

Benthic invertebrate food selectivity in northern Lake Michigan following the invasion of
dreissenid mussels (*Dreissena polymorpha* and *D. bugensis*)

A Senior Honors Thesis

Presented in Partial Fulfillment of the Requirements for graduation with distinction in
Evolution and Ecology in the undergraduate colleges of The Ohio State University

By

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June 2005

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Introduction

Exotic species have plagued the Laurentian Great Lakes in recent decades (Mills et al. 1993). Perhaps the most successful invaders are dreissenid mussels, *Dreissena polymorpha* and *D. bugensis*. Since their introduction via ballast water in Lake St. Clair in 1988 (Herbert et al. 1989), dreissenids have successfully colonized hard substrata throughout the Great Lakes and most eastern waters of North America (Griffiths et al. 1991, Johnson and Carlton 1996). High densities of 1,000-45,000 individuals m⁻² (Hebert et al. 1991, Lowe and Pillsbury 1995) and high filtration rates (Fanslow et al. 1995, but also see Yu and Culver 1999) have dramatically altered invaded ecosystems. The most apparent, large-scale effects of dreissenid invasion include: (i) decreased phytoplankton density (Holland 1993, Leach 1993, Nicholls and Hopkins 1993, Fahnenstiel 1995b, MacIsaac 1996, Caraco et al. 1997); (ii) increased water clarity (Hebert et al. 1991, Leach 1993, Fahnenstiel 1995a), and therefore an increased size of the littoral zone (Lowe and Pillsbury 1995); and (iii) increased nutrient availability to the benthos from feces and pseudofeces deposited by dreissenids (Griffiths 1993, Lowe and Pillsbury 1995).

Thus, the dreissenid mussel invasion changed the spatial allocation of resources from pelagic to benthic regions. Greater light transparency and nutrient enrichment on the benthos from dreissenid fecal material has facilitated a dramatic increase in benthic algal productivity in the littoral zone (Lowe and Pillsbury 1995). Not only has post-invasion benthic primary productivity increased, but the benthic algal community has also shifted from tychoplanktonic diatoms to periphytic diatoms and filamentous green algae (Zygnematales and Siphonocladales) with associated epiphytes (Lowe and

Pillsbury 1995, Pillsbury et al. 2002, Carter and Lowe, unpublished data). The abundant benthic algae, dense clumps of dreissenids, and nutrient-rich organic matter have increased the structural complexity of benthic habitats, and initially promoted increases in the density, biomass, and species diversity of benthic macroinvertebrates (Dermott et al. 1993, Griffiths 1993, Stewart and Haynes 1994, Stewart et al. 1998a, Stewart et al. 1998b).

The dreissenid invasion has thus created a novel benthic habitat in the littoral zones of the Great Lakes. Several investigations have examined changes in the composition and productivity of the new benthic algal community (Lowe and Pillsbury 1995, Pillsbury et al. 2002, Carter and Lowe, unpublished data), while other investigations have documented the effects of dreissenid invasion on benthic invertebrate communities (e.g. Griffiths 1993, Stewart et al. 1998b, Haynes et al. 2005). However, the interaction between the algal and invertebrate communities has been largely ignored. Understanding the relationship between these two trophic levels is critical in understanding the long-term effects of dreissenid invasion on the ecosystem dynamics of the Great Lakes.

This study focused on the interaction between the new benthic algal community and invertebrate grazers. The objective of this study was to examine whether grazers are exploiting the new benthic algal food source. Specifically, I hypothesize that invertebrates have shifted their dietary habits to accommodate this dreissenid-mediated benthic algal resource.

Materials and Methods

Study Site

The study site was off the western coast of Skillagalee Island (Latitude: 45° 40' 37.9199" N, Longitude: 85° 10' 17.7600" W), located 11 km northwest of Cross Village, Michigan in northern Lake Michigan (Fig. 1). The location of this off-shore, uninhabited site minimized the effects of human disturbances. The benthic habitat, approximately 200 m from the island, consisted of patches of large rocks and cobble that are ideal for dreissenid mussel colonization. Firmly and loosely attached filamentous green algae and dense clusters of dreissenids covered the rocky substrata.

Collection

Seven rocks between 11-20 cm in diameter were collected by SCUBA at a depth of 5 m below the water surface. Rocks were collected by placing a one gallon Zip-Lock® plastic bag over the rock, lifting the rock from the bottom, and closing the bag as the rock was lifted. This method allowed the collection of associated dreissenids, algae, and invertebrates on each rock while minimizing any loss of organisms. Bags were brought to the surface and placed in coolers for transport to the laboratory.

At the laboratory, each rock was initially placed in an aerated 10-gallon aquarium filled with distilled water to perform a manipulative experiment, but this plan was subsequently abandoned. After approximately 24 hours, each rock was placed in a metal dissecting pan and the dreissenids, macroinvertebrates, and algae were removed with a razor blade. Scraped contents were separated into groups of dreissenids, algae,

amphipods, isopods, chironomids, and gastropods. As a quality control measure, each pan was sequentially examined by a minimum of three people to ensure adequate removal of all organisms.

Algae

The separated algal community of each rock was placed in a mason jar and approximately 1-3 mL of 50% glutaraldehyde solution was added to preserve all algal cells. Algal samples were settled for a minimum of 4 days and then concentrated by siphoning out supernatant water. The algal samples were then homogenized by blending for 15 s in a kitchen blender. The algal community of each rock was enumerated using a Palmer-Maloney nanoplankton counting chamber on an Olympus BX-51 light microscope at 400X. Based on random fields of view, a minimum of 300 cells were counted and grouped based on different valve morphologies. 50 mL of the homogenized algal slurry was placed in a 1 L beaker and chemically oxidized with 100 mL of nitric acid. The remaining diatom valves and nitric acid suspension was diluted with approximately 900 mL of distilled water and then decanted after allowing the valves to settle on the bottom for at least 24 hours. This dilute-decant procedure was repeated at least 2 more times. Samples were air dried on #1 22 mm² cover slips and mounted on microscope slides with Naphrax® mounting medium. A minimum of 600 diatom valves were counted and identified from each rock sample. The cleaned valves were identified to species based on the proportions of different morphological groups from the live counts, using Prescott (1962, 1978), Krammer and Lange-Bertalot (1986, 1991a, 1991b), and Krammer (1997a, 1997b, 2002) as taxonomic guides. Algal biovolumes for each

taxon were calculated using average dimensions of each taxon ($n > 6$) and applying the measurements to geometric shapes that approximated the size of each taxon (Hillebrand et al. 1999).

Invertebrates

After sorting and separation from the metal dissecting pans, 0.5-1 mL of 50% glutaraldehyde solution was added to each vial of invertebrates. This immediately euthanized the invertebrates, and preserved all algal cells in their guts. From each rock, 1 gastropod and 3 amphipods, isopods, and chironomids, respectively, were randomly selected for gut analysis. Individuals were identified on a Nikon Type 102 dissecting microscope using Smith (2001) and Merritt and Cummins (1996) as taxonomic guides. Each individual was gently shaken in a petri-dish bath of distilled water for approximately 10 s to remove epizoic algae. The head capsule of chironomids was removed and the gut was extracted with fine forceps along the anterior-posterior axis. The head and legs were removed from amphipods and isopods to facilitate gut removal in the above fashion. Gastropod shells were removed with dissecting scissors and forceps, and the gut was removed. Each gut was placed on a clean microscope slide with approximately 1 mL of distilled water. The gut was then homogenized with forceps and a razor blade. Soft algae were enumerated and identified on an Olympus BH-2 light microscope at 200-400X. The microscope slide was then placed on a hot plate and burned on high heat for a minimum of one hour to burn off all organic matter and leave only cleaned diatom valves. 22 mm² cover slips were then mounted on the slides using Naphrax® mounting medium. All diatoms in the entire gut were counted and identified

to species on Olympus BH-2 and BX-51 light microscopes at 400-1000X using Prescott (1962, 1978), Krammer and Lange-Bertalot (1986, 1991a, 1991b), and Krammer (1997a, 1997b, 2002) as taxonomic guides.

Data analysis

Diatom taxa were grouped together based on their substratum preference (Table 1) (Stoermer 1980). Because filamentous green algae and associated diatom epiphytes dominate the post-invasion benthic algal community, epiphytic diatoms are a robust indicator of grazing on this new food source. Thus, the epiphytic diatom group included *Cocconeis pediculus*, *Diatoma vulgare*, *Rhoicosphenia curvata*, *Gomphoneis herculeana*, and *Gomphonema* spp. (after Rosen et al. 1981, Sheath and Morison 1982, Lowe et al. 1982, Stevenson and Stoermer 1982). Other, non-epiphytic diatoms included epipelagic, epilithic, and tychoplanktonic taxa – forms that were present prior to dreissenid invasion. Accordingly, a group of epipelagic diatoms, *Navicula cryptotenella* and *N. tripunctata* (after Stoermer 1980, Vilbaste and Truu 2003), were grouped together to represent grazing on the traditional, pre-invasion algal community.

Two similarity indices, SIMI (McIntire and Moore 1977) and Simplified Morisita's (Krebs 1989), were used to examine the degree of similarity between gut contents and the algal community. Diatoms were separated into three groups: epiphytic diatoms ("epiphytes", Table 1), all non-epiphytes ("non-epiphytes"), and the entire community (epiphytes + non-epiphytes, "all"). Three comparative tests were conducted using diatom biovolume data. First, the gut community was compared to the epiphyte group to examine the degree of similarity between gut contents and the epiphyte group.

Second, the gut community was compared to the non-epiphyte group to examine the degree of similarity between gut contents and non-epiphytes. Third, the gut community was compared to the entire algal community to examine the degree of similarity between gut contents and the entire algal community. A 3 x 4 matrix was constructed to run the 3 aforementioned tests for each of the 4 invertebrate groups.

T-tests were conducted to compare the relative abundance of the diatom groups in guts and the algal community (Minitab, version 13.2). Abundance data were transformed to biovolume to more accurately represent the three-dimensional space of the benthos. First, the relative biovolume abundance of epiphytic taxa was pooled together for all invertebrates (n=62) and compared to the rock epiphytic data (n=7). More detailed t-tests were then conducted to separately compare each invertebrate taxon (amphipods n=21, isopods n=18, chironomids n=17, gastropods n=6) to the epiphytic data for each rock (n=6 for isopods, chironomids, and gastropods, respectively; n=7 for amphipods). The same t-tests were then calculated as above using the epipelagic diatom group.

Results

Benthic Algal Community

All diatom taxa encountered in this study are listed in Appendix 1. Mean abundance x biovolume data for each species on each rock (n=7) is given to describe the three-dimensional space of the benthos and provide a detailed representation of invertebrate food choices.

Similarity Indices

SIMI and Morisita's similarity indices both indicate that gut contents are most similar to the entire benthic algal community (Table 2). Amphipod gut contents are most similar to the entire algal community, with intermediate similarity to non-epiphytes, and are least similar to the epiphyte complex. Likewise, isopod gut contents are most similar to the entire algal community, exhibit intermediate similarity to non-epiphytes, and are least similar to epiphyte complex. Chironomid gut contents exhibit highest similarity with the entire algal community, intermediate similarity to non-epiphytes, and are least similar to the epiphyte complex. Gastropod gut contents are most similar to the entire algal community, exhibit intermediate similarity with non-epiphytes, and are least similar to the epiphyte complex.

T-tests

The relative abundance of epiphytic diatoms was significantly higher in invertebrate guts than in the benthic algal community ($p = 0.04$, Fig. 2). More detailed analysis of the individual invertebrate taxa revealed different t-test results (Fig. 3). Each invertebrate taxon contained a greater proportion of epiphytes in their guts compared to the community, and the isopod content of epiphytes was statistically significant ($p = 0.012$).

Epipellic diatom consumption by the entire invertebrate community was significantly higher compared to the availability in the benthic algal community ($p = 0.39$, Fig. 4). T-tests by separate invertebrate taxon indicated that each taxon contained a greater proportion of epipellic diatoms in their guts compared to the community (Fig. 5), and isopod epipellic consumption was statistically significant ($p = 0.016$).

Discussion

Selectivity or electivity of a resource can be an arbitrary term. In this study, selectivity is defined as the consumption of a food resource in a greater proportion than it occurs in the environment (Botts and Cowell 1992).

The results indicate that benthic invertebrates, as a whole, are opportunistically grazing on available benthic diatoms, both epiphytic and epipellic. The indices of community similarity show a strong degree of similarity between the entire benthic diatom community and the composition of invertebrate guts. The relatively high similarity between guts and non-epiphytes, and low similarity between guts and epiphytes, suggests that invertebrates are opportunistically ingesting all available diatoms. Because both SIMI and Morisita's indices yielded similar results, this contention is extremely robust.

The t-test results provide a more detailed analysis of invertebrate grazing. Collectively, invertebrates appear to selectively ingest epiphytic diatoms (Fig. 2). Though statistically significant, more detailed analysis by invertebrate group indicates that not all invertebrate taxa are significantly selecting epiphytes (Fig. 3). While only isopod grazing is statistically significant, it is worth noting that the relative abundance of epiphytes was 2- to 4-fold greater in invertebrate guts compared to the benthic diatom community. This suggests that each invertebrate taxon may selectively graze on at least a biologically significant amount of epiphytes.

Like epiphytic diatoms, epipellic diatoms appear to be significantly selected by invertebrates as a group (Fig. 4). Analysis by invertebrate taxon shows that, again, only isopod selectivity is statistically significant. Similarly, the other invertebrate groups ingested a greater proportion of epipellics than occur in the benthic diatom community, although the difference is smaller (1- to 3-fold) compared to epiphytes. This still represents a biologically significant selectivity of epipellic diatoms.

Grazer-periphyton interactions are complex and highly dependent on numerous factors, including grazer mouthpart morphology (Feminella and Resh 1991, Pan and Lowe 1994, Merritt and Cummins 1996) and taxonomy (Merritt and Cummins 1996), and also periphyton particle size (McLachlan et al. 1978, Moore 1979, Botts and Cowell 1992), physiognomy (Lowe and Hunter 1988, Steinman 1996) and composition (Gresens and Lowe 1994, Steinman 1996). Although the present study failed to incorporate several of the aforementioned factors, it did include periphyton physiognomy and composition, and also grazer taxonomy, although at an admittedly coarse level. Thus, caution must be exercised when drawing general conclusions from this study.

In spatiotemporally immense systems such as the Great Lakes, the behavioral mobility of grazers may be more important than in lotic systems, where abiotic factors (e.g. flow, substratum) continually change and play a larger role in structuring communities. Accordingly, the present findings may be explained in terms of the behavioral mobility of invertebrate taxa. Chironomids and gastropods are restricted to the substratum, and amphipods swim just above the substratum and also borrow into loose sediment to avoid light (Smith 2001). In contrast, isopods have a much greater crawling ability and can move up the vertical axis of *Cladophora* filaments (R.L. Lowe,

personal observations). This suggests that isopods can more easily exploit the new epiphytic food resource better than other invertebrates. Their superior crawling ability may also enable them to easily switch from epipellic to epiphytic resources, and vice-versa.

The more restricted mobility of chironomids, gastropods, and amphipods may explain their reduced selectivity of epiphytes relative to isopods. Their biologically significant ingestion of epiphytes may result from grazing lower on *Cladophora* filaments, on and just above the holdfast, and also on senescent filaments that have settled on the benthos.

All invertebrates appear to have shifted their diets to take advantage of the new epiphytic food source. Concomitantly, they have not abandoned their traditional epipellic food source, even though epipellic diatoms have dramatically declined and been replaced by filamentous Chlorophytes since dreissenid invasion (Lowe and Pillsbury 1995, Pillsbury et al. 2002). Selectivity of epipellics may be a new phenomenon resulting from a reluctance or inability of invertebrates to abandon traditional food resources. Unfortunately, pre-invasion data on grazer food preferences in the Great Lakes is not available to test this hypothesis.

The present study elucidates an important but unknown component of the dreissenid mussel story. Numerous investigations have focused on how the dreissenid invasion has impacted benthic invertebrate communities in the Great Lakes. After the invasion, nearshore invertebrate communities experienced increases in abundance (Dermott et al. 1993, Griffiths 1993, Stewart and Haynes 1994, Gonzales and Downing 1999, Stewart et al. 1998a), biomass (Stewart et al. 1998a, 1998b), and species richness

(Griffiths 1993, Stewart et al. 1998b), which was followed by a return to pre-invasion levels (Haynes et al. 2005). However, investigators attributed this resilience to increased habitat complexity from dreissenid shells (Dermott et al. 1993, Griffiths 1993, Stewart and Haynes 1994, Gonzales and Downing 1999, Stewart et al. 1998a, 1998b) increased nutrient availability (Stewart and Haynes 1994, Stewart et al. 1998a, 1998b), and a shift from *Dreissena polymorpha* to *D. bugensis* dominance (Haynes et al. 2005).

Furthermore, these investigations have not implicated the causal mechanism for benthic invertebrate success. The present study suggests that a shift in invertebrate dietary habit may be responsible for continued benthic invertebrate success. Specifically, the ability of grazers to exploit the new epiphytic food resource may be the causal mechanism that explains why benthic invertebrates have been so resilient since the dreissenid invasion.

Further investigation of grazer-periphyton interactions in this system may more clearly elucidate how invertebrates use the new epiphytic food resource. Replicated mesocosms of epiphytized *Cladophora* subjected to different grazer treatments (e.g. amphipod, isopod, chironomid, gastropod, all, none) could detect invertebrate competition for benthic food resources. Also, a Y-maze with an epiphytic monoculture (e.g. *Cocconeis pediculus*) on one branch and an epipelagic monoculture (e.g. *Navicula tripunctata*) on the other may reveal grazer preferences for different diatom taxa. Such studies may also indicate food preference based on diatom size, morphology and nutrition. Further, crustaceans possess highly developed chemosensory systems (Ache 1982, Atema 1988, and Zimmer-Faust 1989, cf. Covich and Thorp 2001), and amphipods and isopods may be able to differentiate between different diatom taxa based on nutritional content. A finer taxonomic resolution of invertebrate taxa may also be

necessary, as much intra-taxon variation in feeding group and mouthpart morphology exists, especially in chironomids (Merritt and Cummins 1996).

In summary, this study has shown that grazers have shifted their dietary habits to utilize the new, dreissenid-mediated benthic algal community in the Great Lakes. This dietary shift is a possible causal mechanism that explains how benthic invertebrates have been so resilient since the dreissenid mussel invasion.

Acknowledgements

This project was supported by research fellowships to T. Bambakidis and Linda N. Novitski from the University of Michigan Biological Station and the Nature Conservancy, and also an Ohio State University College of Biological Sciences undergraduate research grant to T. Bambakidis. I wish to thank the University of Michigan Biological Station, the Snow lab at Ohio State University, and the Lowe lab at Bowling Green State University for laboratory facilities; Peter S. Curtis for helpful advice and logistical support; Jay F. Martin for serving on my committee; Dave Smith, our boat captain; Paula Furey and Art Martin for SCUBA; and P. Furey and Jessica Knapp for thoughtful input and for reviewing earlier versions of this manuscript. This project would not have been possible without the following individuals: Linda N. Novitski, for helping with experimental design and implementation, generating much of the community data, and patiently helping with all aspects of this project; Rex L. Lowe, for sparking and facilitating my interest in algal ecology with his contagious enthusiasm and endless encouragement; and my parents, Anna and Peter, for their love and support in all of my educational endeavors, without whom none of this would have been possible.

TABLE 1. Diatom groups used in data analysis. Groups are based on substratum preference.

Epiphytic Taxa
<i>Diatoma vulgare</i>
<i>Cocconeis pediculus</i>
<i>Gomphonema</i> sp. 1
<i>Gomphoneis herculeana</i>
<i>Gomphonema olivaceum</i> complex
<i>Gomphonema pumulum</i> complex
<i>Rhiocosphenia curvata</i>

Epipellic Taxa
<i>Navicula cryptonenlla</i>
<i>Navicula tripunctata</i>

TABLE 2. SIMI and Simplified Morisita's (MOR) community similarity values comparing gut contents to epiphytes, non-epiphytes, and the entire algal community. Values range from 0 (completely dissimilar) to 1 (completely similar). Calculations based on mean biovolume data.

Comparison	Amphipod		Isopod		Chironomid		Gastropod	
	SIMI	MOR	SIMI	MOR	SIMI	MOR	SIMI	MOR
Gut vs. Epiphytes	0.089	0.087	0.144	0.144	0.314	0.313	0.510	0.463
Gut vs. Non-Epiphytes	0.905	0.812	0.963	0.888	0.947	0.925	0.672	0.524
Gut vs. All	0.908	0.832	0.968	0.912	0.960	0.949	0.695	0.562

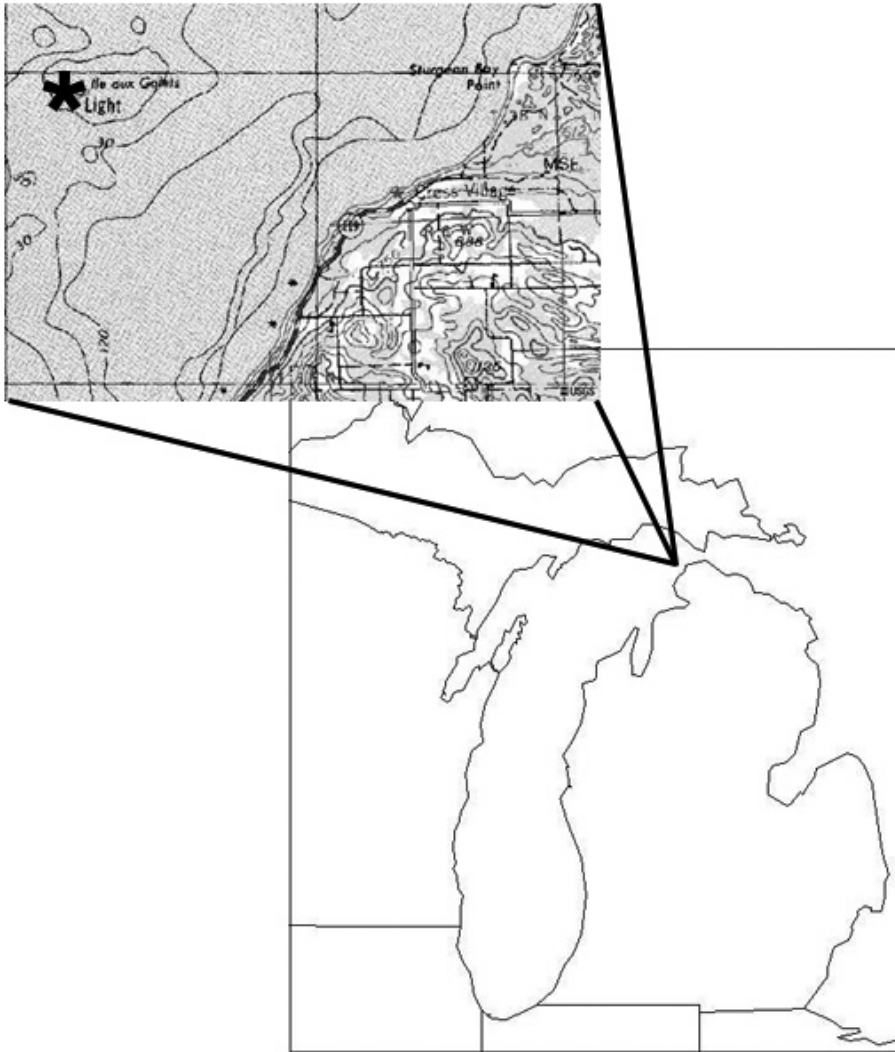


FIG. 1. Location of the study site in northern Lake Michigan.

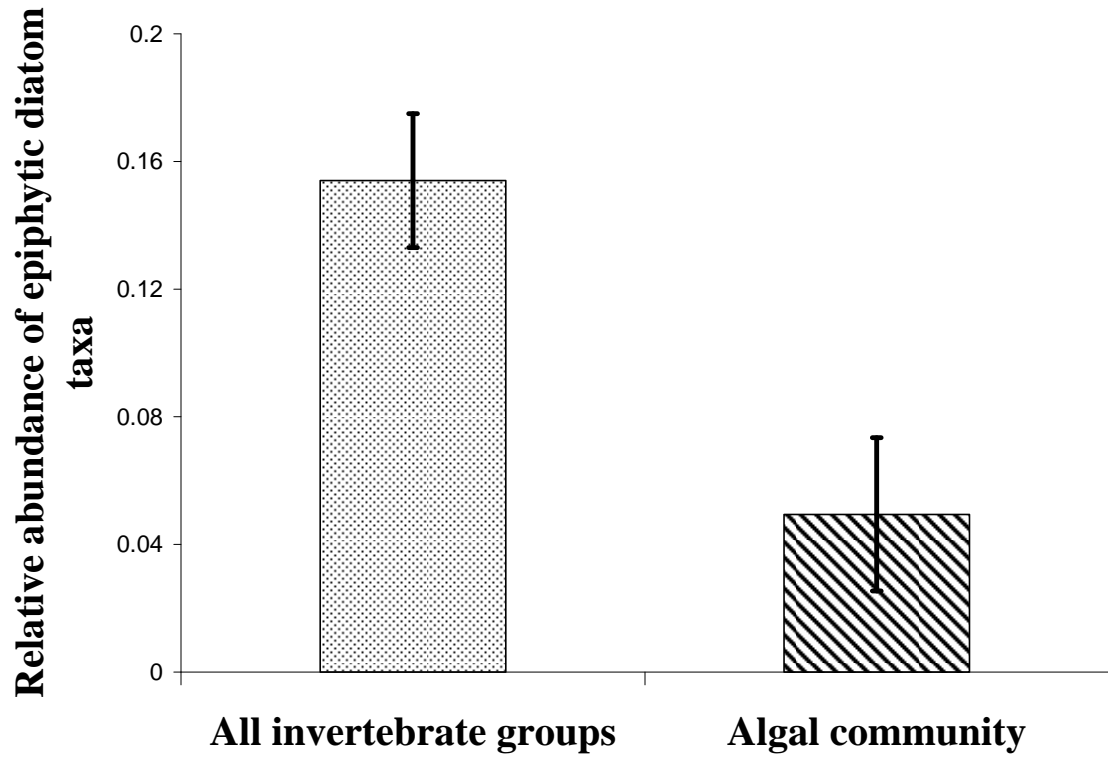


FIG. 2. Mean (\pm SE) relative abundance of epiphytic diatoms in all invertebrate guts and the benthic algal community. Calculations based on biovolume. $p = 0.004$.

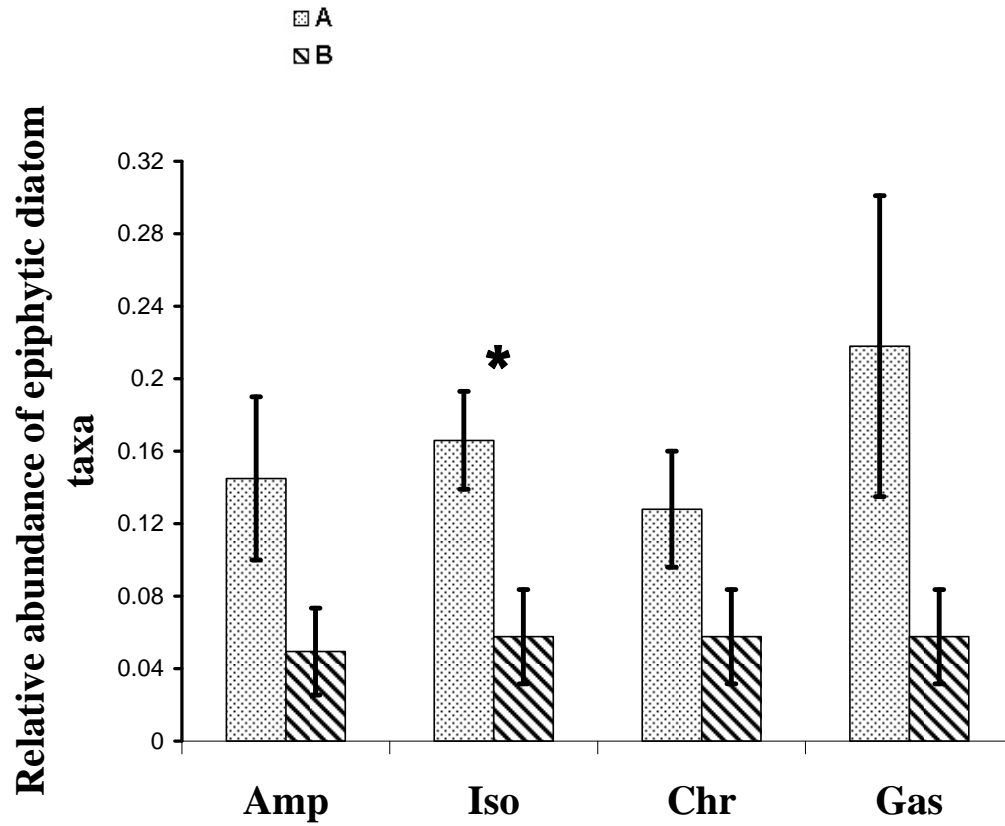


FIG. 3. Mean (\pm SE) relative abundance of epiphytic diatoms in different invertebrate guts (A) and the benthic algal community (B). Calculations based on biovolume. Asterisk denotes statistical significance. Amp = amphipods, Iso = isopods, Chr = chironomids, and Gas = gastropods.

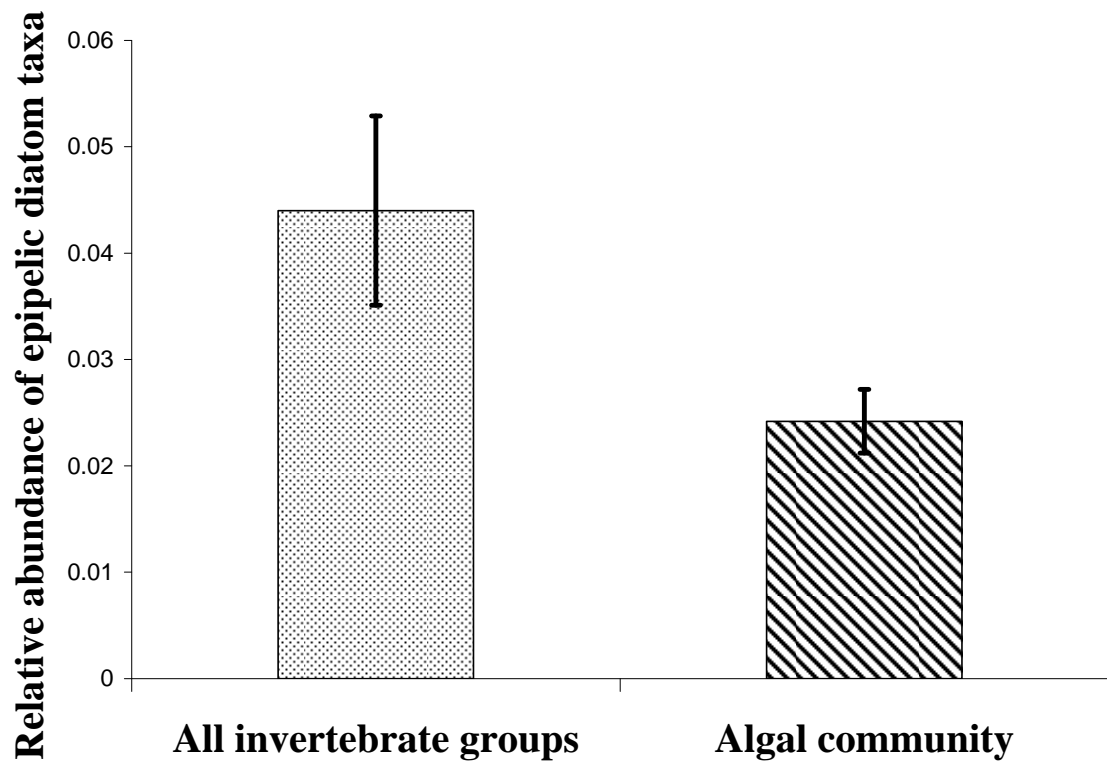


FIG. 4. Mean (\pm SE) relative abundance of epipellic diatoms in all invertebrate guts and the benthic algal community. Calculations based on biovolume. $p = 0.039$.

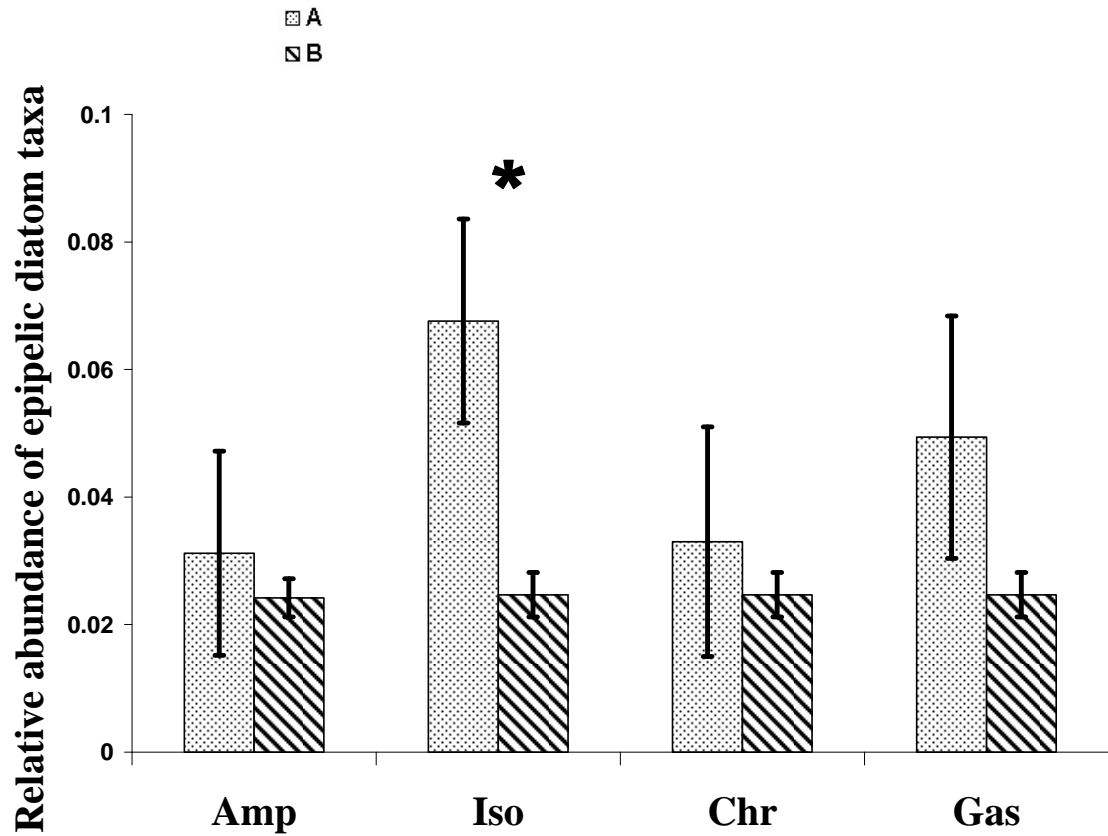


FIG. 5. Mean (\pm SE) relative abundance of epipellic diatoms in different invertebrate guts (A) and the benthic algal community (B). Calculations based on biovolume. Asterisk denotes statistical significance. Abbreviations as in Fig. 3.

APPENDIX 1. Diatom taxa encountered from the benthos and invertebrate guts of northern Lake Michigan. Mean abundance x biovolume values on the rocks (n=7) are given in the right column. Species complexes were created for closely related or indistinguishable taxa.

Centrics	Mean biovolume (μm^3)
<i>Aulacoseira</i> sp.	28.72
<i>Cyclotella meneghiniana</i> Kütz.	8.68
<i>Cyclotella</i> aff. <i>praetermissa</i> Lund	72.71
<i>Cyclotella ocellata</i> Pant.	1302.88
<i>Stephanodiscus rotula</i> (Kütz.) Hendey	28.72
Araphids	
<i>Asterionella formosa</i> Hass.	346.90
<i>Diatoma mesodon</i> (Ehrenb.) Kütz.	94.25
<i>Diatoma tenuis</i> Agardh.	1283.17
<i>Diatoma vulgare</i> Bory	2712.33
<i>Fragilaria capucina</i> Desm.	253373.32
<i>Staurosirella pinnata</i> (Ehrenb.) D.M. Williams & Round	118.15
<i>Nitzschia palea</i> (Kütz.) W.Sm.	953.30
<i>Synedra ulna</i> (Nitzsch.) Ehrenb.	2967.00
<i>Tabellaria flocculosa</i> (Roth) Kütz.	714.17
Monoraphids	
<i>Cocconeis neodiminuta</i> Krammer	60.96
<i>Cocconeis pediculus</i> Ehrenb.	2429.83
<i>Cocconeis placentula</i> Ehrenb.	819.96
<i>Achnantheidium minutissimum</i> (Kütz.) Czarn.	3297.22
Biraphids	
<i>Amphora inariensis</i> Krammer	1338.72
<i>Amphora pediculul</i> s (Kütz.) Grunow	325.39
<i>Cymbella excisa</i> Kütz.	2420.24
<i>Cymbella</i> sp. 1	239.03
<i>Cymbella lange-bertalotii</i> complex	10547.96
<i>C. lange-bertalotii</i> nov. spec	
<i>C. helvetica</i> Kütz.	
<i>C. compacta</i> Østrup	
<i>C. sp. aff. mexicana</i> (Ehrenb.) Cleve	
<i>Encyonema prostratum</i> complex	4678.47
<i>E. prostratum</i> (Berk.) Kütz.	
<i>E. cespitosum</i> Kütz.	
<i>E. silesiacum</i> (Bleisch ex Rabenh.) D.G.Mann	
<i>Encyonemopsis microcephala</i> complex	1413.49

<i>E. microcephala</i> Grunow	
<i>E. minuta</i> Krammer & Reichardt	
<i>E. subminuta</i> Krammer & Reichardt	
<i>Navicula minusculoides</i> Hustedt	
<i>Encyonema minutum</i> (Hilse ex Rabenh.) D.G.Mann	172.21
<i>Epithemia</i> sp.	0 ^a
<i>Eunotia paludosa</i> Grunow	8.10
<i>Eunotia</i> sp. aff. <i>bilunaris</i> Ehrenb.	6.95
<i>Gomphonema</i> sp. 1	196.24
<i>Gomphonema olivaceum</i> complex	3656.80
<i>G. olivaceum</i> (Lyngb.) Kütz	
<i>G. truncatum</i> Ehrenb.	
<i>Gomphonema pumuilum</i> complex	1004.48
<i>G. pumilum</i> (Grunow) Reichardt	
<i>G. sp. aff. pumilum</i> (Grunow) Reichardt	
<i>G. occultum</i> Reichardt & Lange-Bertalot	
<i>Gomphoneis herculeana</i> (Ehrenb.) Cleve	9346.69
<i>Navicula clementis</i> Grunow	72.56
<i>Navicula cryptonenlla</i> Lange-Bertalot	3615.52
<i>Navicula tripunctata</i> (O.F.Müll.) Bory	3972.75
<i>Rhiocosphenia curvata</i> (Kütz.) Grunow	224.79

^a Species not found in the benthic community, but in invertebrate guts.

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