zebra mussels (Dreissena polymorpha Pallas) and other benthic invertebrates, I investigated the effects of goby predation on invertebrates within zebra mussel colonies. Using a 2x3 factorial design, I examined the effects of gobies (present or absent) and zebra mussel densities (zero, low, and high) on non-mussel invertebrates. Ten ceramic tiles of each zebra 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 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 ( $p < 0.01$ ), 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 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 x round goby interaction showed that total invertebrate biomass responded positively to the combined effect of high zebra mussel density and goby absence. Results from this study demonstrate that these two non-indigenous species (round gobies and zebra mussels) are altering benthic algal resources and benthic invertebrate community structure in nearshore areas of southwestern Lake Michigan.

## CHAPTER I

### FISH PREDATION EFFECTS ON BENTHIC INVERTEBRATES

Views differ as to the role of fish predation in trophic control of benthic communities in aquatic systems (Holomuzki and Stevenson 1992). Although some studies suggest that benthic invertebrate species composition and density are influenced by fish predation (Bowlby and Roff 1986, Gilliam et al. 1989, Power 1990), others report no effect on benthic invertebrate assemblages (Flecker and Allan 1984, Healey 1984, Luecke 1990). Although fish predation may be important in structuring benthic communities, many other factors can alter benthic community structure as well. Different biotic and abiotic factors may be important in structuring benthic communities (Dudgeon 1991). Organizing factors include predation, competition, spatial heterogeneity, and abiotic environmental factors. In this review I will discuss the role of predation in structuring aquatic benthic communities and how predation influences other structuring forces.

#### **Direct and Indirect Effects of Fish Predation**

Predation can impact an aquatic community when keystone predators suppress dominant competitive relationships which lead to increases in species diversity (Paine 1966, Gilinsky 1984). In a pond littoral zone,

bluegill (Lepomis macrochirus) concentrated on a few preferred prey which altered competitive relationships among macroinvertebrates and possibly lead to higher densities of many species (Gilinsky 1984). Morgan and Ringler (1994) found that sculpin (Cottus cognatus) density had little or no effect on size distribution and secondary production of most benthic invertebrates. Densities of shredders and scrapers/gatherers, however, increased two- to three-fold when sculpins were removed while densities of filter-feeders decreased. This shift in functional feeding groups indicated changes in competitive relationships between benthic macroinvertebrates.

Fish predation can impact on benthic invertebrate communities in some systems and have no detectable impact in others. Studies conducted in streams and lakes have documented direct, indirect, or no effects from fish predation. Predation can affect benthic invertebrate density, biomass, diversity, and secondary production.

In lakes, direct effects of fish predation were demonstrated by Bendell and McNicol (1995) who showed invertebrates were more numerous when fish were absent. Thorp and Bergey (1981) however, found that vertebrate predators did not affect benthic macroinvertebrate communities in littoral zones with soft sediments. Indirect effects can cascade far down the food web. Power (1990) showed that in the presence of fish, invertebrate predators were reduced, allowing grazing chironomids to reach high densities and reduce algal biomass. When vertebrate predators were

absent, however, chironomid densities were reduced, resulting in an increase in algal standing crop.

The impacts of fish predation also have been demonstrated in stream systems. Bowlby and Roff (1986) showed that in the presence of piscivorous fish, abundance and biomass of stream benthic invertebrates was higher than in streams without piscivorous fish. Flecker (1984) also reported that sculpin (Cottus bairdi and Cottus girardi) predation on midges played an important role in the overall structure of a stream invertebrate community. Other studies however, have reported contrary results. Flecker and Allan (1984) showed that fish predation by sculpin (Cottus sp.), dace (Rhinichthys sp.), trout (Salvelinus fontinalis), and sucker (Catostomus commersoni) had no effect on the benthic invertebrate community. Similarly, Holomuzki and Stevenson (1992) found that the effects of sunfish (Lepomis sp.) in an intermittent stream did not influence the general organization of the food web.

### **Invertebrate Responses to Predation**

Some prey have been reported to be able to detect predators and use certain behaviors to avoid or reduce encounters with potential predators. Some of these behaviors include reduced prey movement, changes in activity times, and changes in habitat use (Holomuzki and Short 1988). For example, in the presence of green sunfish (Lepomis cyanellus), the isopod

Lirceus fontinalis sought refuge in Cladophora and reduced movement on sandy substrates (Holomuzki and Short 1988). This behavior was most likely due to a chemical cue, because Lirceus only responded in water “conditioned” with green sunfish.

Under some circumstances invertebrates must migrate to new environments where they may be more vulnerable to predation. In response to hypoxia, Kolar and Rahel (1993) reported the movement of invertebrate taxa to areas of higher oxygen concentration despite the presence of a predator. Taxa most vulnerable to fish predation, however, waited longer to migrate when a predator was present. These behaviors demonstrate the ability for some invertebrates to respond to predator presence.

### **Spatial Heterogeneity**

Spatial heterogeneity also can play a large role in structuring aquatic communities because it often provides benthic invertebrates with refugia from predation. Diehl (1992) showed that submerged vegetation provided refugia for macroinvertebrates while reducing foraging efficiency of perch (Perca fluviatilis). Hershey (1985) found that chironomid density was higher among macrophytes, and that the macrophytes served as a refuge against predators. Reice (1991) tested the role of fish predation in a stream system and concluded that leafpacks also function as a refuge, because fish predation did not affect macrobenthic species richness or diversity.

## **Abiotic Environmental Factors**

Although benthic invertebrate assemblages can be structured by fish predation, water chemistry also has an influence on invertebrate community structure (Jackson and Harvey 1993). Jackson and Harvey (1993) found that the chemical environment of aquatic systems was very important in structuring invertebrate communities. Water chemistry, especially pH, may play a role in reducing less stress-tolerant species such as fish and crayfish which reduce invertebrates through predation. Therefore, water chemistry may be in some cases, an indirect mechanism that releases invertebrates from fish or large invertebrate predation.

## **Conclusions**

Although conclusions concerning the effects of fish predation on benthic invertebrates may be contradictory, most studies have found that fish predation plays some role in structuring aquatic invertebrate communities. Because the influence of predation diminishes at lower trophic levels (Bowlby and Roff 1986), not all fish predation interactions will have the same strength or outcome. Despite these different interactions, predation either directly or indirectly can be an important organizer for benthic invertebrate communities.

CHAPTER II  
RESPONSES TO ROUND GOBY AND ZEBRA MUSSEL INVASION IN  
SOUTHERN LAKE MICHIGAN

Historically, the introduction and spread of exotic organisms has occurred repeatedly within the Great Lakes (Mills et al. 1994). Invasions of exotic species 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, which may impact southern Lake Michigan are the zebra mussel (Dreissena polymorpha Pallas) and the round goby (Neogobius melanostomus Pallas), and both 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 Great Lakes. Densities as high as 342,000/m<sup>2</sup> have been reported from areas with suitable substrates (MacIsaac 1994). The establishment of zebra mussels into North America has coincided with increases in depth of light penetration and benthic algal biovolume, while phytoplankton populations have declined (Lowe and Pillsbury 1995, MacIsaac 1996). These shifts in energy flow from pelagic to benthic may influence benthic algal food sources and benthic invertebrate community

structure.

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 (Marsden et al. 1996). Mollusks represent a major component of round goby diets in both the Great Lakes and their native habitats (Jude et al. 1992, Kovtun et al. 1974). In the Great Lakes, zebra mussels comprise up to 82% of the diet of gobies 80-90 mm in length (Jude et al. 1995). Although gut analysis studies have provided information on goby diets in the Great Lakes (Ghedotti et al. 1995, Jude et al, 1995), few data are available on how goby predation impacts benthic communities. Goby predation on zebra mussels may have important implications for other benthic invertebrates that use zebra mussel colonies as refugia. To determine the impacts of round gobies and zebra mussels on nearshore invertebrate communities in Lake Michigan, I examined responses of benthic invertebrates to various zebra mussel densities and goby presence or absence.

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



response of benthic invertebrates to goby predation.

## **Methods**

### Study Site

Calumet Harbor is located in southwestern Lake Michigan on the Illinois/Indiana border. The study area was approximately 4 m offshore and located at a depth of 3 m. The substrate was mostly large cobbles and boulders, and adult round gobies were abundant at the study site.

### Experimental Design: Zebra Mussel Density Effects

To determine the effect of zebra mussel density on benthic invertebrates, three densities of zebra mussels (zero = 0/m<sup>2</sup>; low = 10,000/m<sup>2</sup>; high = 100,000/m<sup>2</sup>) were colonized in the laboratory on 10 x 10 cm unglazed ceramic tiles attached to bricks. Zebra mussels were collected from Calumet Harbor, IL and sorted into three size classes. Each tile was colonized with approximately 50% small mussels (3.0-7.9 mm), 45% medium-sized mussels (8.0-10.9 mm) and 5% large mussels (11.0-15.0 mm). These ratios reflected the size-structure of zebra mussels on natural substrates at the study site in the Spring of 1995. Tiles were placed in a tank with recirculating water for three weeks to allow zebra mussels to attach. Treatment densities were attained by placing the appropriate number of zebra mussels on each tile and replacing mussels that had

migrated off the tiles. During the colonization period, zebra mussels were fed a mixed assemblage of phytoplankton from a laboratory culture three times weekly.

### Experimental Design: Goby Predation Effects

After the third week of colonization in the laboratory, cages were constructed around the tiles to either exclude gobies or allow for goby predation. Cages were constructed from plastic mesh screening (mesh opening = 5x8 mm) in the shape of a four-sided pyramid. The mesh size allowed free movement of non-mussel invertebrates into and out of the cages. Goby exclusion cages enclosed the entire tile, whereas goby predation cages had one side of the cage open to allow gobies access to the tiles.

Five replicates of each treatment (5 replicates x 3 zebra mussel densities x 2 goby treatments = 30 tiles) were placed randomly along a single line, parallel to the shore at approximately 3 m depth. In addition, the open side of each goby predation cage was oriented randomly. The experiment was conducted for ten weeks in 1995 (11 July - 18 September). SCUBA divers observed round gobies feeding in predation cages on several occasions during day and night, but no other fish were seen in the cages. Crayfish were abundant in the cobble around 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 cages remained intact during the experiment. At the completion of the experiment, tiles were collected by SCUBA divers and placed into 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 the tiles 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). Invertebrate and chlorophyll a data were analyzed using a two-way ANOVA (2x3 factorial design: 2 levels of goby predation x 3 levels of zebra mussel density). Chlorophyll a and all invertebrate density data, excluding total chironomid density, were log transformed to meet homoscedasticity and normality assumptions.

## Results

All invertebrate densities are expressed as mean number/100 cm<sup>2</sup> ( $\pm$  SE). To determine if zebra mussel density treatments were maintained during the experiment, the number of live zebra mussels remaining in goby exclosures at the completion of the experiment was analyzed using a one-way ANOVA on log-transformed data. The mean of all three zebra mussel density treatments were significantly different from each other after the 10 week experiment ( $p < 0.001$ ). No zero density tiles gained zebra mussels. Zebra mussel density in the low density treatments exposed to gobies were not significantly different from densities in goby predation cages and goby exclosure cages. Mean densities at the end of the experiment were 34 mussels/100 cm<sup>2</sup> ( $\pm 2.7$ ) for tiles open to predation and 41 mussels/100 cm<sup>2</sup> ( $\pm 4.5$ ) for goby exclosure cages. High density treatments, however, had significantly more mussels remaining in the goby exclosure cages ( $p < 0.01$ ). Zebra mussel density in goby exclosure cages had a mean of 211 mussels/100 cm<sup>2</sup> ( $\pm 9.0$ ), whereas goby predation cages had a mean of 100 mussels/100 cm<sup>2</sup> ( $\pm 1.3$ ) at the end of the experiment.

A total of 20 genera of amphipods, isopods, gastropods, and insects were collected from the experimental tiles (Table 1).

## Zebra Mussel Effects

Mean density of total non-mussel invertebrates was 3 -4 times greater in the presence of zebra mussels (high:  $59.1/100 \text{ cm}^2 \pm 6.9$ ; low:  $40.5/100 \text{ cm}^2 \pm 2.2$ ) than on zero density tiles ( $14.1/100 \text{ cm}^2 \pm 2.4$ ) ( $p < 0.001$ , Figure 1a). Agraylea (Hydroptilidae), Gammarus (Gammaridae), and Chironomidae occurred in significantly higher densities in the presence of zebra mussels (Figures 1 and 2).

Because chironomids comprised a substantial proportion (54%) of the total number of invertebrates collected, chironomid density may have masked invertebrate differences between low and high zebra mussel density treatments. To assess this, total invertebrate densities were adjusted to exclude chironomids. Excluding chironomids from the analysis revealed a significant positive relationship between densities of non-mussel invertebrates and zebra mussel density (high-low:  $p < 0.05$ ; high-zero:  $p < 0.001$ ; low-zero:  $p < 0.001$ ; Figure 1c). Mean densities increased from  $5.8/100 \text{ cm}^2 (\pm 1.4)$  at zero mussel densities, to  $19.3/100 \text{ cm}^2 (\pm 2.9)$  at low mussel densities, to  $43.6/100 \text{ cm}^2 (\pm 8.1)$  at high mussel densities.

Caecidotea densities were significantly greater on high zebra mussel treatments than in the absence of zebra mussels ( $p < 0.05$ ). There were no differences ( $p > 0.05$ ) in Caecidotea densities among other zebra mussel density treatments (Figure 2b).

Agraylea responded positively to the presence of zebra mussels.

Agraylea densities were two-fold greater in the presence of zebra mussels ( $p < 0.05$ , Figure 2c), however low and high density zebra mussel colonies had similar densities of Agraylea ( $p > 0.05$ ).

Gammarus responded positively to all three zebra mussel density treatments (high-low:  $p < 0.01$ ; high-zero:  $p < 0.001$ ; low-zero:  $p < 0.01$ ; Figure 2d). Mean densities of Gammarus increased from 4.4/100 cm<sup>2</sup> ( $\pm 1.2$ ) at zero zebra mussel densities, to 13.8/100 cm<sup>2</sup> ( $\pm 2.5$ ) at low zebra mussel densities, to 37.6/100 cm<sup>2</sup> ( $\pm 7.8$ ) at high zebra mussel densities.

Thirteen genera of chironomids were identified from the experimental tiles. The most abundant genera were Polypedilum, Psectrocladius, Paratanytarsus, Parachironomus, and Cricotopus. Total chironomid density was significantly higher ( $p < 0.001$ ) in the low and high zebra mussel density treatments compared to the zero zebra mussel treatment, however midge densities on low and high zebra mussel density tiles were not significantly different from each other ( $p > 0.05$ , Figure 1b). The most common genera, Cricotopus and Paratanytarsus, increased two-fold in the presence of zebra mussels compared to zero density treatments. Responses of other chironomids are presented in Table 2.

### Round Goby Effects

Total invertebrate densities were influenced by the presence of

gobies. When gobies were excluded, invertebrate densities increased by 33% from 41.4/100 cm<sup>2</sup> ( $\pm 6.2$ ) to 59.4/100 cm<sup>2</sup> ( $\pm 9.0$ ) ( $p < 0.01$ , Figure 3a). Total invertebrate densities remained significantly different ( $p < 0.05$ ) when chironomids were removed from the analysis (Figure 3c).

The only taxon significantly affected by goby presence was the predatory caddisfly, Oecetis. Densities of Oecetis increased five-fold in goby enclosure treatments ( $p < 0.05$ , Figure 4a). Gobies had no significant effect on densities of other taxa (Figures 3 and 4, Table 2).

### Zebra Mussel and Goby Impacts on Algae

Chlorophyll a concentrations on tiles were quantified to examine possible indirect effects of zebra mussels or gobies on food availability for algivorous benthic invertebrates. Chlorophyll a was influenced by both zebra mussel density and goby presence. Chlorophyll a concentrations were two-fold greater at low zebra mussel densities ( $p < 0.001$ , Figure 5a) than on the zero and high density treatments. Chlorophyll a concentrations in the presence of gobies were 33% greater than in goby enclosures ( $p < 0.01$ , Figure 5b).

### Zebra Mussel and 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 ( $p < 0.01$ ). Total non-mussel invertebrate biomass, however, did exhibit a positive response to the combined effects of high zebra mussel density and goby absence (Figure 6).

## **Discussion**

### Zebra Mussel Density Effects

Results from the present study show that densities of most non-mussel benthic invertebrates had a positive response to zebra mussels. This is consistent with Griffiths (1993) who reported increased abundance of many genera of invertebrates after zebra mussel invasion. These increases may result from additional substrate complexity caused by zebra mussel shells and colony formation and/or an elevation in the rate of nutrient deposition to the benthos from fecal and pseudofecal production of zebra mussels (Griffiths 1993, Botts et al. 1996). Although nutrient enhancement may play a role in invertebrate density increases (Hamburger et al. 1990), Botts et al. (1996) have shown that the additional structural complexity caused by zebra mussels is the largest contributor to increases in invertebrate densities.

### Goby Effects

Studies have examined round goby diets in both laboratory and field



populations (Ghedotti et al. 1995, Jude et al. 1995). These studies have been effective in showing that round gobies have preserved prey preferences in their transfer to the Great Lakes (Jude et al. 1992, Kovtun et al. 1974). Although differences in prey species composition exist between the round goby's native habitat and the Great Lakes, diet composition in both habitats was similar throughout all size classes of round goby (Jude et al. 1992, Kovtun et al. 1974). Despite field and laboratory studies on round goby diets and food preferences, no studies have addressed how the presence of the 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 gobies. The most likely explanation for this reduction is goby predation. Several studies have shown decreases in benthic invertebrate density either through direct or indirect effects of fish predation (Gilinsky 1984, Dudgeon 1991, Harvey and Hill 1991, Hershey 1985, Bendell and McNicol 1995).

### Community Responses

Zebra mussel colonization adds structural complexity to benthic architecture and channels nutrients to benthic invertebrates via fecal and pseudofecal production (Lowe and Pillsbury 1995). 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 algivorous (see Table 1) and likely reduced chlorophyll a levels in treatments with high zebra mussel density. The net result is that chlorophyll a levels in high mussel density conditions and concomitant high grazer densities, are similar to those without zebra mussels and hence no nutrient enrichment from mussel feces and pseudofeces. Thus, low zebra mussel density treatments exhibited the highest chlorophyll a concentrations.

Chlorophyll a on experimental tiles was significantly higher in the presence of gobies. The most likely explanation is that goby predation on grazing invertebrates released algae from grazing pressure. When gobies were excluded, however, invertebrate numbers were significantly higher (33%) resulting in lower chlorophyll a concentrations. Similar results have been reported from studies examining the effects of crayfish (Orconectes rusticus) predation on benthic invertebrates (Lodge et al. 1994, Charlebois and Lamberti 1996). Crayfish predation in both studies released algae from invertebrate grazing, causing increases in chlorophyll a (Lodge et al. 1994, Charlebois and Lamberti 1996).

With the invasion of round gobies and zebra mussels into Lake Michigan, food web dynamics of nearshore benthic communities have changed. Results from this study 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 (Figure 7).

The results from this study demonstrate that the introduction and establishment of two non-native benthic species, the round goby and zebra mussel, can alter direct and indirect interactions in nearshore benthic communities. Changes in these interactions can have important implications for food web dynamics in the littoral zone of southwestern Lake Michigan.

### Summary

The presence of zebra mussels increases benthic invertebrate density. Although an increase in substrate complexity caused by zebra mussels may provide refugia for some benthic invertebrates against predators, the presence of round gobies in Calumet Harbor had a negative impact on total benthic invertebrate densities. Goby predation had a positive impact on chlorophyll a concentrations by releasing algae from grazing pressure. Results from this study suggest that round gobies may modify the effects of zebra mussel colony formation on benthic invertebrate community structure.

Table 1 Benthic invertebrate taxa colonizing experimental tiles in Calumet Harbor, IL. Functional feeding groups (FFG) listed in the last column are as follows: C-G = collector-gatherer, SCR = scraper, SHR = shredder, and PRED = predator (from Merritt and Cummins 1996, Thorp and Covich 1991).

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

Table 2 Effects of zebra mussel density and goby presence/absence on Chironomidae. (+ =  $p < 0.05$ , ++ =  $p < 0.01$ , +++ =  $p < 0.001$ , ns = not significant)

	Zebra Mussel Density	Goby Presence/Absence
<i>Cricotopus</i>	+	ns
<i>Parachironomus</i>	ns	ns
<i>Paratanytarsus</i>	+++	ns
<i>Polypedilum</i>	Interaction	Interaction
<i>Psectrocladius</i>	++	ns
Total Chironomidae	+++	ns

Figure 1 (a) Total non-mussel invertebrate responses to zebra mussel densities (mean  $\pm$  SE), (b) Chironomid responses to zebra mussel densities (mean  $\pm$  SE), and (c) Total invertebrate responses to zebra mussel densities excluding midges (mean  $\pm$  SE). Bars with different letters are significantly different from each other ( $p < 0.05$ ).

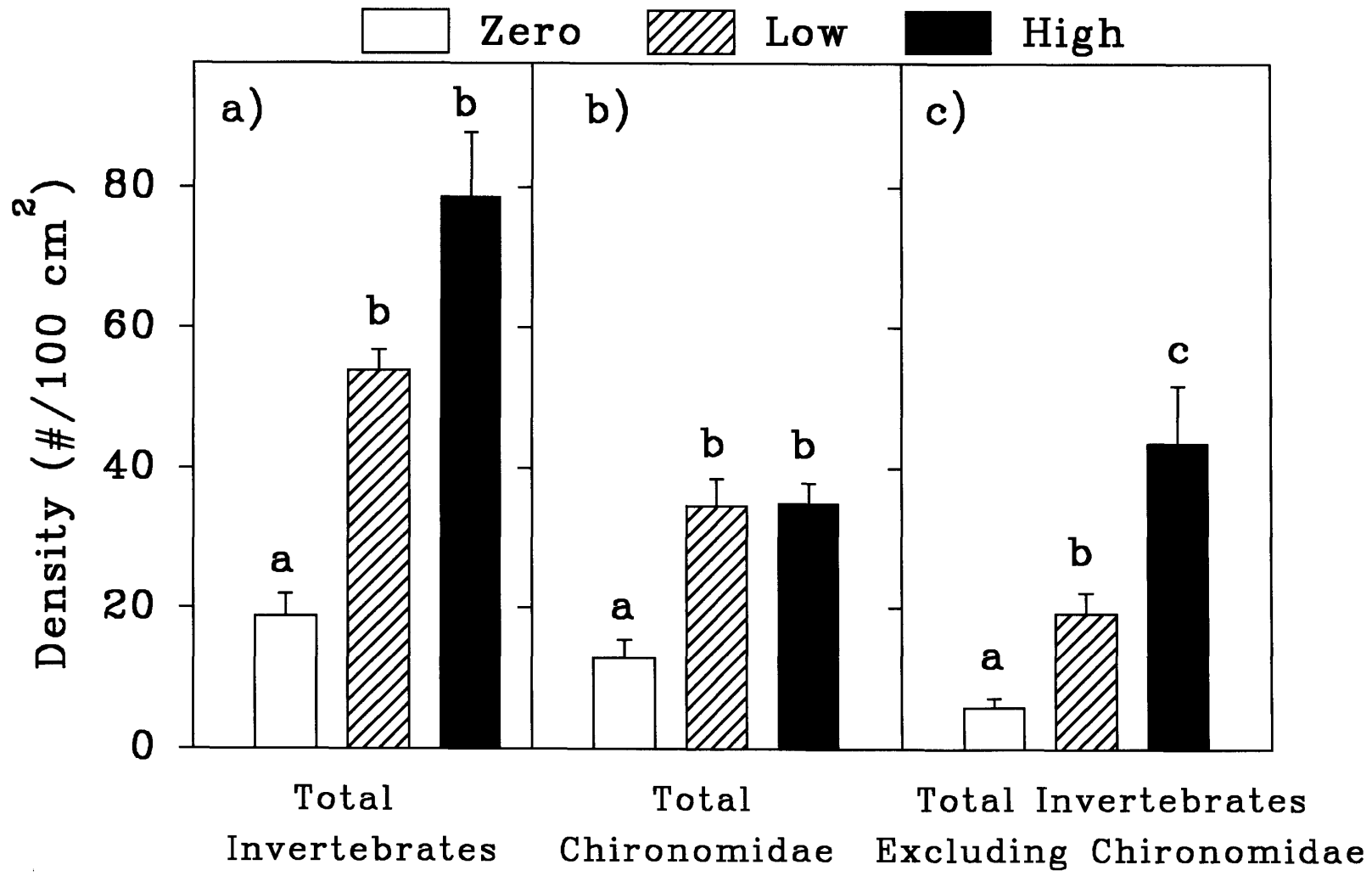


Figure 2 Invertebrate responses to zebra mussel densities (mean  $\pm$  SE). Bars with different letters are significantly different from each other ( $p < 0.05$ ).



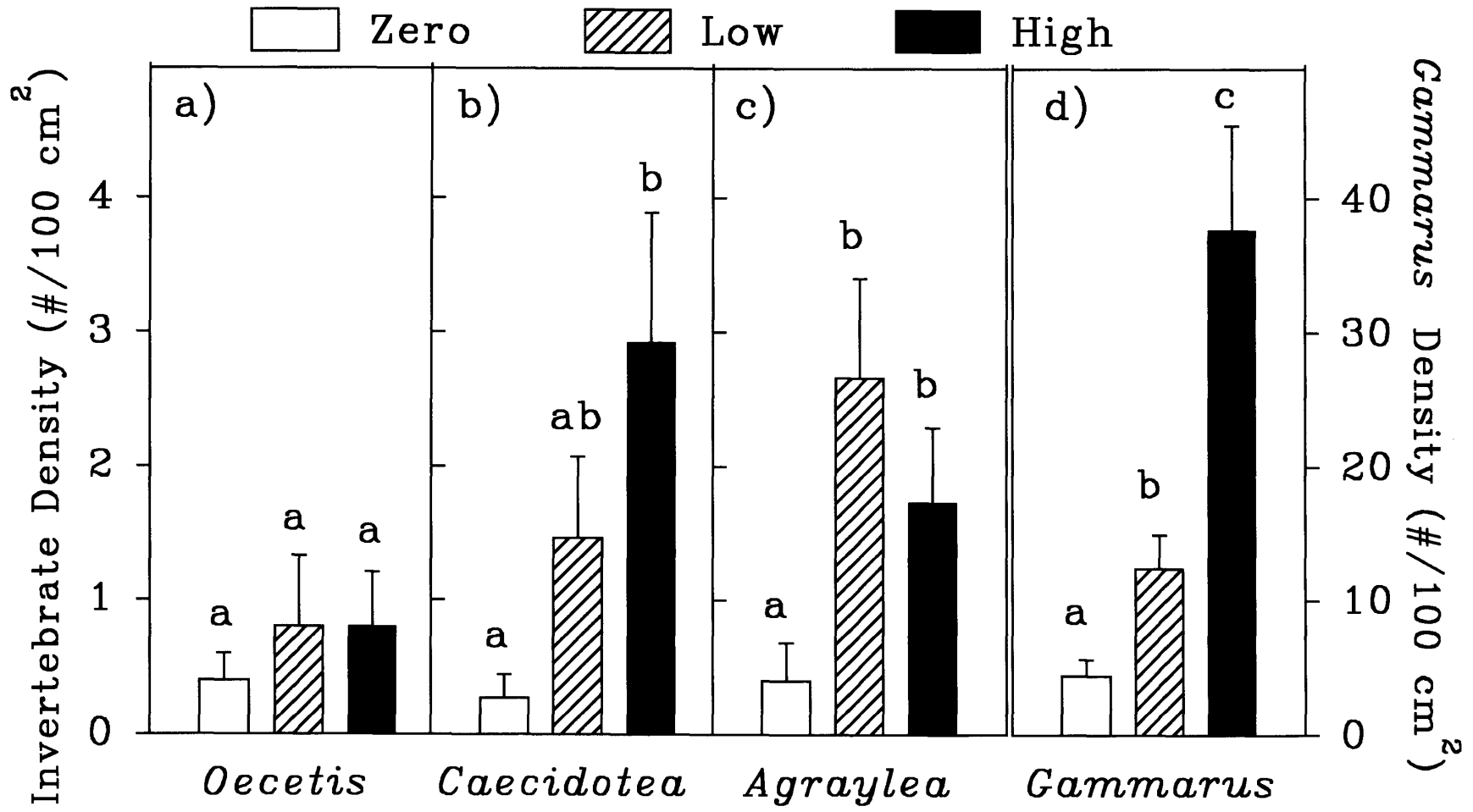


Figure 3 (a) Non-mussel invertebrate responses to goby predation (mean  $\pm$  SE), (b) Chironomid responses to goby predation (mean  $\pm$  SE), and (c) Total non-mussel invertebrate responses, excluding chironomids, to goby predation (mean  $\pm$  SE). Bars with different letters are significantly different from each other ( $p < 0.05$ ).

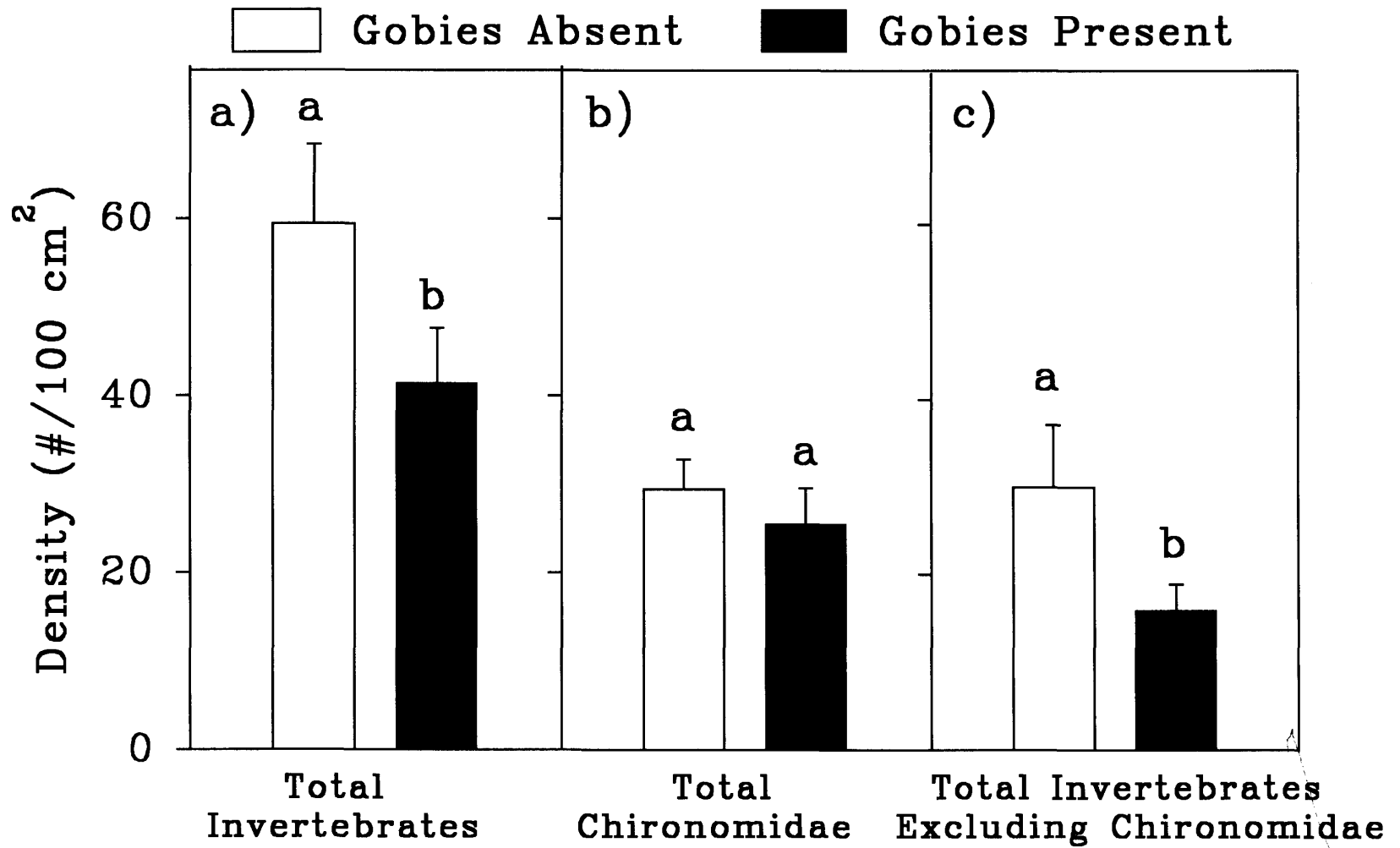


Figure 4 Invertebrate responses to goby predation (mean  $\pm$  SE). Bars with different letters are significantly different from each other ( $p < 0.05$ ).

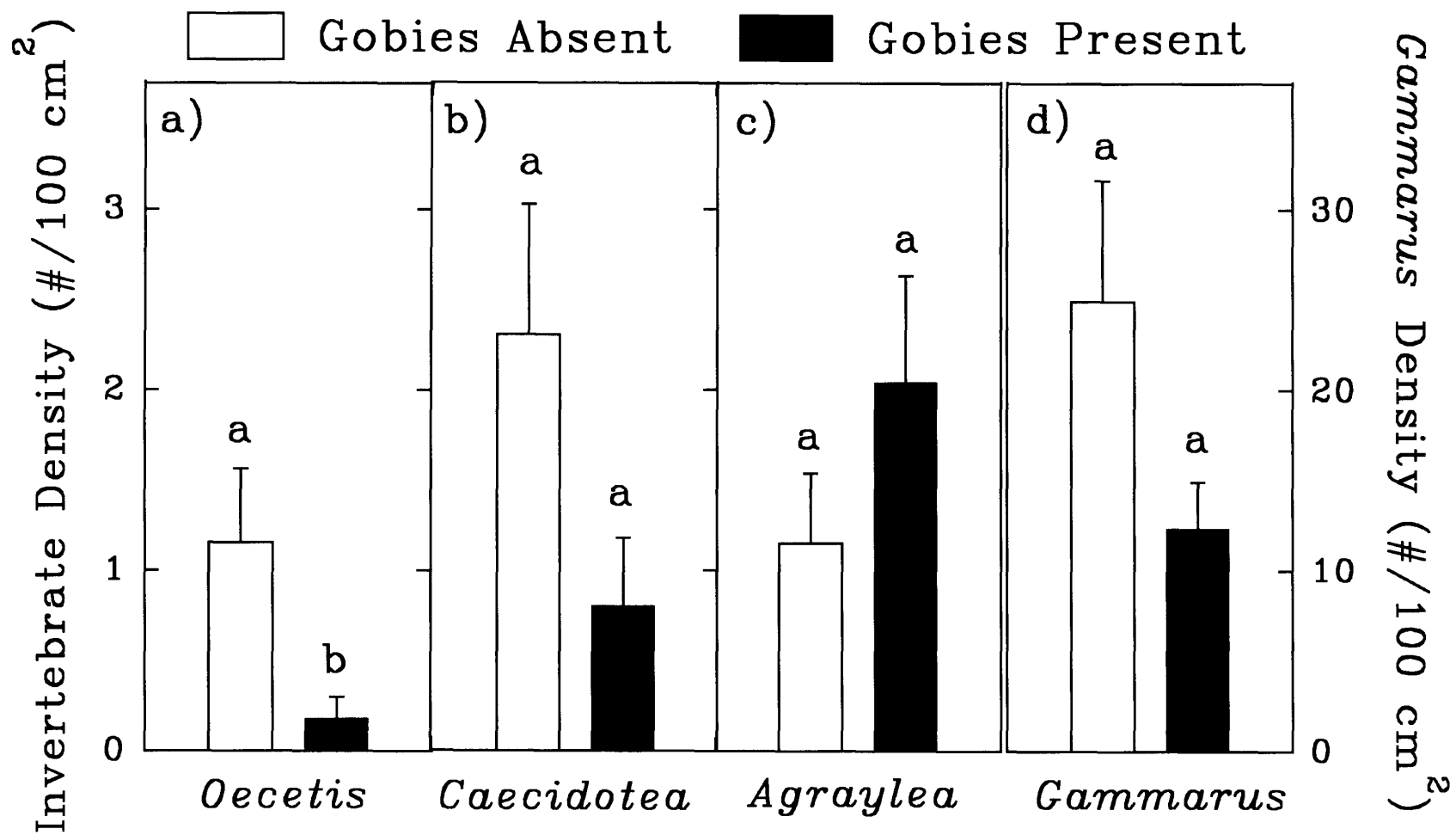


Figure 5 Benthic chlorophyll a responses to (a) Zebra mussel density and (b) Goby presence (mean  $\pm$  SE). Bars with different letters are significantly different from each other ( $p < 0.05$ ).

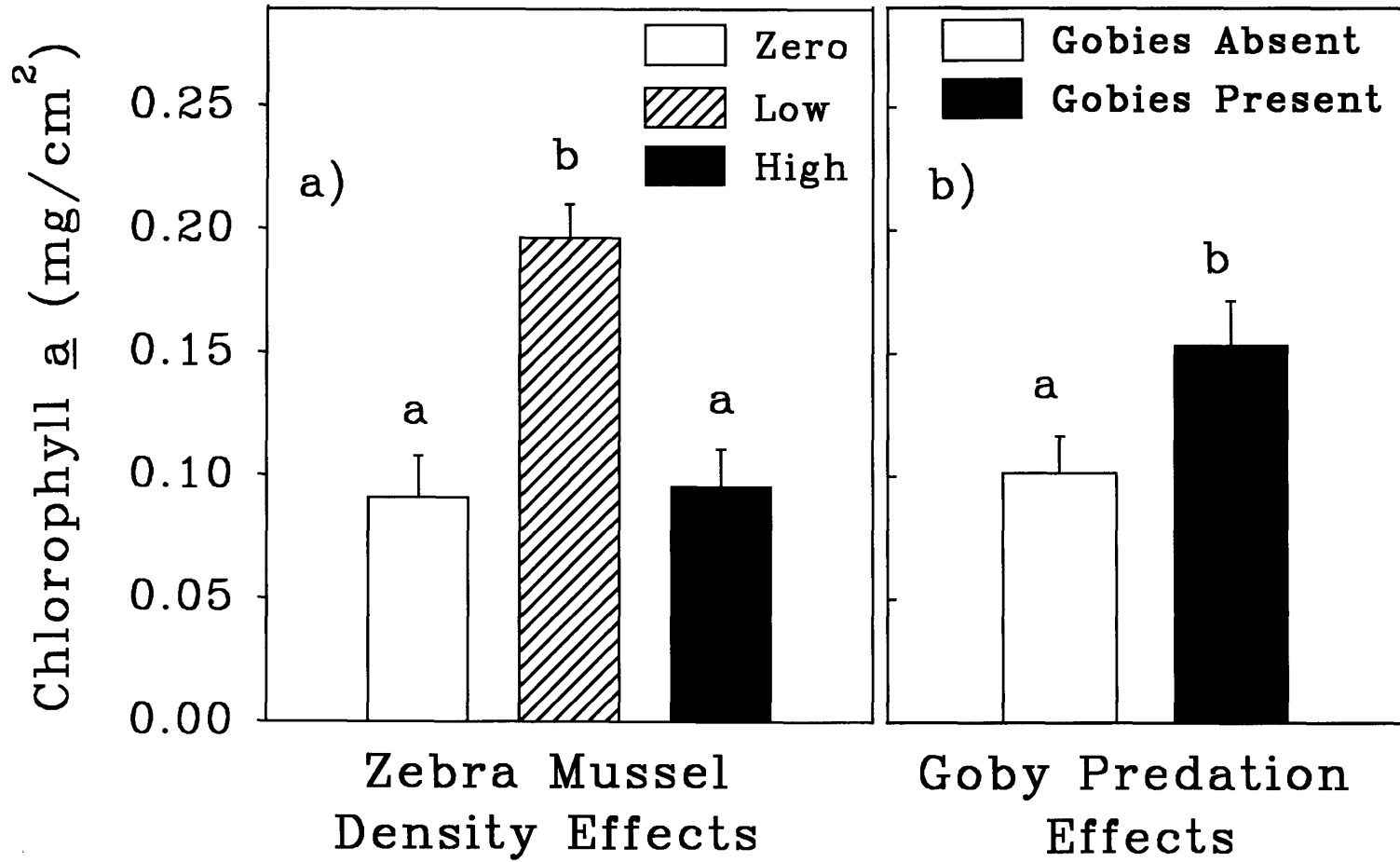


Figure 6 Relationship between zebra mussel density and goby predation on total invertebrate biomass (mean  $\pm$  SE).



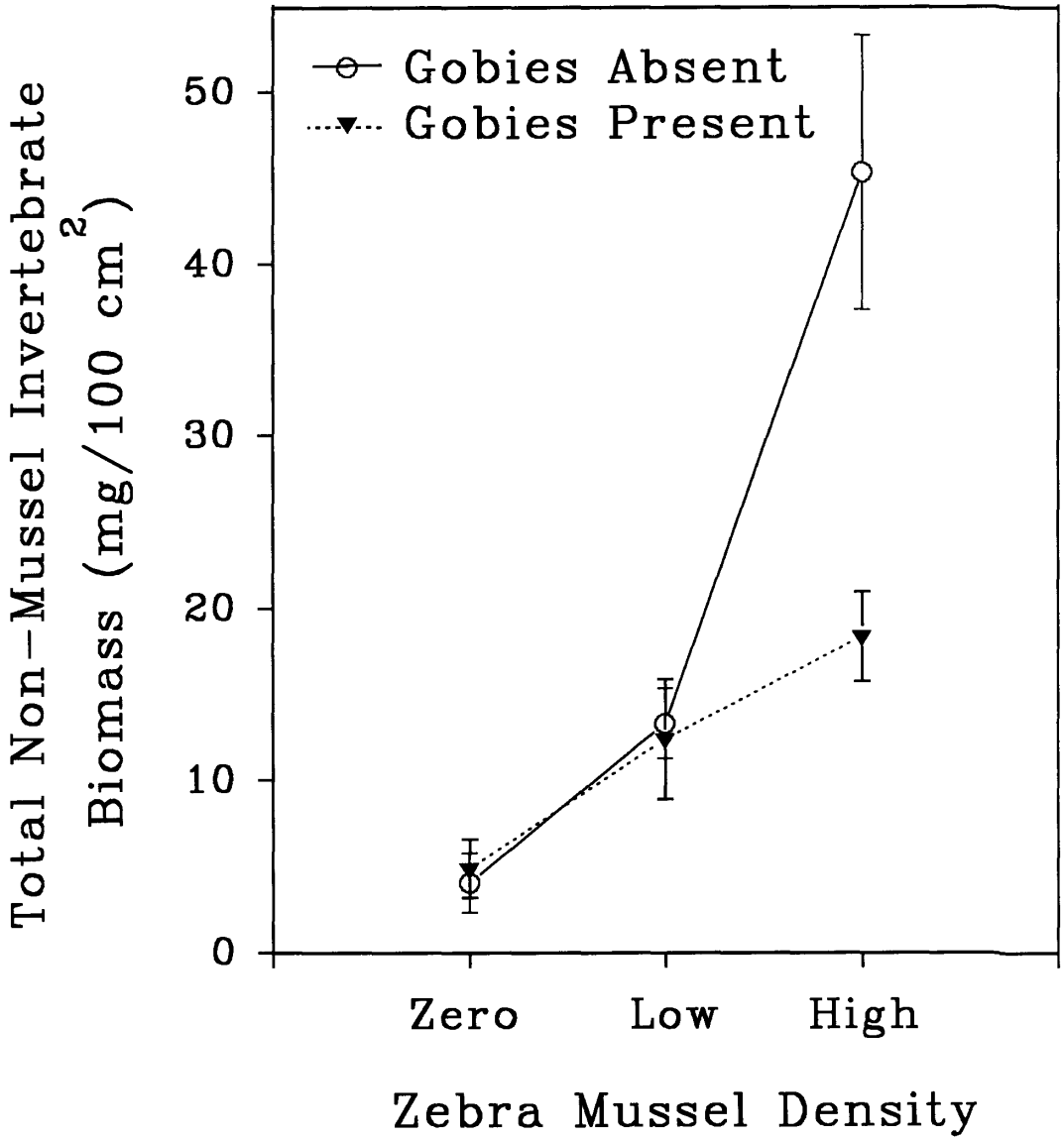
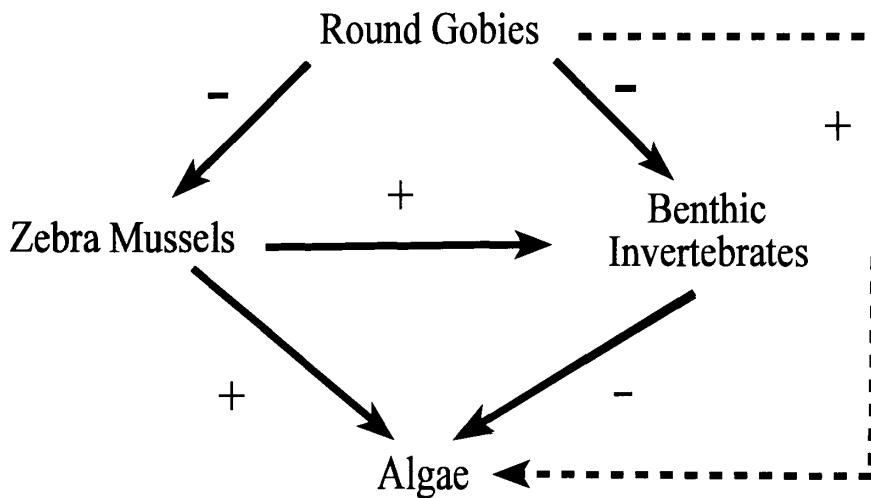


Figure 7 Conceptual diagram of interactions in nearshore, littoral zone, benthic communities in southwestern Lake Michigan. Direct interactions are indicated by a solid line, indirect interactions are indicated by a dotted line. Direction of arrows indicate the direction of interaction. A positive effect is indicated by a +, a negative effect is indicated by a -.



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The thesis is therefore accepted in partial fulfillment of the requirements for the degree of Master of Science.

11/27/96  
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