

# Habitat or Food? The Demise of the Benthic Food Web in Lake Michigan (GLFT 2008.960)

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## ACKNOWLEDGEMENTS

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We thank Dennis Donahue of NOAA's Lake Michigan Field Station and the crew of the R/V *Laurentian* for their help and support of our research cruise. We thank Thomas Nalepa (NOAA-GLERL) for providing *Diporeia* collections, historical animal densities, interpretation, and manuscript preparation. We thank Will Daniels (Science Museum of Minnesota) and Kim Greene and James Hart (University of Michigan) for their help in the lab and aboard the research ship. Shawn Schottler, Dan Engstrom, Erin Mortenson, and Alaina Fedie (Science Museum of Minnesota) are thanked for their help with core dating, sediment mixing models, and geochemistry, Joy Ramstack and Rebecca Bixby for statistical analysis, and Norman Andresen for assistance with diatom analysis. This project received funding from the Great Lakes Fishery Trust (Project 2008.960) and we gratefully acknowledge that support.

## PROJECT PROFILE

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### **Synopsis**

**Project Title:** Habitat or Food? The Demise of the Benthic Food Web in Lake Michigan (GLFT 2008.960)

**Grantee Organization:** Science Museum of Minnesota

**Project Team:** Mark Edlund (Science Museum of Minnesota), David Jude (University of Michigan), Thomas Nalepa (NOAA-GLERL), Norman Andresen (Andresen Consulting, Ypsilanti, Michigan), Joy Ramstack Hobbs (Science Museum of Minnesota)

**Contact Person:** Mark Edlund, Science Museum of Minnesota, mbedlund@smm.org

**Grant Amount:** \$148,008

**Time Frame:** 1/1/2009 to 3/31/2011

**Focus Areas:** Food Web, Aquatic Invasive Species

#### **Brief Project Summary:**

There is a strong connection between the disappearance of the benthic invertebrate *Diporeia* and the introduction and spread of zebra and quagga mussels in the Great Lakes. To test whether competition for food resources is the primary cause of *Diporeia* decline, we analyzed gut contents of *Diporeia* collected during spring from 1987-2009 at three stations in Lake Michigan. *Diporeia* was shown to be a highly selective feeder for three large diatom species groups. Analysis of sediment cores documented dramatic shifts in Lake Michigan diatom communities including lower abundance of the preferred food of *Diporeia* after the introduction of dreissenid mussels.

### **Project in Context**

The Great Lakes have been impacted by natural and anthropogenic changes, nutrient loading, atmospheric deposition, climate change, fisheries management, and exotic species introductions. The multiplicative impacts of these stressors are manifested in dramatic shifts in water quality, energy flow, food web dynamics, and fisheries structure. Among the most noted stressors in Lake Michigan has been the establishment of zebra and quagga mussels in the late 1980s-1990s and their subsequent spread throughout the basin. Coincident with establishment of these anchored, filter feeders in the Great Lake have been increases in water clarity, changes in nutrient loading and dynamics, shifting of energy from the pelagic to the benthic zone, colonization of available substrates, creation and colonization of large shell zones, major changes in benthic algal and invertebrate dynamics, botulism outbreaks, and bottom-up fish condition and community shifts. Perhaps the most publicized recent change in the Great Lakes has been decline of the benthic invertebrate *Diporeia* in the Great Lakes, except Lake Superior. *Diporeia* had long been the most abundant benthic macroinvertebrate in the Great Lakes. *Diporeia* is a deposit feeder that once inhabited all of the deeper regions of the Great Lakes comprising over 70% of the deepwater benthic biomass. *Diporeia* served as the benthic-pelagic trophic link in the Great Lakes assimilating over 60% of sedimented carbon, primarily through the ingestion of lipid-rich spring-bloom diatoms. As a result *Diporeia* accumulate abundant lipids and are a primary and preferred fish prey for many deepwater and nearshore fish species including sculpins, lake whitefish, bloater, perch, alewife, and smelt. In Lake Michigan alone, there has been a 94% decline in *Diporeia* between 1995 and 2005. Initial losses were in shallow and nearshore areas, but more recently *Diporeia* numbers have plummeted in the deeper zones of

Lake Michigan, as well as refugial areas. There is obvious correspondence between the decline of *Diporeia* and the invasion and spread of zebra and quagga mussels throughout the Great Lakes (except Superior); however, establishing the mechanistic link between *Diporeia* decline and mussels has been a research challenge. The *Diporeia* decline is widely regarded as resulting from direct competition for food resources following establishment of zebra and quagga mussels; however, no clear mechanism for limitation and conflicting evidence from distributional surveys, laboratory tests, and sediment traps confounds establishing competition and food limitation as the direct link between zebra/quagga mussels and the demise of *Diporeia*.

### ***Goals of the Effort***

Several hypotheses have been forwarded concerning the disappearance of *Diporeia* from southern Lake Michigan and its connection to the introduction and spread of dreissenid mussels (zebra and quagga) throughout the lake. The key research question addressed in this study – the food limitations hypothesis – is whether the quantity and quality of food resources used by *Diporeia* have changed during the spread of dreissenid mussels. To answer this research question, our study used paleolimnological analysis of multiple southern Lake Michigan sediment cores to reconstruct a history of algal food resources from 1960 to 2009 in conjunction with gut content analysis of historical *Diporeia* collections made between 1987 and 2009, covering the pre-dreissenid, post-dreissenid, and period of rapid colonization of the deepwater sediments by quagga mussels.

### ***Results***

This project analyzed, first, the dietary preference of *Diporeia* collected in Lake Michigan from 1987-2009, and second, the changes in food resources from 1960-2009 available to *Diporeia* based on analysis of algal remains in sediment cores. In contrast to previous research that did not specially prepare guts for microscopical analysis, we found that *Diporeia* were very selective in their spring diets and showed high preference for three large-sized diatom species groups that have been historically common in winter and spring plankton of Lake Michigan: *Aulacoseira islandica*, *A. subarctica*, and large *Stephanodiscus*. Sediment core analysis corroborated what gut analysis showed; that these three highly preferred diatom groups have become less abundant in Lake Michigan during the demise of *Diporeia*. Small increases in biogenic silica deposition may suggest minor increases in quantity of food reaching the sediments, but any increase has primarily been a consequence of increased numbers of low quality and negatively preferred planktonic araphids and small-sized *Cyclotella* and *Stephanodiscus* spp. reaching the sediments.

### ***Significance***

This is the first study that has combined paleolimnological techniques with gut content analysis to disentangle the mechanism of food limitation during the demise of *Diporeia* in southern Lake Michigan. The preferred prey items of *Diporeia* have continued to decrease in relative abundance, while selectivity for them has increased over time as *Diporeia* must contend with finding fewer preferred prey species among increasing numbers of lower quality food – there is less wheat and more chaff. Our findings of strong preference and selectivity for specific diatom species by *Diporeia*, coupled with corroborating evidence from sediment cores of significant changes in quality and potentially quantity of the pelagic rain of planktonic diatoms, provide a more detailed mechanism and further support that food limitation – through loss of preferred prey species – has played a significant role during the demise of *Diporeia* populations and expansion of dreissenids in southern Lake Michigan. We cannot fully rule out other factors and interactions that may be impacting *Diporeia* populations, but know that the loss of this keystone

species in Lake Michigan and the Great Lakes will have far-reaching impacts on the nearshore and pelagic fisheries as the benthic-pelagic link is severed.

### **Capacity-Building – Education and development of students**

a. *Elementary and Middle School Outreach*—While processing samples at the NOAA Lake Michigan Field Station, we had the opportunity to showcase our work and the changes that are occurring in Lake Michigan to two groups of students who were touring facilities along the Muskegon waterfront. About 50-60 students from the Sand Lake School District spent time with us learning how the food web is changing in Lake Michigan.

b. *Undergraduate Training*—Four undergraduates participated in our research cruise and/or assisted in gut content analysis, *Diporeia* population dynamics, and geochemical analyses in labs at the University of Michigan and the St. Croix Watershed Research Station.

### **Communications**

#### **Publications**

Two manuscripts are being prepared for submission based on project results:

- a. Edlund, M.B., Jude, D.J. and Nalepa, T.F. (in prep.) Pre- and post-dreissenid diets of *Diporeia* in southern Lake Michigan and their relationship to abundance of diatoms in sediment cores. *Journal of Great Lakes Research*
- b. Edlund, M.B., Jude, D.J. and Nalepa, T.F., Andresen, N.A., and Ramstack Hobbs, J. (in prep.) Recent changes in southern Lake Michigan diatom communities based on paleolimnological analysis of multiple sediment cores. *Journal of Great Lakes Research*

#### **Presentations**

- a. Dr. Edlund gave a presentation "Are We Losing our Great Lakes?" to the "Friends of the St. Croix Watershed Research Station" of the Science Museum of Minnesota on April 1, 2011.
- b. Dr. Edlund and Dr. Jude (with Dr. Tom Nalepa, NOAA) will be presenting a paper "Historical perspectives on the *Diporeia* demise: paleolimnological and gut content evidence of food limitation," at the 2011 IAGLR meeting being held in Duluth, Minnesota, May 24-27, 2011.

#### **Other**

##### *1. Outreach Activities*

- a. A public relations writer from the University of Michigan, Mr. Jim Erickson <[ericksn@umich.edu](mailto:ericksn@umich.edu)>, accompanied us on our research cruise aboard the R/V *Laurentian* and produced several written pieces and a short video clip:
  - i. Article and video clip in University of Michigan online alumni magazine *Michigan Today* "Great Lakes: 'Amazing change'", available at: <http://michigantoday.umich.edu/2009/07/story.php?id=7510>
  - ii. Article in July 27, 2009 issue of the *University Record*, "Researchers study change in Great Lakes" available at: [http://www.ur.umich.edu/0809/Jul27\\_09/02.php](http://www.ur.umich.edu/0809/Jul27_09/02.php)
  - iii. Article in the University of Michigan's School of Natural Resources and Environment magazine *Stewards* (Fall 2009 issue), "Putting the mussel on the Great Lakes", available at: [http://www.snre.umich.edu/stewards/fall\\_09](http://www.snre.umich.edu/stewards/fall_09)

The release of Mr. Erickson's pieces prompted additional interest from the media that resulted in interviews from the *Detroit Free Press* (David Jude interviewed), *Traverse City Eagle* (David Jude), and Interlochen Public Radio (Mark Edlund interviewed by Bob Allen).

## **Synopsis**

### **Background/Overview**

1. Briefly summarize the project description as outlined in the original proposal.

We proposed to use paleolimnological analysis of four dated sediment cores from nearshore and offshore areas of Lake Michigan to resolve the historical relationships among the diversity, quantity, and quality of the algal food resources, particularly diatoms, and how these parameters impacted or linked population dynamics of zebra/quagga mussels and *Diporeia*. To corroborate the results of our paleolimnological analyses, we also proposed to do gut analysis using historical preserved collections of southern Lake Michigan *Diporeia* that have been collected between 1981-2009.

2. Briefly summarize any significant changes to the work performed in comparison to the plan of work originally proposed and funded. If changes were made, describe how they affected your ability to achieve the intended outcomes for the work.

Two changes were made to our original proposal. First, we added a fifth coring site to our fieldwork. This station was X2, located NW of Muskegon in 100 m of water. It proved to be a site with a conformable but extremely low sedimentation rate. After completing Pb-210 dating on X2, we determined that this core would not provide the temporal resolution necessary for this study. Second, due to what appeared to be poor preservation, we were unable to do gut content analysis on *Diporeia* specimens collected at shallow station H31. This prevented us from making comparisons with the sediment core from nearby station H41. However, among the three stations that were fully analyzed, trends recorded in sediment cores and in diet preferences of *Diporeia* were similar.

### **Outcomes**

Please characterize key outcomes of the project related to *knowledge, training, relationships, and practice*. Not all projects will have outcomes of all types.

3. To what extent and how (if at all) did this research project advance scientific knowledge of the issue?

This study used a combination of paleolimnological analysis of multiple sediment cores from southern Lake Michigan with gut content analysis of historical *Diporeia* collections from the same coring sites. We tested the food limitation hypothesis thought to link the demise of *Diporeia* populations with the introduction and spread of zebra and quagga mussels in Lake Michigan. Key outcomes of the project were in the areas of feeding ecology of *Diporeia*, diet shifts by *Diporeia* during the spread of dreissenid mussels in southern Lake Michigan, and recent changes in algal food quantity, quality, and composition. In contrast to previous studies that did not specifically prepare *Diporeia* guts for microscopical analysis, *Diporeia* was shown to have high selectivity for three large-sized diatom species groups in their spring diets: *Aulacoseira islandica*, *A. subarctica*, and large *Stephanodiscus*. Based on sediment core analysis, we showed that food resources for *Diporeia* began to change even before the introduction of dreissenid mussels, but that changes were exacerbated during dreissenid colonization. Changes included reduced abundance of the preferred and high-quality, large-sized prey species and greater

abundance of araphid planktonic diatoms and small-sized *Cyclotella* and *Stephanodiscus* species. All sediment cores show increased absolute abundance of diatoms in the more recent sediments deposited at each core site, ranging from two- to six-fold increases; however, the increase has primarily been a consequence of increased numbers of low-quality and negatively preferred planktonic araphids and small-sized *Cyclotella* and *Stephanodiscus* spp. reaching the sediments. Biogenic silica profiles confirm little change in overall quantity of food reaching the sediments. Combining gut content and sediment core analyses, we show the preferred prey items of *Diporeia* have been decreasing in relative abundance, while selectivity for them has increased over time, as *Diporeia* must contend with finding fewer preferred prey species among increasing numbers of lower quality food. Our key findings of strong preference and selectivity for specific diatom species by *Diporeia*, coupled with corroborating evidence from sediment cores of significant changes in quality and potentially quantity of the pelagic rain of planktonic diatoms, provide a more detailed mechanism and further support that food limitation – through loss of preferred prey species – has played a role during the demise of *Diporeia* populations and expansion of dreissenids in southern Lake Michigan.

4. *To what extent and how (if at all) did this project contribute to the education and advancement of graduate or undergraduate students focused on Great Lakes fishery issues?*

Four undergraduates participated in our research cruise and/or assisted in gut content analysis, *Diporeia* population dynamics, and geochemical analyses in labs at the University of Michigan and the St. Croix Watershed Research Station. Two of the four students have since entered graduate programs in aquatics. Additionally, we had the opportunity to showcase our work and the changes that are occurring in Lake Michigan to two groups of students who were touring facilities, including NOAA's Lake Michigan Field Station, along the Muskegon waterfront. About 50-60 students from the Sand Lake School District spent time with us learning how the food web is changing in Lake Michigan using displays, demonstrations, and discussion.

5. *To what extent and how (if at all) did this work help you or others on your team build new relationships with others in the research or management communities?*

PI Edlund had worked as a field technician with PI Jude while in graduate school, but we had not had the opportunity to meld our areas of expertise in a research project. This project allowed that to finally happen. We also needed to join forces with Dr. Tom Nalepa (NOAA-GLERL) to gain access to historical *Diporeia* collections. Last, success from this project have been leveraged in a new project to explore linkages between botulism outbreaks and food web changes in nearshore northern Lake Michigan, a project that teams PI Edlund with NPS and USGS researchers.

6. *To what extent and how (if at all) do the findings have action implications for fishery managers? If the research has direct management implications, do you have any knowledge of use of the findings by managers? If the research does not have direct management implications at this stage, to what extent did the research advance the process of identifying management responses to critical issues?*

The Great Lakes are undergoing upheavals at all trophic levels, with the *Diporeia* decline having some of the most wide-ranging impacts, especially on important forage species and juvenile and adult yellow perch. Managers are struggling with how to manage declining stocks of, e.g., yellow perch and forage species that depend on *Diporeia* as an important component of their diet. It is important to know why the *Diporeia* decline occurred and this project has provided an answer on how the algal community (quality, quantity and composition) was modified during the

*Dreissena* colonization and further correlated those changes with historical estimates of *Diporeia* diet shifts and abundance at multiple sites in Lake Michigan. We have established a mechanism for the decline; that changes in food source and quality, especially loss of high-quality and preferred prey items for *Diporeia*, coincided with introduction and spread quagga and zebra mussels. Our study refocuses and refines competing hypotheses back toward food limitation, providing impetus for preventing quagga entry into other ecosystems, and focusing control efforts on this adaptive organism.

7. *Considering the above or other factors not listed, what do you consider to be the most important benefits or outcomes of the project?*

The most important outcomes of this project are: (1) that paleolimnological techniques could be paired with gut content analysis to retrospectively understand food web changes in the Great Lakes, and (2) our discovery that *Diporeia* are highly selective feeders and that loss of high-quality preferred prey items was coincident with their demise.

### **Related Efforts**

8. *Was this project a stand-alone effort, or was there a broader effort beyond the part funded by the GLFT? Have other funders been involved, either during the time of your GLFT grant or subsequently?*

This project was a stand-alone effort in its original conception.

9. *Has there been any spin-off work or follow-on work related to this project? Did this work inspire subsequent, related research involving you or others?*

Three additional research avenues have been explored based on the methods developed in this study and our subsequent results. A new project was funded by the NPS to examine three sediment cores from the Sleeping Bear Dunes area to explore linkages between botulism outbreaks and food web changes in nearshore northern Lake Michigan. Second, *Diporeia* diet samples from other zebra mussel infested waters, but where *Diporeia* remain abundant such as the New York Finger Lakes, will be examined. Third, the historical *Diporeia* samples that were gathered for this study are being further analyzed for isotopes to determine changing contribution of food sources over time.

### **Communication/Publication of Findings**

10. *List publications, presentations, websites, and other forms of formal dissemination of the project deliverables, tools, or results, including those that are planned or in process.*

#### **Publications**

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## Outreach Activities

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    - ii. Article in July 27, 2009 issue of the *University Record*, "Researchers study change in Great Lakes" available at: [http://www.ur.umich.edu/0809/Jul27\\_09/02.php](http://www.ur.umich.edu/0809/Jul27_09/02.php)
    - iii. Article in the University of Michigan's School of Natural Resources and Environment magazine *Stewards* (Fall 2009 issue), "Putting the mussel on the Great Lakes", available at: [http://www.snre.umich.edu/stewards/fall\\_09](http://www.snre.umich.edu/stewards/fall_09)
11. Please characterize your efforts to share the findings of this research with state, federal, Tribal, and interjurisdictional (e.g., Great Lakes Fishery Commission) agencies charged with management responsibilities for the Great Lakes Fishery. If other audiences were priority for this research, please characterize your outreach efforts to those audiences as well. (Please note: you may wish to consult midterm reports in which specific audiences for the findings, and means of outreach to these audiences, were identified.)

The three primary investigators on this project, Edlund, Jude, and Nalepa, work for a private non-profit museum, the University of Michigan, and NOAA, respectively. As such results of this work reach diverse audiences including the public (Edlund via presentations), students and research colleagues (Edlund and Jude through teaching and seminars), and federal agencies (Nalepa, NOAA). We further will present our results at a the 2011 IAGLR meeting in May 2011 and reach a broad international audience. Last, we engaged University of Michigan public relations in outreach efforts to convey the issues and rationale for this project (see 10 above).

12. Please identify technical reports and materials attached to this report by name and indicate for each whether you are requesting that GLFT restrict access to the materials while you seek publication. (Please note that the maximum amount of time during which GLFT will restrict access to the results of funded research is six months, unless notified that more time is needed.)

We suggest the following citation for this Research Final Report and do not request that GLFT place any restricted access on these materials.

Edlund, M.B. and Jude, D.J. 2011. Habitat or Food? The Demise of the Benthic Food Web in Lake Michigan (GLFT 2008.960). Final report on Project 2008.960 submitted to the Great Lakes Fishery Trust from the St. Croix Watershed Research Station, Marine on St. Croix, Minnesota, 55047.

13. **Manuscripts.** *Grantees submitting one or more publications or pending publications in lieu of a stand-alone technical report must submit a cover memo that confirms that all aspects of the funded research are incorporated in the published work, and in cases of multiple publications, identifies or crosswalks the grant-funded objectives to the published article containing results.*

No manuscripts submitted to date (but see 10 above).

14. **Compilation reports.** *Grantees working on several related sub-projects under a single grant may submit a series of sub-project reports rather than a single, integrated report. However, grantees must submit a cover sheet or introduction that outlines and crosswalks grant objectives with the location of the results in the compilation document.*

N/A

### **Reflections**

15. *Please describe any unanticipated benefits, challenges or surprises, and/or important lessons learned over the course of the project.*

After about 15 years of not working on the Great Lakes, this project has been a springboard for PI Edlund to re-engage in Great Lakes issues and research.

16. *What recommendations (if any) would you make to the GLFT to improve its research grantmaking process?*

My suggestion would be to work to have greater contact with project investigators, especially in regard to reporting and accounting. There is nothing wrong with the policies in place at GLFT, but it is my sense that scientists are much too focused on the scientific aspects of the work to readily shift gears to reporting and accounting. For me, a couple phone calls each year of the project would make those efforts go more smoothly and keep everyone abreast of progress, of how project ideas may be developing or changing, and availability of resources and guidelines for grant administration and reporting.

## FULL TECHNICAL REPORT

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**PROJECT TITLE:** Habitat or Food? The Demise of the Benthic Food Web in Lake Michigan (GLFT 2008.960)

<sup>1</sup>Edlund, M.B., <sup>2</sup>Jude, D.J., <sup>3</sup>Nalepa, T.F., <sup>4</sup>Andresen, N.A. and <sup>1</sup>Ramstack Hobbs, J.

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<sup>3</sup>Great Lakes Environmental Research Laboratory (GLERL), NOAA, Ann Arbor, Michigan 48107

<sup>4</sup>Andresen Consulting LLC, Ypsilanti, MI 48197

### PROJECT SUMMARY:

*Diporeia* spp. is a key component of the benthos of the Great Lakes, converting the pelagic algal rain to secondary production, which is critical for most fish species in the Great Lakes. However, declines in *Diporeia* populations in the Great Lakes since the 1980s have been rapid and widespread. There is a temporal relationship between decline of *Diporeia* and spread of zebra *Dreissena polymorpha* and quagga *D. rostriformis bugensis* mussels in the Great Lakes, but establishing a mechanistic link has been a research challenge. *Diporeia* declines are thought to result from competition for food resources with zebra/quagga mussels, but conflicting evidence suggests food limitation may not be the direct link. To test the food limitation hypothesis, we analyzed gut contents of *Diporeia* collected between the 1980s and 2009 from two offshore (>100 m depth) and one nearshore sampling station (~50 m depth) in southern Lake Michigan. We further used paleolimnological analysis of sediment cores from nearshore and offshore southern Lake Michigan to resolve historical relationships among food resources, *Diporeia* diet shifts, and diet selectivity during the pre- and post-dreissenid invasion. Results showed that in spring *Diporeia* fed selectively and almost exclusively on large centric (*Stephanodiscus* spp.) and filamentous centric diatoms (*Aulacoseira* spp.). Diets differed among *Diporeia* size classes, sampling stations, and years. Springtime diets in offshore *Diporeia* populations showed significant shifts during the 2000s that included greater proportions of small *Cyclotella* spp., small *Stephanodiscus* spp., and araphid planktonic diatoms, coincident with widespread *Diporeia* declines and rapid expansion of quagga mussels into offshore regions of Lake Michigan. Sediment cores recorded changes in diatom communities from 1960 to 2009 including declines in *Aulacoseira* and large *Stephanodiscus*, and increases in small centrics especially after dreissenid introduction. Accounting for high selectivity in spring *Diporeia* diets, the community changes in the sediment record are consistent with changes observed in the diet of *Diporeia*, and suggest the decline in *Diporeia* populations has been exacerbated by a shift in diatoms from more nutritious and highly preferred species to less nutritious and negatively selected species.

## INTRODUCTION

Unprecedented recent changes in the food web of the Laurentian Great Lakes have occurred in response to multiple environmental drivers including: nutrient control efforts; the introduction, spread, and control of nonindigenous species; and climate change (Medenjian et al. 2002, Vanderploeg et al. 2002, Wuebbles et al. 2010). In southern Lake Michigan (SLM) changes have been realized at all levels of the food web (Fahnenstiel et al. 2010a). At the base, there has been loss of the winter/spring diatom bloom (Kerfoot et al. 2010, Vanderploeg et al. 2010), large declines in phytoplankton productivity (Fahnenstiel et al. 2010b), and changes in phytoplankton community and size structure (Fahnenstiel et al. 2010b). Size structure and composition of zooplankton communities have changed with loss of small-bodied (Barbiero et al. 2009) and large-bodied (i.e. *Mysis*) plankters (Pothoven et al. 2010). As a result, forage fish numbers have fallen precipitously (Madenjian et al. 2002) and overall fish condition has declined (Pothoven et al. 2001, DeBruyne et al. 2008).

Perhaps the most publicized recent change in Lake Michigan, and in fact, all the Great Lakes except Lake Superior, has been declines of the benthic amphipod *Diporeia* spp. (e.g. Dermott 2001, Nalepa et al. 2006b, 2007), largely coincident with the spread of zebra and quagga mussels throughout the lakes (Nalepa et al. 2009, 2010). *Diporeia* has long been the most abundant benthic macroinvertebrate in the Great Lakes, averaging over 7000 individuals/m<sup>2</sup> and accounting for over 70% of the benthic biomass (Nalepa 1987, 1989). As a deposit feeder, *Diporeia* served as the benthic-pelagic trophic link in the Lake Michigan and assimilated over 60% of sedimented carbon (Gardner et al. 1990, Fitzgerald and Gardner 1993), primarily through ingestion of spring-bloom diatoms, (especially lipid-rich *Aulacoseira* spp.; Quigley 1988, Fitzgerald and Gardner 1993). Some studies suggest high assimilation of bacteria-mediated C in other areas of the Great Lakes (Guiguer and Barton 2002). As a result, *Diporeia* accumulate abundant lipids (Gardner et al. 1985, Quigley et al. 1989) and are a primary and preferred prey for many deepwater and nearshore fish species including sculpins, lake whitefish, bloater, yellow perch, alewife, and rainbow smelt (Wells 1980, Wojcik et al. 1986, Nalepa et al. 2006a).

In Lake Michigan alone, there has been a 94% decline in *Diporeia* between 1995 and 2005 (Nalepa et al. 2006b). Initial losses were noted in shallow and nearshore areas, but more recently *Diporeia* numbers have plummeted in the deeper regions of Lake Michigan coincident with the spread of quagga mussels to these areas (Nalepa et al. 2009). Confounding interpretations of the negative response of *Diporeia* to dreissenids has been the loss of *Diporeia* in areas of the lake distant from areas colonized by dreissenids. The result of the *Diporeia* loss has not yet been fully realized; however, its impact on the Lake Michigan food web is evident (Madenjian et al. 2002). For example, lake whitefish abundance, growth, and body condition in Lake Michigan may have decreased in response to *Diporeia* loss (Pothoven et al. 2001, Mohr and Nalepa 2005, DeBruyne et al. 2008; but see Kratzer et al. 2007).

There is an obvious correspondence between the decline of *Diporeia* and the invasion and spread of zebra and quagga mussels (*Dreissena polymorpha* and *D. rostriformis bugensis*) throughout the Great Lakes (except Lake Superior); however, establishing the mechanistic link between *Diporeia* decline and mussels has been a research challenge (Nalepa et al. 2001, 2006a). Although the *Diporeia* declines are widely regarded as resulting from direct competition for food resources following establishment of zebra and quagga mussels, conflicting evidence from distributional surveys, laboratory experiments, and measures of benthic food inputs have confounded the certainty of establishing food limitation as the mechanistic link between zebra/quagga mussels and the demise of *Diporeia* (Landrum et al. 2000, Nalepa et al. 2006a).

We examined gut contents from historical (Nalepa et al. 2006a) and recently collected *Diporeia* to better understand timing and scale of population declines and how these declines were related to changes in their algal diet. We analyzed gut contents for diatom composition to determine whether springtime diet of *Diporeia* varied across the Lake Michigan basin, among size classes of *Diporeia*, and over time as a function of dreissenid introduction. We further compared what *Diporeia* were eating to abundance and changes in the diatom flora found in sediment core material dated from 1960 to 2009.

## **MATERIAL AND METHODS**

### ***Diporeia* collection and preservation**

May to early June collections of *Diporeia* from previous studies (Nalepa 1995, Nalepa et al. 1998, 2000, 2005, 2006a, b) were selected so as to obtain samples over three periods within the dreissenid invasion history of Lake Michigan: pre-dreissenid (1987), post-dreissenid (1992 or 1998), and the period of quagga mussel expansion (2004 and 2009). All archived specimens of *Diporeia* were preserved in a formaldehyde solution. Previous research identified the spring period as the critical feeding and growth period for *Diporeia* (Gardner et al. 1985, Evans et al. 1990). We selected formaldehyde-preserved specimens from three southern Lake Michigan stations where the history of population changes were well documented (Nalepa et al. 2006a, b). The three stations, B4, C5, and H22 (Fig. 1), represented both nearshore and offshore regions, and *Diporeia* populations at these sites had different decline rates (Table 1; Nalepa et al. 2006a). In addition, in May 2009, benthic samples at the three sites were taken with a PONAR grab and washed through a 500 micron mesh screen. *Diporeia* were immediately sorted, narcotized in carbonated water, and preserved in 5% formaldehyde solution. Quagga mussels were found at all stations sampled in 2009 in southern Lake Michigan.

### **Sediment core collection and processing**

To determine trends in the composition of diatoms settling to the bottom, intact sediment cores were collected with a box corer (25 cm x 25 cm; Ocean Instruments, San Diego) at five stations (B-4, C-5, H-22, H-41, X2; Fig. 1, Table 2) in May 2009. A single box core was taken at each site, and intact sediment cores were obtained in duplicate by inserting a 6.5 cm ID polycarbonate tube into the box-core sediments using a gentle vacuum. Each sub-core subsequently was sectioned into 0.25-cm increments to 7 cm core depth, 0.5-cm increments to 15 cm core depth, and 1-cm increments to ~30-35-cm depth. The core sections were stored at 4°C in the dark until radioisotopic inventory, and biological and geochemical analyses.

### ***Diporeia* subsampling, gut preparation, and diatom counting**

Approximately 100 *Diporeia* individuals were randomly removed from collection vials, measured to the nearest 0.1 mm under a stereomicroscope at 20x magnification, sexed, and percent gut fullness was determined (Auer et al. 2009). Individuals were then divided into three length size classes (<3 mm, 3-5 mm, and >5 mm), and the entire gastrointestinal tracts of five individuals from each size class were removed, rinsed with double distilled water, placed together onto microscope slides, and contents macerated according to Edlund and Francis (1999). The slide was dried at 100°C then placed on a hotplate set at ca. 300°C for 1 hr to ash organic material. Next a drop of Zrax mountant (MicrAP Enterprises, Pittsburgh, Pennsylvania) was placed on a clean 22 x 22 mm No. 1 coverglass, inverted over the ashed gut material on the slide,

and placed on a hot plate set for 250°C for 4-6 min. Air bubbles were squeezed from the slide during cooling and excess mountant removed with a razor blade. Diatoms were counted under oil immersion and differential interference contrast optics capable of 1000x magnification. Either four hundred identifiable fragments or four random transects were counted on each preparation. Chrysophyte cysts and diatoms were identified to the lowest taxonomic level and proportion of a full diatom valve estimated for each fragment. Diatom counts were converted to whole valve units (Glover 1982) and reported as relative abundance by species. Triplicate slides, each slide with the pooled gut contents of five *Diporeia* individuals from a single size class and collection date, were counted for all 1987 and 2009 *Diporeia* size classes from station B4 to assess method variability and test for differences among years and size classes.

### **Sediment dating and geochemistry**

Each core was radiometrically dated using  $^{210}\text{Pb}$  following standard alpha spectroscopy methods (Appleby and Oldfield 1978, Appleby 2001).  $^{210}\text{Pb}$  activity was measured from its daughter product,  $^{210}\text{Po}$ , which is considered to be in secular equilibrium with the parent isotope. Aliquots of freeze-dried sediment (~0.5 g) were spiked with a known quantity of  $^{209}\text{Po}$  as an internal yield tracer and isotopes distilled at 550°C after treatment with concentrated HCl. Polonium isotopes were directly plated onto silver planchets from a 0.5 N HCl solution. Activity was measured for  $1-3 \times 10^5$  s using an Ortec alpha spectrometry system. Core dates and sedimentation rates are calculated using the constant rate of supply model (Appleby and Oldfield 1978). Dating and sedimentation errors represent first-order propagation of counting uncertainty (Binford 1990).

To determine the amount of sediment mixing,  $^7\text{Be}$  was quantified in samples from the top 5 cm of each core within two weeks of core collection.  $^7\text{Be}$  has a half-life of only 25 days and remains detectable for ca. one year. The depth at which  $^7\text{Be}$  is detectable allows us to determine extent and correction factors for sediment mixing (Clifton 1991). Freeze-dried samples were measured for  $^7\text{Be}$  using a high-resolution germanium diode gamma detector and multichannel analyzer. Accuracy and precision are better than 10% for a 12 h measurement of concentrations of  $\sim 30\text{ bq kg}^{-1}$  and detector efficiency is approximately 2% as determined against a NIST-certified standard (Rocky Flats soil / SRM4353).

Subsamples of sediment from each of the core sections were dried at 105°C for 24 hr to determine dry density, then heated at 550°C and 1,000°C to determine organic and carbonate content from post-ignition weight loss, respectively (Dean 1974, Heiri et al. 2001). Data are expressed as percentage of dry sediment weight.

For biogenic silica analysis, freeze-dried subsamples (~30 mg) from each sediment core were digested for biogenic silica analysis using 40 mL of 1% (w/v)  $\text{Na}_2\text{CO}_3$  solution heated at 85°C in a reciprocating water bath for 5 h (Conley and Schelske 2001). A 0.5-g aliquot of supernatant was removed from each sample at 3, 4, and 5 h. After cooling and neutralization with 4.5 g of 0.021N HCl solution, dissolved silica was measured colorimetrically on a Lachat QuikChem 8000 flow injection autoanalyzer as molybdate reactive silica.

### **Diatom analysis of sediment cores**

Weighed subsamples of freeze-dried sediment (~0.25 g) from core sections dated between 1960 and 2009 taken at four of the five coring sites (see Results; the core from X2 was determined to be unsuitable for diatom analysis) was prepared for microscopy following Renberg (1990). Following oxidation of organic matter, a known quantity of microspheres was added to each sample to estimate absolute abundance of diatoms (Maher 1981), and the oxidation byproducts

and saline carrier for microspheres removed using centrifugation and multiple rinses with distilled water. The remaining diatom material and microspheres were dried onto coverglasses and mounted on microslides using Zrax (MicrAP Enterprises, Pittsburgh, Pennsylvania). Four hundred siliceous remains (diatom valves and chrysophyte cysts) were counted along one or more random microslide transects, along with any microspheres, on a Leica Ortholux microscope using full oil immersion optics capable of N.A. 1.32 and 1250X. All diatom fragments were identified to the lowest taxonomic unit possible using iconographic treatments (e.g., Krammer and Lange-Bertalot 1986-1991), regional floras (e.g., Patrick and Reimer 1966, 1975; Reavie and Smol 1998; Camburn and Charles 2000; Fallu et al. 2000), and primary literature (Kreis and Stoermer 1979; Stoermer et al. 1979, 1981; Theriot et al. 1988). Diatom fragments were reconstituted to whole valve equivalents (Glover 1982, Stoermer et al. 1990). Diatom counts were converted to proportional or percent abundance against total siliceous microfossils and absolute abundance (diatom valves per g of dry sediment).

### Numerical analysis

Gut content data were analyzed to determine whether *Diporeia* diets changed over time, varied among *Diporeia* size classes, and varied among sampling stations. Data were further compared to sediment diatom communities to determine whether *Diporeia* fed selectively. For some tests and graphics, diatom species in gut contents were grouped; e.g., the group "Large *Stephanodiscus* spp." included *S. niagarae*, *S. alpinus*, *S. subtransylvanicus*, and *S. transylvanicus*. Two-way ANOVA followed by *post hoc* Tukey HSD pairwise comparisons were used to test for diet differences among size classes and years (SPSS for Windows, Rel. 17.0 2008. Chicago: SPSS, Inc.). Chesson's Index ( $\alpha_i$ ) was used as a measure of diet selectivity and was calculated for each diatom prey category in the *Diporeia* diets *versus* abundance of prey items in sediment cores to determine if each diatom species was positively or negatively selected by *Diporeia* (Chesson 1978). Chesson's Index ( $\alpha_i$ ) is independent of sample size and composition and calculated as follows:

$$\alpha_i = (d_i/e_i) / (\sum d_i/e_i)$$

where  $\alpha_i$  is the selectivity for prey item  $i$ ,  $d_i$  is the percentage of prey item  $i$  in the diet (*Diporeia* gut contents),  $e_i$  is percentage of prey item  $i$  in the environment (sediment core sample), and  $n$  is total number of prey categories in guts and sediment cores ( $n = 26$  prey categories). For Chesson's Index, neutral selection corresponds to  $\alpha_i = 1/n$ , positive selection corresponds to  $\alpha_i > 1/n$ , and negative selection corresponds to  $\alpha_i < 1/n$ . To provide more of a gradient in assigning the selection index, we broke down the assignment of the selection index  $\alpha_i$  into the following categories, where  $1/n$  was equal to 0.04:

Neutral selection (0) when  $\alpha_i = 0.04$

Moderately negative selection (-) when  $0.02 \leq \alpha_i < 0.04$

Negative selection (--) when  $0 \leq \alpha_i < 0.02$

Moderately positive selection (+) when  $0.04 < \alpha_i \leq 0.08$

Positive selection (++) when  $\alpha_i > 0.08$ .

Relative abundances of diatom species in each core are summarized using stratigraphic plots of core date against percent abundance of the predominant diatom species or species groups. To explore changes and relationships among diatom communities within each sediment core, various multivariate statistical analyses were also performed in the software package R (Ihaka & Gentleman 1996). Diatom species found at >1% abundance in two or more core strata were included in analyses. Detrended Correspondence Analysis (DCA) was determined to be the most suitable analysis based on gradient lengths (Ramstack et al. 2008) and was used to summarize diatom compositional or species turnover. Core depths were plotted in ordinate space, their DCA axis 1 and 2 scores extracted and plotted with each core stratigraphy. Changes along DCA Axis 1 are the dominant species gradient in the cores and when stratigraphically plotted the axis 1 scores represent species turnover in standard deviation (SD) units between samples or core depths.

## RESULTS

### ***Diporeia* size distribution and gut fullness**

*Diporeia* lengths varied between 1.5 mm and 9.0 mm and were commonly represented by a bimodal distribution (Fig. 2) or more rarely with a unimodal or trimodal distribution, providing evidence of multiple year classes. Female *Diporeia* were much more common than males in the large size classes where sex could be easily determined (data not shown). Of note is the lack of small-sized *Diporeia* in samples just previous to local extirpation of *Diporeia* (e.g., H22-1992, C5-2009). There was little discernable pattern in gut fullness among samples. *Diporeia* from most sampling dates, stations, and size classes had high variability in gut fullness among individuals (Fig. 3). *Diporeia* taken from 1987 to 2004 at station C5 had consistently high gut fullness, whereas samples from Station H22 had lower gut fullness.

Diatoms were well represented in most guts examined, although gut contents of *Diporeia* from several sampling dates from the early 1980s did not contain well-preserved diatoms and were rejected for this study. Poor preservation was most likely an artifact resulting from poor handling and preservation of the *Diporeia*, e.g., no narcotization and egestion of gut contents or loss of diatoms during storage as evidenced by dissolution artifacts.

### **Changes in *Diporeia* diet**

#### *Station B4 (124-m depth)*

Among the three stations, B4 was the only station with complete collections of all size classes of *Diporeia* in each of the four years that were analyzed (1987, 1998, 2004, and 2009). Diatom assemblages in gut contents were compared with diatom assemblages in similarly dated levels in the B4 sediment core. Additionally, gut contents were analyzed in triplicate preparations of each size class from the 1987 and 2009 collections at station B4 to assess method variability and test differences between years and size classes. Variability of relative abundance estimates of predominant diatom species groups in *Diporeia* guts was < 15% (Fig. 4), with somewhat higher variability (< 20%) among the more easily fragmented diatom species (e.g., large *Stephanodiscus* spp., *Aulacoseira islandica*). For the primary prey groups of *Diporeia*, relative abundance in diets was significantly different between 1987 and 2009 (Fig. 4). The proportion of *Aulacoseira islandica* ( $F$ -stat 7.080,  $p = 0.21$ ), *A. subarctica* ( $F$ -stat 13.945,  $p = 0.003$ ), and large *Stephanodiscus* spp. were lower in the diets in 2009 compared with 1987 ( $F$ -stat 69.442,  $p < 0.0005$ ), whereas the proportions of small *Cyclotella* spp. ( $F$ -stat 127.065,  $p < 0.0005$ ), the

planktonic araphids ( $F$ -stat 101.855,  $p < 0.0005$ ), and small *Stephanodiscus* spp. were higher ( $F$ -stat 16.612,  $p = 0.001$ ). Pairwise comparisons showed significant differences in diet among *Diporeia* size classes in only two prey categories. There were significant differences in diet among all *Diporeia* size classes for large *Stephanodiscus* spp. ( $F$ -stat 20.690,  $p < 0.0005$ , L/M  $p = 0.030$ , L/S  $p < 0.0005$ , M/S  $p = 0.12$ ). There was also significant differences in diet between large and small and medium and small *Diporeia* for *Aulacoseira subarctica* ( $F$ -stat 13.879,  $p = 0.001$ , L/S  $p = 0.001$ , M/S  $p = 0.006$ ). Overall, the proportion of large *Stephanodiscus* spp. was higher in diets of smaller *Diporeia*, whereas *A. subarctica* was less abundant in small *Diporeia* diets than in diets of large and medium *Diporeia*.

Gut content analysis of *Diporeia* collections from 1987, 1998, 2004, and 2009 showed that between 1987 and 2004, three prey classes dominated the diets of *Diporeia*—*Aulacoseira islandica*, large *Stephanodiscus* spp, and *A. subarctica*—together accounting for over 80% of diatoms in the diet (Fig. 5). From 1987 to 2004, large *Stephanodiscus* spp. were most common in the diets of small *Diporeia*, *Aulacoseira subarctica* was most common in large *Diporeia* diets, and the three prey groups shifted in dominance in medium-sized *Diporeia* diets (Fig. 5). Diets from 1987 to 2004 contrast sharply with *Diporeia* diets in 2009. The dominant prey groups in the earlier period (*Aulacoseira islandica*, large *Stephanodiscus* spp, and *A. subarctica*) accounted for less than 50% of the *Diporeia* diet in 2009. Small *Cyclotella* and *Stephanodiscus* species, along with planktonic araphid diatoms, accounted for over 50% of the *Diporeia* diets in 2009. Comparison of diet trends in *Diporeia* with changes in diatom assemblages in sediment cores at station B4 showed that the dramatic shift in diet between the periods 1987 to 2004 and 2009 paralleled similar shifts in sedimented diatom assemblages. Whereas the three prey groups of *Aulacoseira islandica*, large *Stephanodiscus* spp, and *A. subarctica* together accounted for about 25% of sedimented diatoms from 1987 to 2004, this percentage dropped to 13.3% in 2009. Among the other major prey groups in the sediment cores, there was marked increase in small *Stephanodiscus* spp., little change in small *Cyclotella* spp., and a slight decrease in planktonic araphid between the time periods 1987-2004 and 2009.

#### *Station C5 (127-m depth)*

*Diporeia* diets were analyzed in spring collections made at station C5 from 1987, 1998, 2004, and 2009. Similar to station B4, diets in pre-2009 collections were dominated by the three prey groups (*Aulacoseira islandica*, large *Stephanodiscus* spp., and *A. subarctica*) that nearly always accounted for over 75% of the diatoms in *Diporeia* diets (Fig. 6). However, there was a trend toward decreased abundance of these primary prey items already in 2004 compared to 1987 and 1998 specimens. *Aulacoseira islandica*, large *Stephanodiscus* spp, and *A. subarctica* accounted for greater than 95% of diet items in 1987 and 1998, but only 66.2% to 89.9% of diet items in 2004 (Fig. 6). Only large *Diporeia* were found in samples collected in spring 2009 at C5. (Fig. 6). Although the three prey groups (*Aulacoseira islandica*, large *Stephanodiscus* spp, and *A. subarctica*) together still accounted for nearly 66% of the diet, the proportion of small *Stephanodiscus* and *Cyclotella* spp. and planktonic araphids increased in the diets of large-sized *Diporeia* in 2009 (Fig. 6). The diatom community preserved in the C5 sediment core showed less change than the community in the B4 core. The proportion of the two *Aulacoseira* spp., *A. islandica* and *A. subarctica*, decreased between 1987 and 2009, from 18.5% to 10.8% respectively; the proportion of *A. islandica* alone decreased from 7.2% to 2.8% over that time period (Fig. 6). Large *Stephanodiscus* species remained at  $< 2.1\%$  in sediments over the entire time period, in contrast to a greater proportion in *Diporeia* diets. Other prey categories

preserved in the sediment core showed subtle changes between 1987 and 2009. The proportion of small *Stephanodiscus* spp. increased from 16.2% to 24.4% and small *Cyclotella* spp. increased slightly from 22.5% to 27.5%. Planktonic araphids were well represented in all sediments samples between 1987 and 2009, accounting for between 23.8% (2009) and 39.6% (2004) of the sedimented diatom community (Fig. 6).

#### *Station H22 (52-m depth)*

Because *Diporeia* disappeared from Station H22 after 1993 (Nalepa 2006a), specimens for gut analysis were only available for samples collected in 1987 and 1992. No small-sized *Diporeia* were collected in the 1992 samples. Similar to stations B4 and C5, spring diets of *Diporeia* in 1987 and 1992 were dominated by three prey categories. *Aulacoseira islandica*, large *Stephanodiscus* spp, and *A. subarctica* together accounted for between 69.4% (1987, large) and 85.7% (1987, small) of the *Diporeia* diets despite their relatively low abundance in the H22 sediment core (Fig. 7). Large *Stephanodiscus* spp. were particularly abundant in guts of small and medium-sized *Diporeia* in 1987; *Aulacoseira subarctica* was very abundant in *Diporeia* diets in 1992 (Fig. 7). Planktonic araphids and other diatom species (primarily benthic taxa or tychoplanktonic species) accounted for the remainder of diet items (Fig. 7). Over the same time period, the diatom community in the H22 sediment core changed significantly. The proportion of the three primary prey species, *A. islandica*, large *Stephanodiscus* spp., and *A. subarctica*, was much lower in the H22 core than in cores from B4 and C5, but showed a similar decrease (Fig. 7). Between 1987 and 1992, the proportion of these prey group decreased from 7.1% to 3.9%. Small *Stephanodiscus* spp. also declined. In contrast, small *Cyclotella* spp. and planktonic araphids increased from 27.3% to 43% and from 11.4% to 19.3%, respectively (Fig. 7).

#### **Selectivity for diatoms in *Diporeia* diets**

Chesson's index ( $\alpha_i$ ) was used to determine prey selectivity for 26 diatom prey species or categories. The index compared abundances in the diets of *Diporeia* collected 1987-2009 at stations B4, C5, and H22 against abundances in specific strata dated between 1987 and 2009 in sediment cores from the same stations. Among prey species, there was a wide range of selectivity that varied among sampling time and among *Diporeia* sizes (Table 3).

#### *Selectivity trends over time*

*Diporeia* showed a strong preference for consuming five diatom species (*Aulacoseira subarctica*, *A. islandica*, *Stephanodiscus niagarae*, *S. subtransylvanicus*, and *S. alpinus*) and these preferences were similar among all three stations and sizes of *Diporeia* (Table 3). There was a tendency for the preferences for these five species to change over time. It was also clear that there were changes in preferences from the pre-dreissenid period (1987) to the post-dreissenid periods, because many diatom groups that were not eaten in 1987, were consumed in the post-dreissenid era. This switch suggests that preferred food items have declined, causing *Diporeia* to have to change its diet to groups on which they were not feeding in the pre-dreissenid period.

The same five diatom species that were highly preferred at station B4 (Table 3a) were also preferred food items at stations C5 (Table 3b) and H22 (Table 3b) according to Chesson's  $\alpha_i$ , but they were not as highly preferred as was observed at station B4 (Table 3a). In addition, trends seen in switching of prey items over time that were clearly evident at station B4 were not documented at stations C5 and H22.

### *Selectivity trends among Diporeia size classes*

For *Aulacoseira subarctica*, there was a distinct trend of increased utilization with increased *Diporeia* size, as small animals showed little preference, medium-sized animals showed moderate preference, and large individuals showed moderate to high preference for this species at all stations for all dates (Table 3). There was a similar relationship between *Aulacoseira islandica* preference and *Diporeia* size, but actual preferences were not as strong as with *A. subarctica* (Table 3). *Stephanodiscus niagarae* was preferred by all sizes of *Diporeia* over all sampling times at station B4 (Table 3a), while these preferences were less strong for the other stations, C5 and H22 (Tables 3b, 3c). *Stephanodiscus subtransylvanicus* was preferred by *Diporeia* of all sizes in about 2/3 of the samples analyzed (Table 3), but there were no large differences among size groups. *Stephanodiscus alpinus* showed trends similar to *S. subtransylvanicus*, in that *Diporeia* showed preferences for this species in about 5/8 of the samples, while there did not appear to be any large differences according to size (Table 3). *Diporeia* of all sizes showed negative selection for the remaining ten diatom groups, with one exception. At station B4 during 2009, four diatom groups (*Cyclotella* "tiny", *Synedra ulna* and varieties, *Discostella pseudostelligera*, and *Cyclotella comensis*) were preferred by most size classes of *Diporeia* (Table 3a).

## **Sediment geochemistry, mixing, and core dating**

### *Core B4*

Loss on ignition analysis showed that sediments at deep station core B4 were primarily inorganics and secondarily composed of carbonates and organics (Fig. 8). Inorganic content increased upcore from ~50% to over 80% between 23 and 18 cm core depth. Over the same depths, carbonate content dropped from ~45% to ~10% and continued to decrease to less than 5% at 5 cm. Organic content increased slowly upcore from 3.5% to 6% at 4 cm and increases up to 11% at the core surface. Biogenic silica was measured in sediments deposited since 1960 and showed an increase upcore from 1.2 to 2.4 % dry sediment weight (Fig. 9).

Inventory of  $^7\text{Be}$  in core B4 showed rapid steady state mixing to 1.0 cm limiting temporal resolution within the top 5.3 yr of sedimentation (Table 4), likely a consequence of *Diporeia* continuing to live at station B4 (see Fig. 9). Total  $^{210}\text{Pb}$  activity decreased from the core surface to 5.5 cm (Fig. 8). From 5.5 to 10 cm there was an anomalous increase in total  $^{210}\text{Pb}$  inventory (Fig. 8). These depths overlaid the likely redox boundary in core B4 that was demarcated by a crust-like iron oxide layer between 9 and 9.5 cm core depth. Below 10 cm, total  $^{210}\text{Pb}$  activity declined again to reach supported levels that were measured at four core depths below 20 cm (Fig. 8). A similar anomalous peak in total  $^{210}\text{Pb}$  activity was seen between 11 and 14 cm in core C5 (see below).

The anomalous activity peak represents  $^{210}\text{Pb}$  that is not supported by either atmospheric deposition of  $^{210}\text{Pb}$  or *in situ* mineralogical uranium decay. There is likely aqueous radium that has been preferentially concentrated at the redox layer/interface. This may be a historic artifact in the core or an ongoing process. In any case, the amount of  $^{210}\text{Pb}$  found at this layer exceeds the amount of  $^{210}\text{Pb}$  expected from mineralogical secular equilibrium. Therefore these intervals should not be included in the c.r.s. dating model (Appleby and Oldfield 1978). For this project, this is not a major concern because the intervals above and below this anomaly don't have excess  $^{210}\text{Pb}$ , and notably the intervals above the redox layer have already reached supported  $^{210}\text{Pb}$ , and this surplus of  $^{210}\text{Pb}$  due to aqueous radium is below the region of interest (1960-2009) for this project. An enrichment of  $^{210}\text{Pb}$  by aqueous radium has not been widely reported in the

literature, will impact older dating interpretations, and warrants further study especially as to the source of the radium.

Our date-depth model for core B4 showed post-1900 sediments are preserved above 10 cm depth and that the last 50 years of sedimentation is preserved in the upper 4 cm of the core (Fig. 8). Above 4.5 cm, there is a slight increasing trend in sedimentation rates from 0.018 to 0.025 g/cm<sup>2</sup> yr (Fig. 8). Below 5 cm, sedimentation rates were not calculable because depths within the anomalous spike in total <sup>210</sup>Pb activity had to be removed in the c.r.s. model.

#### *Core C5*

Sediment geochemistry at deep station C5 was dominated by inorganics, followed by carbonate and organic content (Fig. 8), and shared a similar depth profile with core B4. Inorganic content increased from ~53% below 27 cm to a peak of over 90% at 14 cm, and then fell upcore to 70% between 5 cm and the core surface. Carbonate content mirrored inorganic content by decreasing from 40% to 5% between 27 and 14 cm and then increased upcore to 20% above 5 cm. Below 9 cm, organic content generally remained less than 5%, but increased upcore to 10%. Biogenic silica content increased upcore from 1.4% to a peak of 3.4 % at 1 cm before declining to 2.3% dry weight at the core top (Fig. 10).

Core C5 maintained its <sup>7</sup>Be inventory to 0.75 cm, suggesting rapid state mixing that incorporates the most recent 2.7 years of sedimentation (Table 4). Total activity of <sup>210</sup>Pb was constant above 4 cm and then decreased logarithmically to 11 cm. Below 11 cm, <sup>210</sup>Pb activity then increased anomalously to 14 cm before decreasing to supported levels of <sup>210</sup>Pb in three levels analyzed below 20 cm. This pattern was similar to the <sup>210</sup>Pb peak seen between 5.5 and 10 cm in core B4 and our interpretation of it is given above. The anomalous increase between 11 and 14 cm coincided with the redox boundary in the core, which was represented by a hardened oxidized layer at 14-15 cm in core C5. Removing the depths with anomalous activity from the c.r.s. dating model produced a date-depth model that showed post-1900 sediments are preserved above 15 cm and that the last 50 years of sediment accumulation is present above 5 cm core depth (Fig. 8). Sedimentation rates have remained relatively constant above 7 cm (ca 1940) at ~0.03 g/cm<sup>2</sup> yr (Fig. 8) and are not interpretable in the region of the anomalous peak in <sup>210</sup>Pb activity between 11 and 15 cm (Fig. 8).

#### *Core H22*

There was little change in sediment geochemistry at shallow station H22 (Fig. 8). Inorganic content dominated the core at ca. 60% below 13 cm and then increased slightly upcore to 60 to 65%. Carbonate content was between 32 and 40% below 13 cm depth and then falls to 30% near the core top. Organic content remained low throughout the core at approximately 5%. Biogenic silica levels decreased during the 1960s from 2% to less than 1% and remained low until the 1980s (Fig. 11). From 1982 to the top of the core biogenic silica increased three-fold from 0.9% to 2.9% at the core top (Fig. 11).

The <sup>7</sup>Be inventory was detected to a depth of 1.25 cm indicating rapid state mixing of the last 0.8 years (Table 4). <sup>210</sup>Pb activity decreased downcore in a stepwise manner to reach supported levels below 42 cm. The upper 41 cm of core included sedimentation since 1850, and the upper 15 cm included sedimentation since 1960. Sedimentation rates at station H22 have varied three-fold in the last 150 years. Sedimentation rates increased from the core base (42 cm, ca. 1860) to over 0.3 g/cm<sup>2</sup> yr at 19 cm (1969), and then decreased upcore to 0.20 to 0.25 g/cm<sup>2</sup> yr (Fig. 8).

### Core H41

Core H41 had a similar loss-on-ignition profile to core H22 with inorganics dominant at 60 to 75% content throughout the core, and a slight increase above 8 cm (Fig. 8). Carbonate content mirrored inorganics with 25 to ~30% content below 8 cm, and a decreasing trend to < 25% above 8 cm. Organic content remained low in core H41 at between 5.5 and 6.5%. In a pattern similar to core H22, biogenic silica decreased during the 1960s and remained at 1.4 to 2.0% through 1991 (Fig. 12). After 1991, biogenic silica content increase upcore from 1.4 to 3.5%, a 2.5-times increase (Fig. 12)

Core H41 had a detectable  $^7\text{Be}$  inventory to 1.25 cm with rapid state mixing of the most recent 2.4 years of sedimentation (Table 4).  $^{210}\text{Pb}$  activity declined logarithmically from the core top and reached supported levels below 31 cm (Fig. 8). The top 31 cm of core included sediments deposited since 1850 with the last 50 years of sedimentation in the top 17 cm of core H41. Sedimentation rates increased from the base of the core to 20 cm and then remained relatively constant at ca.  $0.13 \text{ g/cm}^2 \text{ yr}$  upcore (Fig. 8).

### Core X2

Core X2 had the lowest inventory of  $^7\text{Be}$  among core sites providing the first evidence of its extremely low sedimentation rate (Table 4).  $^7\text{Be}$  was detectable and mixed to only 0.5 cm, which incorporated the most recent 4.9 years of sedimentation (Table 4).  $^{210}\text{Pb}$  activity decreased downcore and reached supported levels below 5 cm (Fig. 8). The top 5 cm of the core incorporated the last 200 year of sedimentation, with the last 50 years contained in the top 2.25 cm (Fig. 8). There was little variation in sedimentation rate at station X2, which remained at about  $0.015 \text{ g/cm}^2 \text{ yr}$  over the last 200 years. Based on these analyses, we determined that station X2 is only a marginal depositional site and because of its slow sedimentation rate we were not able to sample core X2 sediments from 1960 to 2009 in sufficient resolution for this project.

## Diatom stratigraphy in sediment cores

Stratigraphies of percent abundance of the predominant diatom species or species groups are plotted for each core against the  $^{210}\text{Pb}$  modeled date for each core section (Figs 9-12). For comparison and to assist in interpreting the timing and impact of diatom community changes, DCA axis scores, total diatom abundance (millions of diatoms per g dry sediment), biogenic silica content, sedimentation rate, and historical densities (animals/m<sup>2</sup>) of *Diporeia* spp., and zebra and quagga mussels are plotted for each core or sampling station (Figs 9-12).

### Core B4

DCA Axis 1 explained 60.1% of the variance in the diatom communities preserved in core B4. Axis 1 scores indicate a steady and directional change in diatom community turnover between 1960 and 2009, rather than abrupt community changes (Fig. 9). Three species or species groups – *Aulacoseira islandica*, *A. subarctica*, and the large *Stephanodiscus* spp. (primarily *S. niagarae*, *S. alpinus*, and *S. subtransylvanicus*) – decrease in percent abundance upcore (Fig. 9). In contrast, the small *Cyclotella* spp. (including *C. delicatula*, *C. comensis*, *C. ocellata*, and three small undescribed morphotypes) and small *Stephanodiscus* spp. (mostly *S. minutulus* and *S. parvus*) increase in relative abundance upcore (Fig. 9). The percent abundance of the planktonic araphid species (especially *Fragilaria crotonensis* and *Asterionella formosa*) showed little

change in core B4. Total diatom abundance remained constant from 1960 to 1998, but has increased five-fold since (Fig. 9).

#### Core C5

Sediments dated from 1970 to 2009 were analyzed for diatom communities at station C5. An earlier age model for core C5 had to be corrected and sediments initially dated at 1960 were adjusted to 1970 (Fig. 8). Over 61.2% of the variance in diatom species composition in core C5 was explained by DCA axis 1. Axis 1 scores became more negative moving upcore indicating a steady directional turnover between 1970 and 2009 (Fig. 10). The two *Aulacoseira* species, *A. islandica* and *A. subarctica*, decreased in percent abundance moving upcore, and shared that pattern with the less abundant large *Stephanodiscus* spp. (mostly *S. alpinus*) (Fig. 10). In contrast, the small *Cyclotella* spp., the small *Stephanodiscus* spp. (*S. hantzschii*, *S. minutulus*, *S. parvus*) and the grouped planktonic araphid diatoms (primarily *Fragilaria crotonensis* and *Asterionella formosa*) increased in relative abundance moving upcore (Fig. 10). The small *Cyclotella* species group in core C5 included *C. comensis*, *C. delicatula*, *C. michiganiana*, *C. ocellata*, and four undescribed and provisionally named morphotypes including *Cyclotella* sp. #6 *GLRD*, *Cyclotella* sp. *mich-like*). Total diatom abundance increased upcore with a slight increase between 1982 and 1986, and a more substantial increase after 1998, which accounted for up to a two-fold increase (Fig. 10).

#### Core H22

DCA axis 1 accounted for 34.8% of the variation in species data from shallow station H22. *Aulacoseira islandica*, *A. subarctica*, and the large *Stephanodiscus* species (mostly *S. alpinus*) were much less abundant at H22 compared to B4 and C5, but showed similar trends in decreasing abundance upcore (Fig. 11). The small *Cyclotella* spp., dominated by *C. comensis* and secondarily by *C. delicatula*, *C. ocellata*, and *C. sp. #6GLRD*, are the most common planktonic group in core H22 and show a large increase in percent abundance between 1976 and 1994, before decreasing in abundance towards the top of the core (Fig. 11). The small *Stephanodiscus* spp. (*S. hantzschii*, *S. parvus*, and *S. minutulus* in core H22) show little pattern in percent abundance until increasing dramatically in the 2009 sample. Abundance of planktonic araphids in core H22 was controlled by abundance of *Fragilaria crotonensis* and secondarily by *Tabellaria flocculosa* (Fig. 11). *Tabellaria flocculosa* was more common between 1960 and 1985, whereas *Fragilaria crotonensis* increased in abundance from 1976 to 1999 before declining in abundance to the core top. Benthic diatoms were an important component of the diatom assemblage in core H22 accounting for 15 to 45% of the community (Fig. 11); their stratigraphy was characterized by peaks in percent abundance in the early 1970s and between 2004 to 2009. Both peaks are primarily reflecting peaks in abundance of *Staurosirella pinnata*, although *Staurosira construens* var. *venter* was also abundant in sediments deposited before 1990. Total diatom abundance in core H22 was very low from the mid-1960s through the early 1980s and at several core levels, counts had to be truncated due to low abundance (1968.8, 1973.9; Fig. 11). Diatom abundance rapidly increased after the early 1980s resulting in about a six-fold increase in diatom abundance between 1984 and 2009 at the core surface (Fig. 11).

#### Core H41

DCA axis 1 explained 49.2% of variance in species data. Core H41 showed the most species turnover among the cores as axis 1 scores shifted positive in the 1970s through 1987, and again

between 2005 and 2008 (Fig. 12). Sediments dated from 1960 to 1969 were characterized by abundance peaks of *Aulacoseira subarctica*, *A. islandica*, the small *Cyclotella* species *C. comensis*, and *Tabellaria flocculosa* (Fig. 12). Sediments dated from 1972 to 1987 had lower abundance of the two main *Aulacoseira* spp., but strong peaks in abundance of *Fragilaria crotonensis*, and three small *Cyclotella* spp. (*C. comensis*, *C. sp. #6GLRD*, *C. sp. mich-like*). Sediments dated from 1991 through 2002 returned to being dominated by *A. subarctica* and *A. islandica* (Fig. 12). Other diatoms that are common during this time include *Tabellaria flocculosa*, the benthic species *Staurosirella pinnata* and *Staurosira construens* var. *venter*, and lower abundance of *Fragilaria crotonensis* (Fig. 12). The uppermost sediments in core H41 are dated 2005-2008 and have relative abundance peaks of *Fragilaria crotonensis*, *Cyclotella delicatula*, *C. sp. #6GLRD*, *C. sp. mich-like*, and *Stephanodiscus parvus* (Fig. 12). Benthic diatom are common in core H41 at 10 to 20% abundance, but increase in abundance in the top three samples dated from 2005 to 2008 (Fig. 12). Similar to core H22, this increase is strongly driven by the percent abundance of *Staurosirella pinnata*. Total diatom abundance in core H41 is characterized by two peaks in abundance, first in the 1998 sample and second in the 2006 sample (Fig. 12). The two peaks in abundance represent three- and six-fold increases in total diatom abundance over relatively steady and lower abundances between 1960 and 1994.

## DISCUSSION

*Diporeia* spp. have historically dominated benthic biomass in offshore regions of the Great Lakes and functioned as the keystone element of the benthic-pelagic linkage (Nalepa 1989, Fitzgerald and Gardner 1993). However, *Diporeia* populations have declined precipitously in Lakes Michigan, Huron, Erie, and Ontario over the past several decades (Nalepa et al. 2006a, 2007, Barbiero et al. 2011). In southern Lake Michigan, the decline started in the nearshore regions in the late 1980s (Nalepa et al. 2006a) and initially coincided with the introduction and spread of the zebra mussel *Dreissena polymorpha*. With the later introduction and spread of the quagga mussel *D. r. bugensis*, the decline of *Diporeia* has continued its progression into offshore regions, areas once thought to be refugia (Nalepa et al. 2009, 2010). The mechanism of *Diporeia* demise has not been determined, although decreased quantity and quality of food resources due to changes in the algal community – food limitation as a result of lower lake productivity or direct competition with dreissenids – is a leading hypothesis (Nalepa et al. 2006a, Watkins et al. 2007, Fahnenstiel et al. 2010, Kainz et al. 2010). Other hypotheses that have been forwarded or tested include dreissenid pseudofeces toxicity, sediment toxicity, predation, and pathogens potentially introduced with dreissenid mussels (Landrum et al. 2000, Messick et al. 2004, Nalepa et al. 2006a, b, Watkins et al. 2007).

The focus of this study was to explore the primary hypothesis surrounding *Diporeia* decline – that changes in the quantity and quality of available food resources resulting from the introduction of dreissenids led to increased mortality in *Diporeia*. We combined gut content analysis of historical collections of *Diporeia* with analysis of diatom remains in sediment cores to examine differences in available food and its utilization between the pre- and post-dreissenid periods. We first discuss our results in the context of new understandings of recent and historical *Diporeia* feeding ecology and then consider the findings in the context of recent biological and geochemical changes specifically in southern Lake Michigan.

## ***Diporeia* feeding ecology**

Numerous studies have helped inform our understanding of the ecology of Great Lakes populations of *Diporeia* spp. (formerly *Pontoporeia hoyi*). *Diporeia* was historically the dominant macrobenthos in the Great Lakes inhabiting both shallow and profundal regions (Evans et al. 1990). For example, *Diporeia* composed historically up to 65% of the biomass, up to 70% of the caloric content, and numerically up to 30% of the macrozoobenthic community in southern Lake Michigan (Nalepa and Quigley 1981, Gardner et al. 1985, Winnell and White 1984). In contrast with other amphipods, *Diporeia* is an intermittent feeder, with deepwater populations having a more continuous feeding pattern than nearshore populations, perhaps in response to predation pressure (Evans et al. 1990). Feeding by *Diporeia* is strongly seasonal in SLM. Gut fullness is higher in May-June than in summer and fall (Quigley 1988, Evans et al. 1990). During spring, *Diporeia* lipid content increases significantly as the sedimented winter-spring phytoplankton bloom was consumed (Gardner et al. 1987). The combination of intermittent/seasonal feeding coupled with high lipid reserves allowed *Diporeia* to exploit the seasonal variability of high quality food resources in the Great Lakes (Gardner et al. 1987).

In spite of its keystone role as a detritivore driving benthic-pelagic coupling in the Great Lakes, the diet of *Diporeia* has not been well characterized. Contrasting studies have suggested, on one hand, that carbon intake by *Diporeia* is primarily bacteria-mediated (Marzolf 1965, Guiger and Barton 2002), whereas other studies showed high assimilation of sedimented algal carbon in the spring and minimal assimilation of microbially mediated carbon from decomposition (Fitzgerald and Gardner 1993). There is compelling research documenting that diatoms are a key component of the *Diporeia* diet; gut fullness is evident following spring and fall diatom bloom periods (Quigley 1988, Evans et al. 1990), sediment avoidance was reversed by enhancing sediments with cultured diatoms (Landrum et al. 2000), and *Diporeia* condition was enhanced in diatom-fed treatments (Kainz et al. 2010). Fitzgerald and Gardner (1993) showed that two *Aulacoseira* species accounted for 53% of the algal C flux to the sediments in spring 1990 at a 45-m deep southern Lake Michigan station, and that 61% of algal C was assimilated by *Diporeia*.

Gut content analysis remains a standard tool for better understanding food web dynamics, prey selectivity, feeding behavior, and energy flow (Chesson 1978, Edlund and Francis 1999, Huntsman et al. 2011). Studies on *Diporeia* have primarily used gut fullness to compare feeding behavior across sites, size classes, and seasons (Quigley 1988). Detailed analyses of Great Lakes *Diporeia* gut contents are few; Evans et al. (1990) reported that 99% of gut contents were "silt and other sediment," but that *Cyclotella* and *Aulacoseira* (as *Melosira*) fragments were frequently observed. Perhaps key to interpreting those observations that show minimal diatom content in guts is that when *Diporeia* are fed an exclusive diet of diatoms, little discernable evidence of the diatoms remains in the gut or fecal pellets, suggesting the efficient capacity of *Diporeia* to crush and grind food particles with both mouthparts and within the foregut (Quigley and Vanderploeg 1991). Studies of other *Diporeia* populations have suggested selectivity in feeding, the importance of algal resources, and variable assimilation efficiency among food types (Moore 1977, 1979).

Critical to determining the case for food limitation as the leading cause of *Diporeia* declines in SLM is the need to document historical changes in availability and utilization of food resources. Our analyses focused on diatoms in the diet of spring collections of *Diporeia* because previous research identified activity in May-June, following the spring diatom bloom, as the critical period for *Diporeia* feeding, growth, assimilation, and lipid storage (Gardner et al. 1987,

Quigley 1988, Evans et al. 1990). Our results confirmed several aspects of historical and modern ecology of *Diporeia*. Highly variable gut fullness across all sampling stations and years supported the intermittent feeding strategy previously reported for *Diporeia* (Quigley 1988, Evans et al. 1990). Body lengths of spring *Diporeia* showed uni- or bimodal size distributions confirming the two-year (rarely three-year) life history for most deepwater Lake Michigan populations of *Diporeia* (Winnell and White 1984). Of note in our results was loss of the small and medium size classes at station C5 in the 2009 samples and similarly loss of a small size class at station H22 in the 1992 samples. Loss of small-sized individuals may be a harbinger of the pending demise of *Diporeia* at these stations. Nalepa et al. (2006) reported continued recruitment in declining *Diporeia* populations but found a lack of survival to adulthood for young. We also showed that diatoms in the diets differed among sampling stations, notably along the depth gradient. *Diporeia* at shallow station H22 had greater abundance of planktonic araphid diatoms and benthic diatoms (plotted as "other" in Figs 5-7) in 1987 and 1992 compared with *Diporeia* collected at the deeper stations B4 and C5 during 1987 and 1998. Similar observations of greater littoral or benthic food resources contributing to *Diporeia* diets at shallower site have been made in lakes Michigan, Huron, and Superior (Evans et al. 1990, Guiguer and Barton 2002, Sierszen et al. 2006).

This was, however, the first study of Great Lakes *Diporeia* to specifically target species-level identification of diatom food resources using a combination of microscopic gut analysis, paleoecological analysis of resource changes, and application of selectivity indices. Results provided three new insights into *Diporeia* feeding ecology: dominance followed by a post-dreissenid decline of three key species in spring diets, high selectivity for those species, and differing selectivity among *Diporeia* size classes.

In all specimens analyzed from the pre- and post-dreissenid periods, three diatom species groups dominated the spring diet at all three sampling stations: *Aulacoseira islandica*, *A. subarctica*, and large *Stephanodiscus* spp. (including *S. niagarae*, *S. alpinus*, *S. subtransylvanicus*). These species have historically been common members of the Lake Michigan spring phytoplankton (Stoermer and Yang 1970, Barbiero and Tuchman 2001). At deep-water stations B4 and C5, *Aulacoseira islandica*, *A. subarctica*, and large *Stephanodiscus* spp. composed greater than 65% of the spring diatom diet in samples from 1987 through 2004. At shallow station H22, the three species composed over 69% of the spring diatom diets in 1987 and 1992. In the most recent 2009 samples from deep-water stations B4 and C5, spring *Diporeia* diets have become more varied with greater contribution of planktonic araphids and small *Stephanodiscus* and *Cyclotella* spp., especially at station B4. The three key diatoms targeted by *Diporeia* declined significantly in their contribution to 2009 spring diets, falling to less than 50% abundance at station B4 and only 65% abundance at station C5. This 2009 diet shift is concomitant with large changes in primary producers that are occurring throughout the southern basin (Fahnenstiel 2010a; see below).

Although gut fullness is often reported to be highest in spring, little evidence has been forwarded on dietary composition of *Diporeia* beyond "detritus" or "sediment". Fitzgerald and Gardner (1993) showed high assimilation of labeled *A. subarctica* (reported as *Melosira italica*), Landrum et al. (2000) amended sediment with cultures of *Fragilaria crotonensis* to reverse sediment avoidance by *Diporeia*, and Quigley and Vanderploeg (1991) fed *Melosira varians* to *Diporeia* to test feasibility of gut content analysis, although *M. varians* is normally only common in nearshore eutrophied areas of Lake Michigan (Stoermer and Yang 1969). Our analysis of guts prepared specifically for enumeration of diatom remains (Edlund and Francis 1999) provided the

first direct evidence of the significance of a few critical winter-spring diatom plankton species in the spring diet of *Diporeia*. Of perhaps greater importance is our finding that *Diporeia* diets have shifted significantly over time. Our data on overall trends in percent composition of diatoms in *Diporeia* diets showed there was greater variety of diatoms in *Diporeia* diets in 2004 and 2009 samples from stations B4 and C5, compared to samples from 1987 and 1998. Analysis of variance showed statistically significant diet differences between 1987 and 2009 at station B4 with a decreased proportion of *Aulacoseira islandica*, *A. subarctica*, and large *Stephanodiscus* spp. in diets, and an increased proportion of planktonic araphids and small *Cyclotella* and *Stephanodiscus* spp.

Application of Chesson's selectivity index to *Diporeia* diets and potential food sources provided further detail on historical and modern feeding ecology of *Diporeia*. *Diporeia* showed high preference for five large-sized prey species including *Aulacoseira subarctica*, *A. islandica* and the large *Stephanodiscus* species *S. niagarae*, *S. alpinus*, and *S. subtransylvanicus*. Further, large *Diporeia* showed an even stronger preference for the two *Aulacoseira* species, whereas small *Diporeia* preferred large *Stephanodiscus* species. We treated large *Stephanodiscus* as separate species in calculating Chesson's index so the strong selection trend in small *Diporeia* for large *Stephanodiscus* spp. as a group was not as clear (compare Figs 5-7 to Table 3). Previous research on *Diporeia* ecology had considered the importance of feeding on the spring diatom bloom, but provided no evidence to suggest that Great Lakes *Diporeia* was capable of selective feeding. That these five large diatom species were found in much greater abundance in *Diporeia* guts than in dated sediment core levels is clear evidence of highly selective springtime feeding by *Diporeia* and suggests even higher selectivity in more recent samples as the five key prey species have been decreasing in relative abundance.

Similarly, other diatom groups were strongly negatively selected in the diets of *Diporeia*. This list includes some common spring diatoms such as *Fragilaria crotonensis* and others that are often members of the summer plankton or deep chlorophyll layer such as small *Cyclotella* species (Barbiero and Tuchman 2001, Kerfoot et al. 2010). Our data suggest that as preferred food items have declined in abundance, *Diporeia* has had to change its diet to feed on diatom groups on which they were not feeding in the pre-dreissenid period.

### **Have recent changes in SLM affected food quantity and quality for *Diporeia*?**

By the 1960s and 1970s, the condition of Lake Michigan had become severely deteriorated from nutrient loading, accumulation of toxic substances, overharvest of fishes, introduced species such as the lamprey *Petromyzon marinus* and alewife *Alosa pseudoharengus*, and destruction of habitat (Jude and Leach 1999, Jude et al. 2005). Passage of the Clean Water Act, the Clean Air Act, and the Great Lakes Water Quality Act addressed nutrient and toxic substances while the introduction of salmonines hastened recovery of the sport fishery. By the 1980s lake conditions were improving. Unfortunately, continued introduction of invasive, and especially Ponto-Caspian species (Vanderploeg et al. 2002) such as the zebra and quagga mussels and the predatory zooplankter *Bythotrephes*, led to severe disruptions in the Lake Michigan ecosystem.

Fahnenstiel et al. (2010a) presented a compilation of studies summarizing the growing body of evidence of rapid recent change in the southern Lake Michigan ecosystem. Changes occurred at all levels of the food web, at nearshore and offshore stations, and resulted in an ecosystem state that was not previously observed. Many of the trends began decades ago (Barbiero et al. 2005), and the current state cannot be attributed to a single cause or process, although introduction and spread of dreissenid mussels must be implicated. Overall, changes in

southern Lake Michigan reflect recent oligotrophication of the system; total phosphorus, phytoplankton productivity, plankton biomass, and spring chlorophyll have declined, while water clarity has increased (Dobiesz and Lester 2009, Fahnenstiel et al. 2010b, Mida et al. 2010). Within the phytoplankton community, dramatic changes in the spring bloom community have resulted in fewer diatoms, chrysophytes, and cryptophytes, coupled with a springtime increase in blue-green algae; less change has occurred in the summer plankton community (Fahnenstiel et al. 2010b). As such, silica utilization has decreased in spring resulting in measurable epilimnetic silica levels remaining in spring and summer (Evans et al. 2011). Nitrates have also increased in spring and summer, as nitrate utilization declined (Mida et al. 2010). Apart from lower biomass and shifts in contribution of major phytoplankton groups, few studies have examined species-level changes in Lake Michigan phytoplankton. Reavie and Barbiero (in press) compared monitoring data from the 1990s with similar data from the late 2000s and showed that spring cell size of centric diatoms in spring has decreased, whereas cell size of spring pennate diatoms has increased in the lake. Strongly contributing to this change are declines in cell size of the large *Stephanodiscus* species, *S. subtransylvanicus* and *S. niagarae*.

Beyond changes in nutrients and primary producers, changes in secondary consumers have also been dramatic in SLM. The invasion and spread of zebra mussels followed by the introduction and spread of quagga mussels has brought the most dramatic change (Nalepa et al. 2009, Fahnenstiel et al. 2010a). The nearshore and profundal environment has been re-engineered (Hecky et al. 2004), energy flow has been shifted to nearshore and benthic zones, and ultimately the dreissenid invasion has been implicated in wide-ranging effects on nearly all aspects of the lakes: water clarity, biogeochemistry, primary producer communities, grazers, fisheries, and benthic macroinvertebrates (Madenjian et al. 2002, Barbiero et al. 2009, 2011, Nalepa et al. 2009, Fahnenstiel et al. 2010b, Pothoven et al. 2010, ).

The widespread decline of the benthic macroinvertebrate *Diporeia* is perhaps the most dramatic change in the benthic environment. Populations had apparently increased in the southern basin during the 1970s and 1980s, especially at depths <50 m, compared with the 1960s (Nalepa 1987) as a result of increased organic material settling to the bottom. The *Diporeia* declines began in the early 1990s, proceeded from nearshore stations to offshore stations (Nalepa et al. 2006a, b), and have continued as quagga mussels rapidly colonized profundal areas of southern Lake Michigan (Nalepa et al. 2009). Initial evidence from population structure (poor recruitment or poor survival of young) and measurements of physiological stress (as low lipid content) in declining populations suggested that food limitation might be the probable cause of the *Diporeia* declines (Nalepa et al. 2006a). However, the case for food limitation has not been fully resolved, because there are instances of *Diporeia*-dreissenid coexistence, continued sedimentation of apparently high-quality food resources, and lack of spatial correspondence between the *Diporeia* decline and dreissenid increase (Nalepa et al. 2006a, b, Watkins et al. 2007).

To link changes in the primary producer community with continued declines in *Diporeia*, this study took a new approach by exploring how *Diporeia* diets have shifted during the course of the dreissenid invasion with consideration of dietary selectivity, and how the quantity and quality of potential food resources have changed over time. The study focused solely on the diatom component of the spring diet, a known and critical dietary component for Great Lakes *Diporeia* (Fitzgerald and Gardner 1993, Nalepa et al. 2006a), although we fully recognize that additional prey items and bacterially mediated carbon may be utilized by *Diporeia*. Our findings show that until recently a few species groups of diatoms (*Aulacoseira islandica*, *A. subarctica*,

and large *Stephanodiscus* spp.) dominated spring diets of *Diporeia*, and there was high selectivity for these species from among the diatoms available in the sediments. Sediment cores taken at similar stations record changes in the sedimented diatom community and their profiles facilitated our interpretation of the link between food resources, dreissenid colonization, and *Diporeia* at each site (Figs 9-12).

Chronologies of diatom changes as derived from the sediment cores at stations B4, C5, and H22 showed similar temporal patterns: the relative proportion of the three diatom species groups preferred by *Diporeia* (*Aulacoseira islandica*, *A. subarctica*, and large *Stephanodiscus* spp.; Figs 9-11) decreased between 1960 and 2009. The change in diatom communities that was recorded in the cores corresponded with overall shifts reported in recent and long-term phytoplankton data from southern Lake Michigan (Barbiero and Tuchman 2001, Fahnenstiel et al. 2010b).

At deep station B4 the decline in the preferred prey was gradual but began in the early 1980s and was accompanied by an increase in small *Cyclotella* and *Stephanodiscus* spp. (Fig. 9). Small *Stephanodiscus* spp. have further increased in abundance since the mid-2000s (Fig. 9). *Diporeia* at station B4 declined in abundance slightly since the 1980s but are still present (Fig. 9; Nalepa et al. 2006a). Quagga mussels were first recorded at station B4 in 2008 (Fig. 9).

At deep station C5, quagga mussels were first recorded in 2007; their arrival at the station coincided with a rapid decline in *Diporeia* density (Fig. 10). Decreasing percent abundance of the preferred diatom species groups began at station C5 ca. 1980; in contrast, araphid planktonic diatoms and the small *Cyclotella* and *Stephanodiscus* spp. increased in relative abundance since 1980 (Fig. 10).

At shallow station H22, the decline of all three preferred prey groups began in the early 1980s to reach the lowest abundances of all three coring sites by 2009. This decline was accompanied by rapid increases in small *Cyclotella* spp. and planktonic araphids, increases that began somewhat earlier in the mid-1970s (Fig. 11). Unique to station H22 are decreased relative abundances of small *Cyclotella* spp. and planktonic araphids since ca. 2000, with increased percent abundance of benthic diatoms between 2000 and 2009 likely in response to clearing of Lake Michigan waters and increased light and nutrient availability at the bottom as a result of dreissenid filtering (Fig. 11). *Diporeia* populations disappeared at station H22 between 1992 and 1994, presaging the arrival of zebra mussels in 1998 and quagga mussels in 2002 (Fig. 11).

Shallow station H41 is not regularly sampled for macrobenthos by NOAA biologists and animal densities of *Diporeia* and zebra and quagga mussels are reported from nearby station H31. In the core from shallow station H41, the preferred prey groups (*Aulacoseira islandica*, *A. subarctica*, and large *Stephanodiscus* spp.) had already declined in abundance between 1960 and 1987, but were well represented in the cores again by the time zebra mussels started heavily colonizing H31 in the early 2000s (Fig. 12). *Diporeia* declined at station H31 between 1994 and 2000 before the site had been heavily colonized by zebra mussels (Fig. 12). Quagga mussels were first recorded at station H31 in 2001 and reached densities of over 7000 animals/m<sup>2</sup> by 2004. Coincident with the colonization of H31 by quagga was the rapid decline of the preferred prey groups of *Diporeia* and increased abundance of less preferred small *Cyclotella* spp. and benthic diatoms. An assessment of *Diporeia* feeding ecology at station H31 was not possible; collections of *Diporeia* were only available from 1992 at station H31 and unfortunately those collections did not have well preserved gut contents.

Changes recorded in the cores suggest that food quality declined in southern Lake Michigan beginning in the 1980s, perhaps in response to nutrient abatement, but became more

pronounced after the introduction and spread of dreissenids. The three diatom groups preferred and selected in *Diporeia* diets, *Aulacoseira subarctica*, the large *Stephanodiscus* spp., and especially *A. islandica*, have historically been common components of the winter and spring phytoplankton of southern Lake Michigan (Stoermer and Yang 1969, Stoermer and Tuchman 1980, Barbiero and Tuchman 2001, Kerfoot et al. 2010, Reavie and Barbiero in press). Paleoecological and historical records show *A. subarctica* to only have become relatively abundant in Lake Michigan beginning in the 1950s (Stoermer and Yang 1970, Stoermer et al. 1985). The three species groups are relatively large diatoms and are further known to rapidly settle from the water column upon stratification and silica limitation, settling fast enough that they avoid zooplankton grazing (Gardner et al. 1987, Fitzgerald and Gardner. 1993, Gibson et al. 2003). Diatoms shift their physiology with sinking and silica limitation to form resting cells and increase their storage of carbohydrates and lipids (Gibson and Foy 1988, Sicko-Goad et al. 1989, Gibson and Fitzsimons 1990), a strategy that has historically provided rapid delivery of highly preferred, large, lipid-rich cells to the sediment surface, which resulted in high grazing and rapid accumulation of storage products by *Diporeia*. All sediment cores indicated a decline in these three species groups concomitant with overwhelming numerical increases in the smaller, much less preferred and often negatively selected species such as the planktonic araphids and the small *Cyclotella* and *Stephanodiscus* spp..

More difficult to reconcile from this study is whether the quantity of food available to *Diporeia* has changed over time. All sediment cores show increased absolute abundance of diatoms in the more recent sediments deposited at each core site; diatoms increased two-fold at station C5 after 1997 (Fig. 10), five-fold at station B4 after 1998, (Fig. 9), and up to six-fold at shallow stations H22 and H41 after the late 1980s (Figs 11, 12). However, these increases in absolute abundance of diatoms contrast with temporal changes in biogenic silica content. Sediment profiles of biogenic silica indicated a much lower change in quantity of food reaching the sediments. Biogenic silica content increased only 0.6 times at station C5 after 1997, was little changed at station B4 after 1998, increased only two-fold at station H22 after the late 1980s, and 2.5-times at station H41 after 1994. These small increases in biogenic silica deposition relative to large increases in diatom numbers were consistent with the observed shift in diatom composition. That is, because of the recent shift to smaller taxa such as planktonic araphids and small-sized *Cyclotella* and *Stephanodiscus* spp., less biogenic silica would be reaching the sediments relative to diatom numbers.

As our diet data showed, species groups that have recently increased in absolute and relative abundance in the sediments are much less preferred and negatively selected in the spring diets of *Diporeia*. The preferred prey items of *Diporeia* have decreased in relative abundance, while selectivity for them has increased over time as *Diporeia* must contend with finding fewer preferred prey species among increasing numbers of lower quality food, thus feeding efficiency declines. Our findings of strong preference and selectivity for specific diatom species by *Diporeia*, coupled with corroborating evidence from sediment cores of significant changes in quality and potentially quantity of the pelagic rain of planktonic diatoms, provide a more detailed mechanism and further support that food limitation – through loss of preferred prey species – has played a role during the demise of *Diporeia* populations and expansion of dreissenids in southern Lake Michigan. We still cannot rule out other factors and interactions that may be impacting *Diporeia* populations throughout the Great Lakes.

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## TABLES

**Table 1.** Sampling station, latitude, longitude, depth at station, and dates of collection of *Diporeia* samples that were analyzed for gut contents.

Lake Michigan Station	Latitude (°N) Longitude (°W)	Depth (m)	Spring <i>Diporeia</i> Samples
H22	42°08.35' N 86°39.83' W	46	05 June 1987, 19 May 1992
B4	42°23.50' N 87°01.00' W	129	04 June 1987, 22 May 1998, 26 May 2004, 11 May 2009
C5	42°49.00' N 86°50.00' W	157	03 June 1987, 11 May 1998, 27 May 2004, 11 May 2009

**Table 2.** Sediment cores collected on 11-12 May 2009 aboard the R/V *Laurentian* on southern Lake Michigan (Mich). Station number, latitude, longitude, depth at station, and length of core recovery are given.

Core	Station	Date	Lat (N)	Long (W)	Depth (m)	Recovery (cm)
Lake Mich C5	C5	11 May 2009	42°48.606'	86°50.167'	127 m	48 cm
Lake Mich B4	B4	11 May 2009	42°23.459'	87°00.930'	124 m	43 cm
Lake Mich H22	H22	12 May 2009	42°08.416'	86°39.871'	52 m	56 cm
Lake Mich H41	H41	11 May 2009	42°52.472'	86°21.301'	57 m	78 cm
Lake Mich X2	H22	11 May 2009	43°11.983'	86°30.963'	101.0 m	37 cm

**Table 3a.** Chesson's preference index ( $\alpha_i$ ) for diatom prey determined from percent composition in *Diporeia* diets and in a sediment core from Lake Michigan station B4 for up to three different *Diporeia* size groups (LG = large, MD = medium, and SM = small) during up to four periods: 1987 (pre-dreissenids) and 1998, 2004, 2009 (post-dreissenids). O = neutral preference ( $\alpha_i = 0.04$ ), P = moderately preferred ( $0.04 < \alpha_i \leq 0.08$ ), PP = preferred ( $\alpha_i > 0.08$ ), N = moderate negative selection ( $0.02 \leq \alpha_i < 0.04$ ), NN = negative selection ( $0 \leq \alpha_i < 0.02$ ). *Diporeia* exhibited neutral or moderately negative preference for the following 11 taxonomic groups (which were deleted from the table to save space) found in the sediments: *Stephanodiscus minutulus*, *Cyclotella delicatula*, chrysophyte cysts, unidentified fragments, *S. parvus*, *Asterionella formosa*, *Cyclotella* sp. "short str rough", *Cyclotella* sp. 1CSP, *Nitzschia* spp., *Cyclotella mich-like*, and miscellaneous rare species.

<b>Station</b>	<b>B4</b>			<b>B4</b>			<b>B4</b>			<b>B4</b>		
<b>Year</b>	<b>1987</b>			<b>1998</b>			<b>2004</b>			<b>2009</b>		
<b><i>Diporeia</i> size class</b>	LG	MD	SM									
<b>Diatom Taxon</b>												
<i>Aulacoseira subarctica</i>	P	O	N	P	PP	NN	P	PP	N	P	P	N
<i>Aulacoseira islandica</i>	PP	P	N	N	N	NN	PP	PP	PP	P	P	O
<i>Steph niagarae</i>	PP	PP	P	PP	PP	PP	PP	PP	PP	P	PP	PP
<i>Stephanodiscus subtransylvanicus</i>	PP	PP	P	PP	P	PP	N	O	N	PP	PP	PP
<i>Steph alpinus</i>	P	PP	P	PP	N	N	P	P	PP	N	N	N
<i>Frag crotonensis</i>	NN	NN	NN	NN	NN	NN	NN	P	NN	P	O	O
<i>Cycl ocellata</i>	NN	NN	NN	NN	NN	NN	P	O	NN	N	N	N
<i>Tab flocculosa</i>	PP	PP	NN	NN	NN	NN	NN	NN	NN	NN	NN	NN
<i>Cyclotella "tiny"</i>	N	NN	NN	NN	NN	NN	NN	NN	NN	P	P	N
<i>Syn ulna + vars</i>	P	N	NN	NN	NN	NN	NN	NN	NN	PP	PP	PP
<i>Cyclotella pseudostelligera</i>	NN	NN	NN	NN	NN	NN	PP	PP	NN	PP	PP	P
<i>Cycl comensis</i>	NN	NN	NN	NN	NN	NN	NN	NN	NN	PP	PP	N
<i>Frag vaucheriae</i>	P	NN	NN	NN	NN	NN	NN	NN	NN	NN	NN	NN
<i>Frag intermedia v. fallax</i>	NN	NN	NN									
<i>Cycl radiosa</i>	NN	NN	NN									

**Table 3b.** Chesson's preference index ( $\alpha_i$ ) for diatom prey determined from percent composition in *Diporeia* diets and in a sediment core from Lake Michigan station C5 for up to three different *Diporeia* size groups (LG = large, MD = medium, and SM = small) during up to four periods: 1987 (pre-dreissenids) and 1998, 2004, 2009 (post-dreissenids). O = neutral preference ( $\alpha_i = 0.04$ ), P = moderately preferred ( $0.04 < \alpha_i \leq 0.08$ ), PP = preferred ( $\alpha_i > 0.08$ ), N = moderate negative selection ( $0.02 \leq \alpha_i < 0.04$ ), NN = negative selection ( $0 \leq \alpha_i < 0.02$ ). See Table 3a for list of diatoms taxa for which *Diporeia* exhibited neutral or moderately negative preference.

<b>Station</b>	C5			C5			C5			C5
<b>Year</b>	1987			1998			2004			2009
<b><i>Diporeia</i> size class</b>	LG	MD	SM	LG	MD	SM	LG	MD	SM	LG
<b>Diatom Taxon</b>										
<i>Aulacoseira subarctica</i>	PP	PP	N	PP	PP	PP	PP	NN	O	PP
<i>Aulacoseira islandica</i>	O	N	N	N	NN	P	PP	N	PP	PP
<i>Steph niagarae</i>	NN	NN	NN	NN	NN	NN	PP	P	PP	NN
<i>Steph subtransylvanicus</i>	PP	PP	PP	PP	PP	PP	NN	NN	NN	PP
<i>Steph alpinus</i>	PP	PP	PP	PP	PP	PP	NN	NN	NN	N
<i>Frag crotonensis</i>	NN	NN	NN	NN	NN	NN	NN	NN	NN	NN
<i>Cycl ocellata</i>	NN	NN	NN	NN	NN	NN	NN	NN	NN	O
<i>Tab flocculosa</i>	N	NN	NN	NN	NN	NN	PP	NN	NN	NN
<i>Cycl "tiny"</i>	NN	NN	NN	NN	NN	NN	NN	NN	NN	N
<i>Syn ulna + vars</i>	NN	NN	NN	NN	NN	NN	NN	NN	NN	N
<i>Cycl pseudostelligera</i>	NN	NN	NN	NN	NN	NN	NN	NN	NN	NN
<i>Cycl comensis</i>	NN	NN	NN	NN	NN	NN	NN	NN	NN	PP
<i>Frag vaucheriae</i>	NN	NN	NN	NN	NN	NN	NN	NN	NN	NN
<i>Frag intermedia v. fallax</i>	NN	NN	NN	NN	NN	NN	NN	PP	NN	NN
<i>Cycl radiosa</i>	NN	NN	NN	NN	NN	NN	PP	NN	PP	N

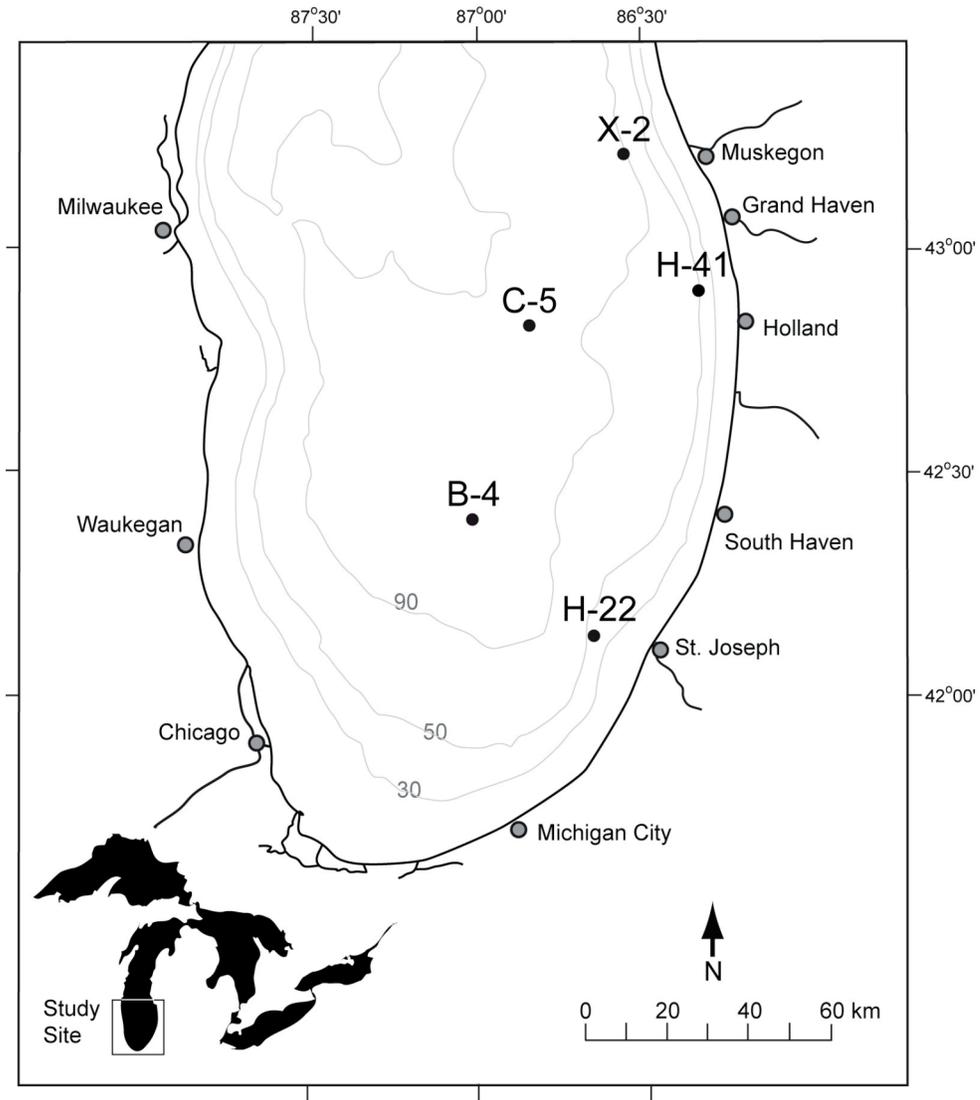
**Table 3c.** Chesson's preference index ( $\alpha_i$ ) for diatom prey determined from percent composition in *Diporeia* diets and in a sediment core from Lake Michigan station H22 for up to three different *Diporeia* size groups (LG = large, MD = medium, and SM = small) during two periods: 1987 (pre-dreissenids) and 1992 (post-dreissenids). O = neutral preference ( $\alpha_i = 0.04$ ), P = moderately preferred ( $0.04 < \alpha_i \leq 0.08$ ), PP = preferred ( $\alpha_i > 0.08$ ), N = moderate negative selection ( $0.02 \leq \alpha_i < 0.04$ ), NN = negative selection ( $0 \leq \alpha_i < 0.02$ ). See Table 3a for list of diatom taxa for which *Diporeia* exhibited neutral or moderately negative preference.

<b>Station</b>	H22			H22	
<b>Year</b>	1987			1992	
<b><i>Diporeia</i> size class</b>	LG	MD	SM	LG	MD
<b>Diatom Taxon</b>					
<i>Aulacoseira subarctica</i>	P	NN	N	PP	PP
<i>Aulacoseira islandica</i>	P	N	N	PP	P
<i>Steph niagarae</i>	NN	NN	NN	PP	PP
<i>Steph subtransylvanicus</i>	N	P	P	NN	NN
<i>Steph alpinus</i>	PP	PP	PP	NN	NN
<i>Frag crotonensis</i>	NN	NN	NN	NN	NN
<i>Cycl ocellata</i>	NN	NN	NN	NN	NN
<i>Tab flocculosa</i>	PP	PP	PP	N	NN
<i>Cycl "tiny"</i>	NN	NN	NN	NN	NN
<i>Syn ulna + vars</i>	NN	NN	NN	NN	NN
<i>Cycl pseudostelligera</i>	NN	NN	NN	NN	NN
<i>Cycl comensis</i>	NN	NN	NN	NN	NN
<i>Frag vaucheriae</i>	NN	NN	NN	NN	NN
<i>Frag intermedia v. fallax</i>	NN	NN	NN	NN	NN
<i>Cycl radiosa</i>	P	NN	NN	NN	NN

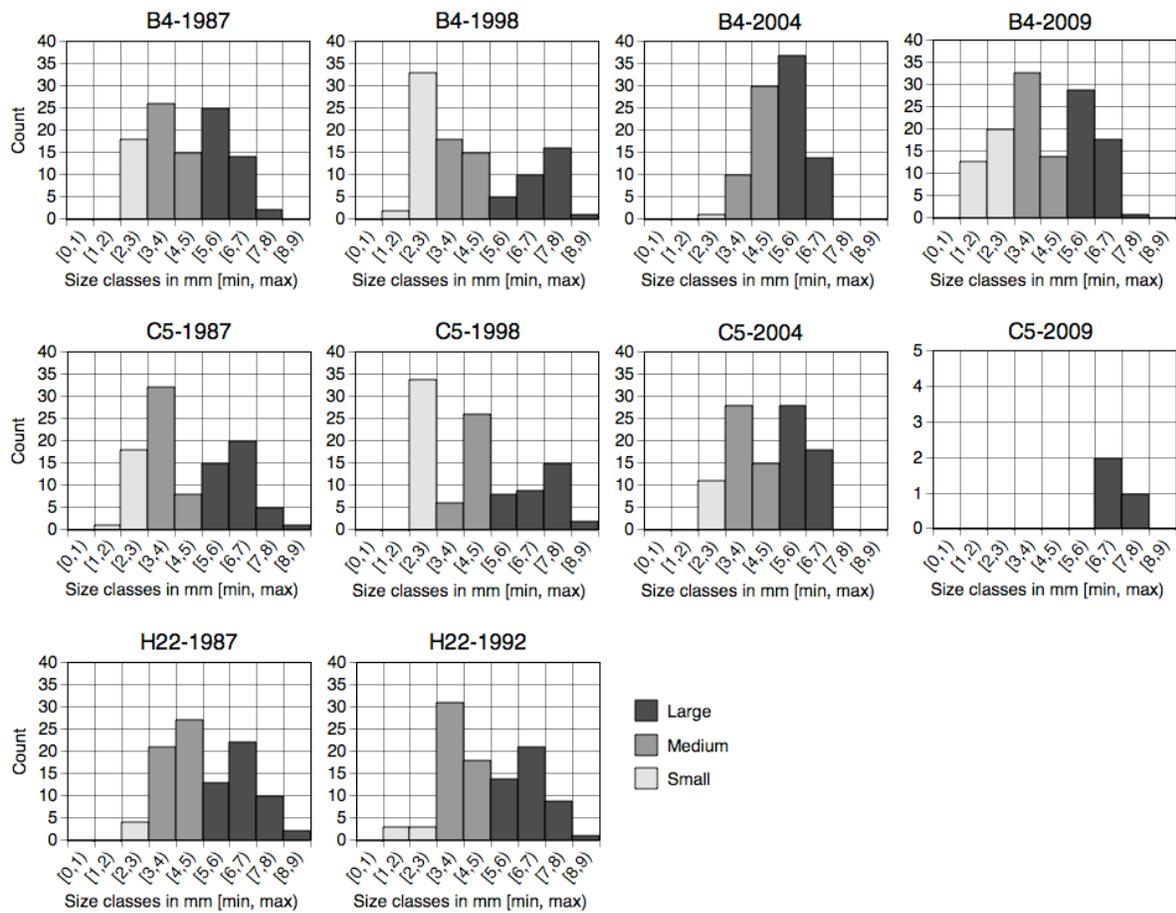
**Table 4.** Inventory (pCi/g of freeze-dried sediment) of  $^7\text{Be}$  and  $^{137}\text{Cs}$  in selected core depths (given in top and bottom [Btm] depths of core section) in box cores from five sampling stations (H22, C5, B4, X2, H41) in southern Lake Michigan. Cells without values represent core levels that were not analyzed. The amount of time included in the mixed depth of each core is given in years.

Depth (cm)		H22		C5		B4		X2		H41	
Top	Btm	Be-7 (pCi/g)	Cs-137 (pCi/g)								
0.00	0.25	5.05	0.61	2.77	4.13	4.42	5.12	0.7	1.64	5.36	0.59
0.25	0.50	5.18	0.65	1.79	4.52	4.32	5.57	0.5	1.13	2.85	0.67
0.50	0.75	3.80	0.64	0.6	4.23	2.56	5.08			2.8	0.83
0.75	1.00					3.42	5.45			0.67	0.85
1.00	1.25	1.22	0.74	0	4.67	0	4.93			0.5	0.7
1.25	1.50										
1.5	1.75	0	0.79								
Years mixed		0.8		2.7		5.3		4.9		2.4	

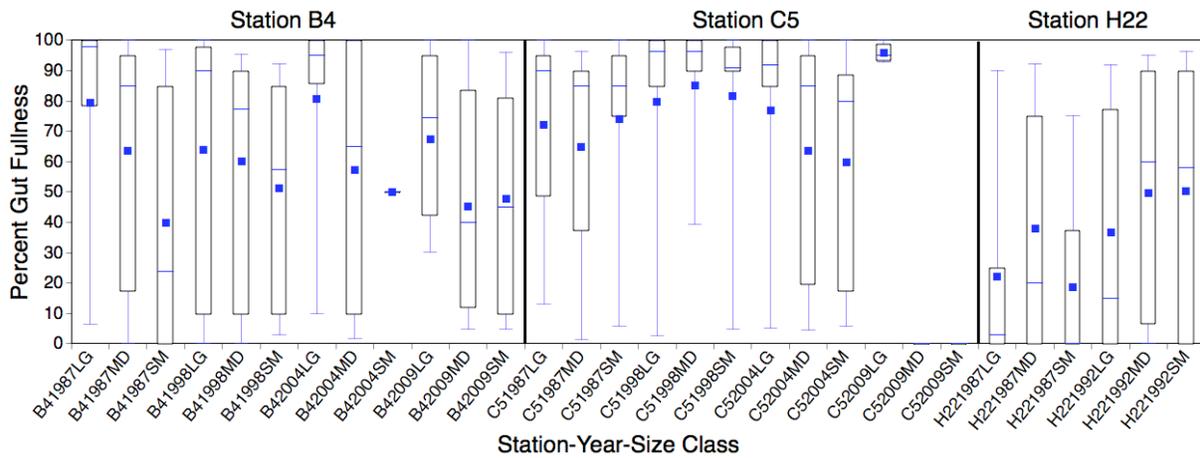
**FIGURES**



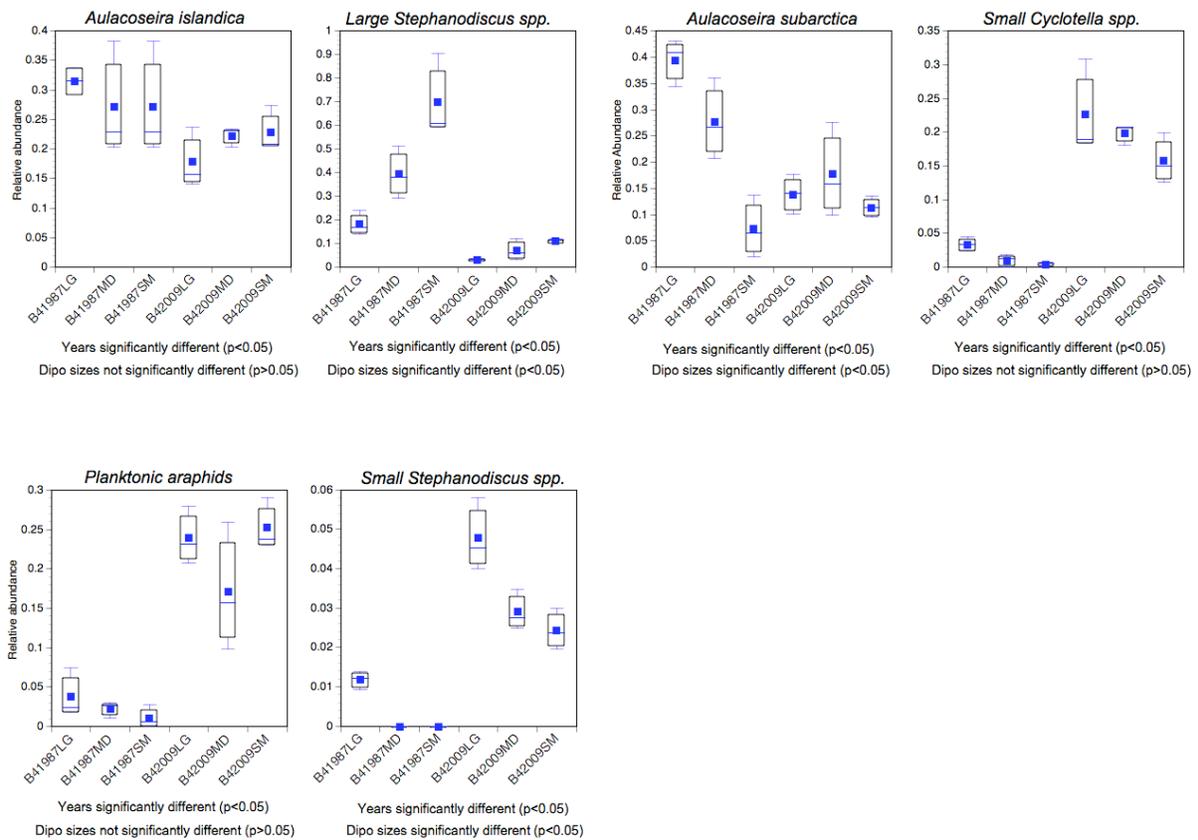
**Figure 1.** Map of southern Lake Michigan with *Diporeia* and sediment core stations indicated. Bathymetric units in meters.



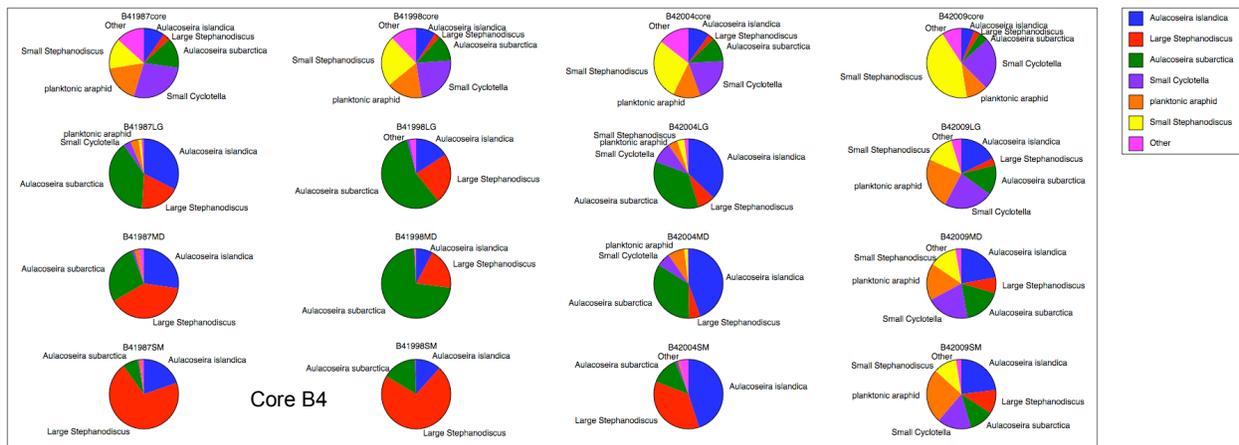
**Figure 2.** Size frequency histograms of *Diporeia* length (mm) at three stations (B4, C5, H22) in southern Lake Michigan. Bar shading refers to *Diporeia* size classes: white-small, gray-medium, black-large (see Methods).



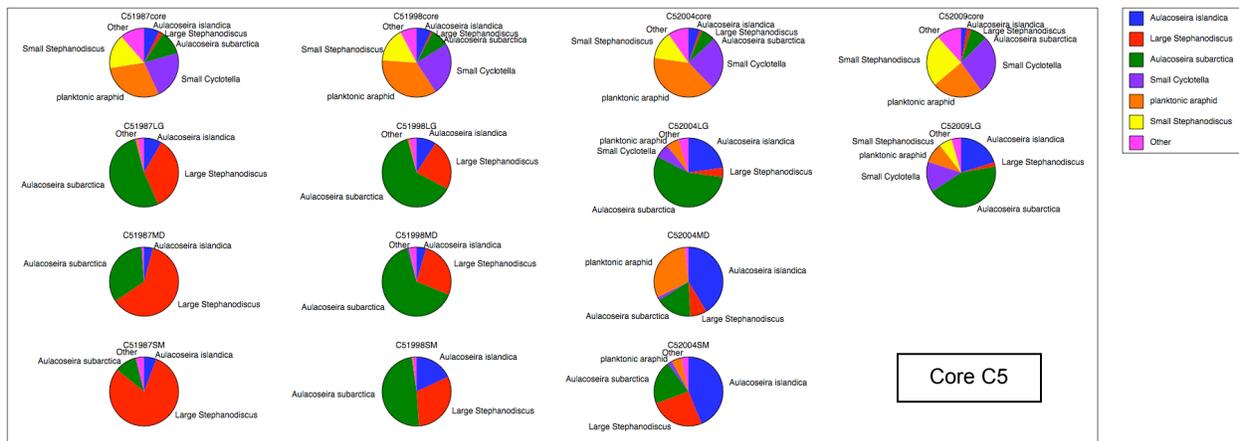
**Figure 3.** Box plots of percent gut fullness in *Diporeia* from three stations in southern Lake Michigan. Sample identifiers reflect sampling station (B4, C5, H22), sampling year (1987, 1992, 1998, 2004, 2009) and *Diporeia* size class (LG-large, MD-medium, SM-small). The top, bottom, and line through the middle of the box correspond to the 75th percentile (top quartile), 25th percentile (bottom quartile), and 50th percentile (median) respectively. Whiskers extend from the 10th percentile (bottom decile) to the 90th percentile (top decile). The blue square symbol represents the mean value.



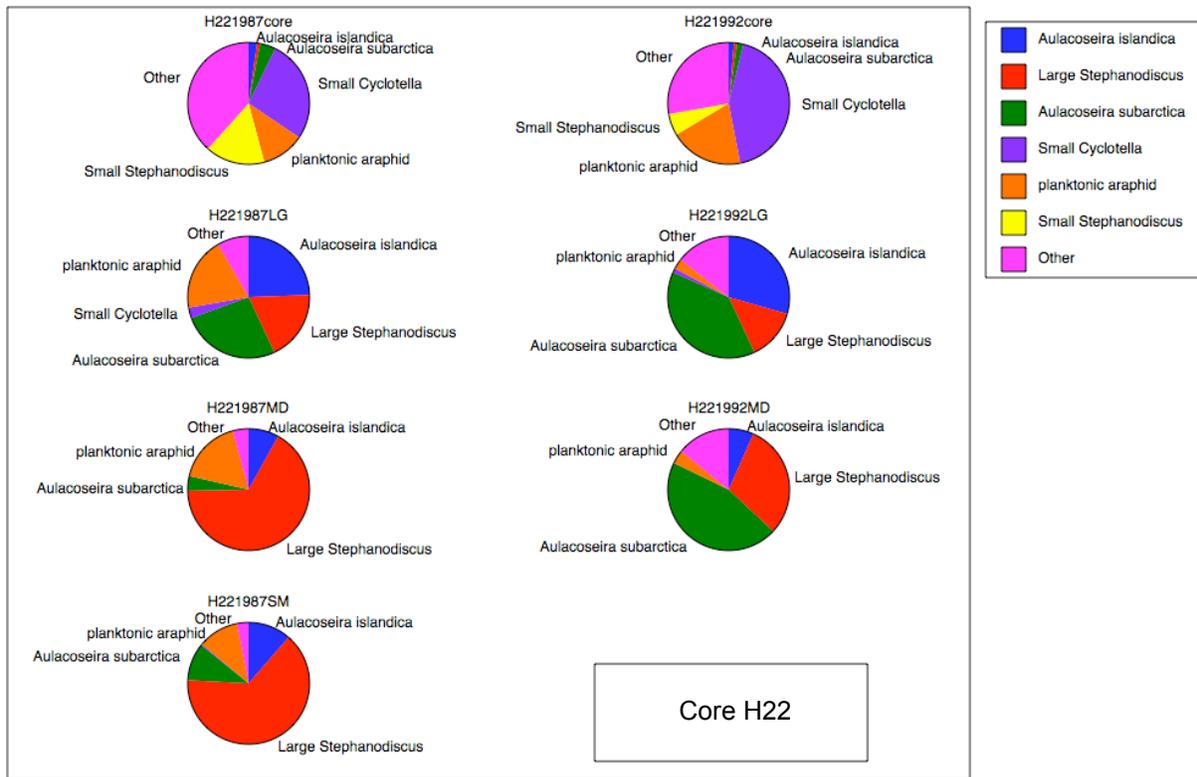
**Figure 4.** Box plots of relative abundance of select diatom species in guts of three size classes (LG-large, MD-medium, SM-small) of *Diporeia* collected from southern Lake Michigan station B4 in 1987 and 2009. Some diatom species have been pooled in morphological or ecological groups. See Fig. 3 for explanation of box plot symbols.



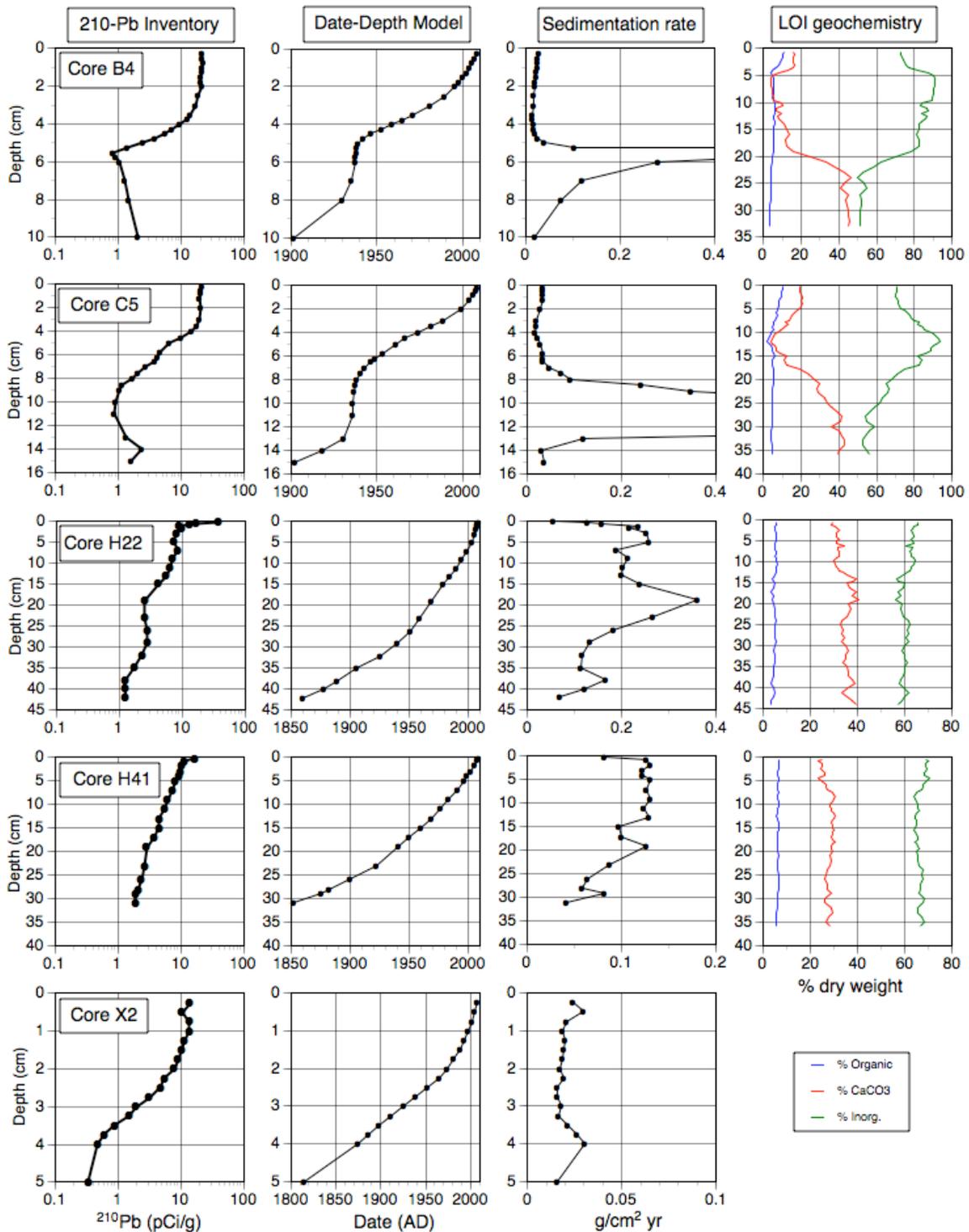
**Figure 5.** Percent contribution by various diatoms in sediment core material and gut contents of three size classes (LG-large, MD-medium, SM-small) of *Diporeia* collected from southern Lake Michigan station B4 in 1987, 1998, 2004, and 2009. Diatom species pooled in morphological and ecological groups.



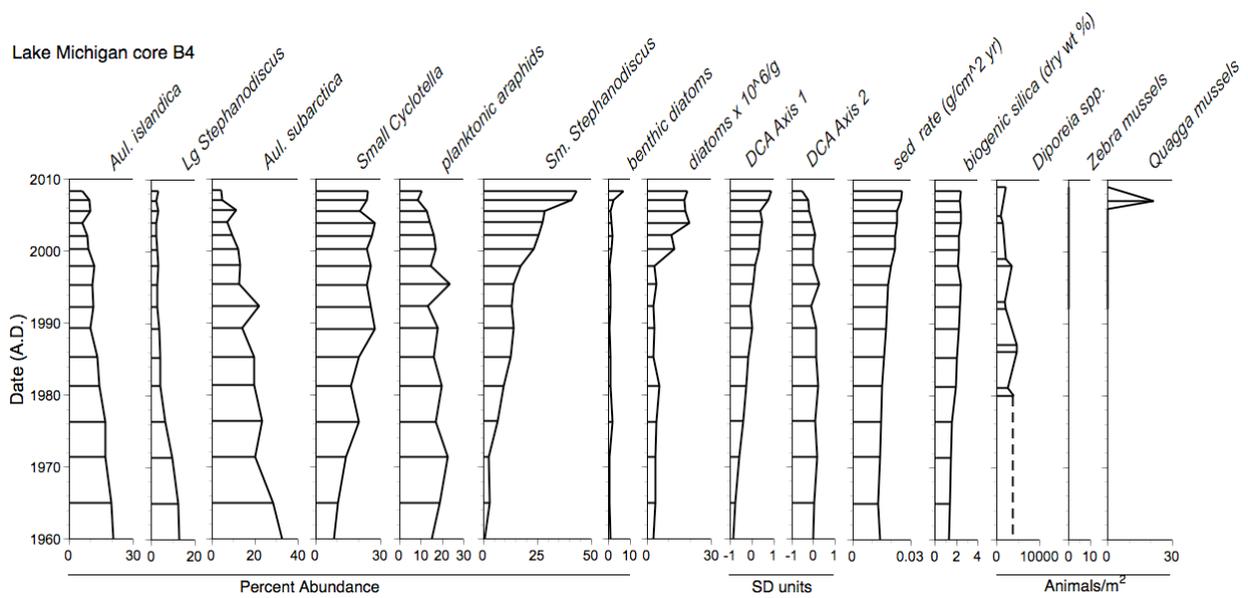
**Figure 6.** Percent contribution by various diatoms in sediment core material and gut contents of three size classes (LG-large, MD-medium, SM-small) of *Diporeia* collected from southern Lake Michigan station C5 in 1987, 1998, 2004, and 2009. Diatom species pooled in morphological and ecological groups.



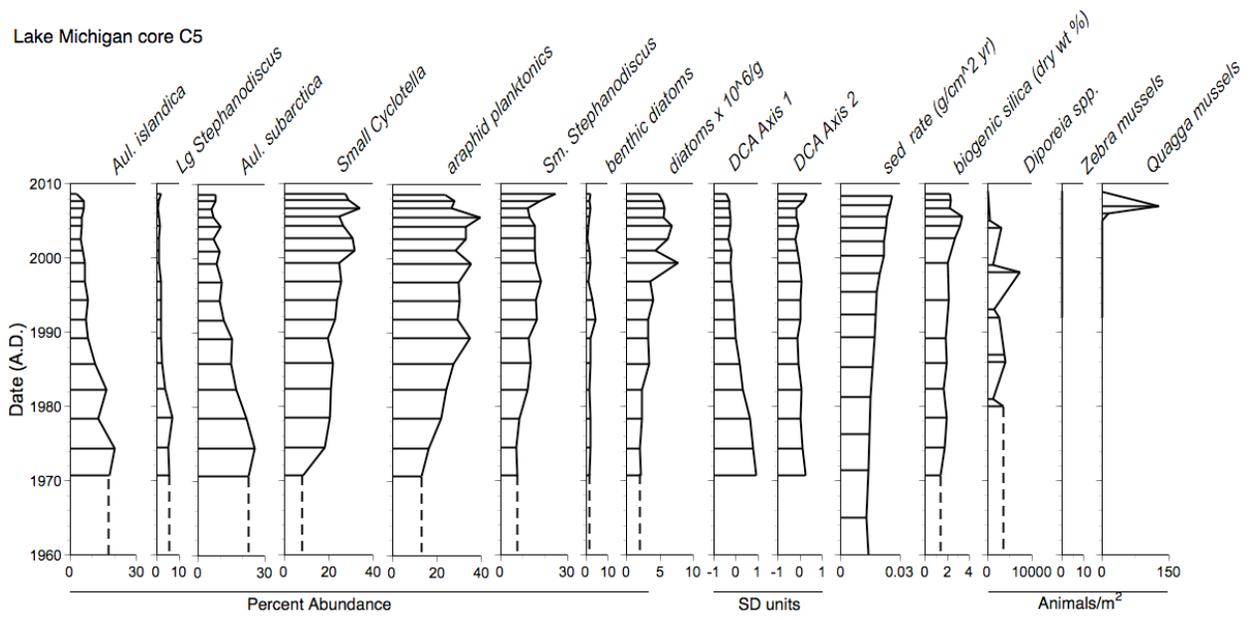
**Figure 7.** Percent contribution by various diatoms in sediment core material and gut contents of three size classes (LG-large, MD-medium, SM-small) of *Diporeia* collected from southern Lake Michigan station H22 in 1987 and 1998. Diatom species pooled in morphological and ecological groups.



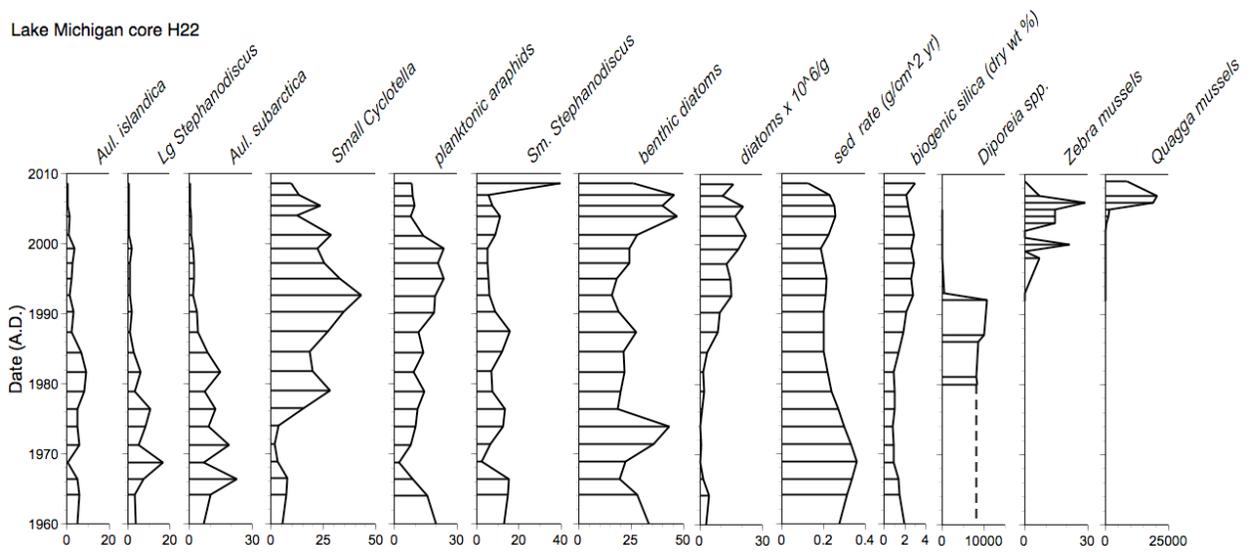
**Figure 8.** Total  $^{210}\text{Pb}$  inventory (pCi/g) with supported levels of  $^{210}\text{Pb}$  indicated by a dashed line, depth-date model (Year AD), sedimentation rates (g/cm<sup>2</sup> yr), and loss-on-ignition geochemistry (percent composition of organics, carbonates and inorganics) for Lake Michigan cores B4, C5, H22, H41, and X2, plotted against core depth (cm).



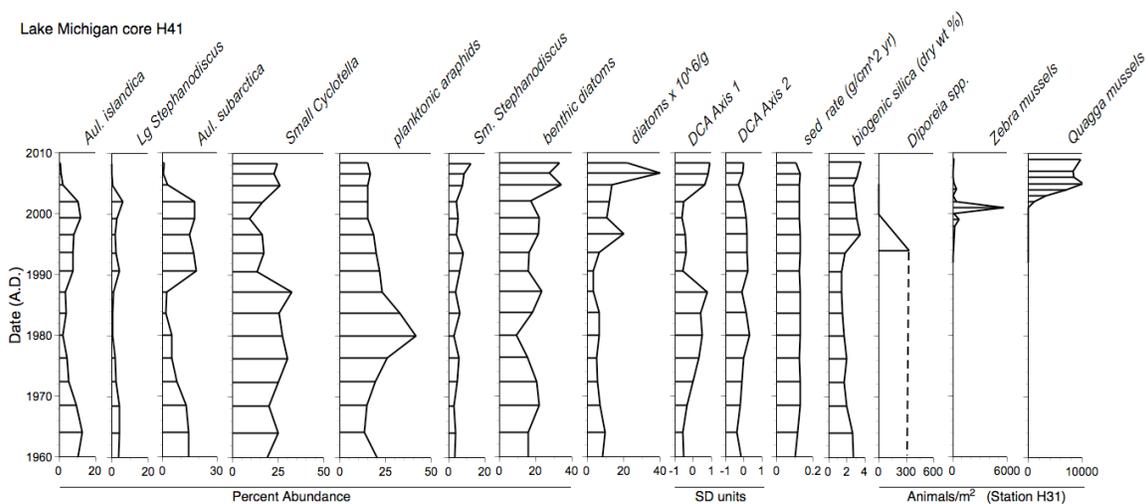
**Figure 9.** Historical biological and geochemical changes at Lake Michigan station B4 based on sediment core analysis and benthic monitoring, *ca.* 1960-2009. The data include: downcore percent abundance of select diatom species or species groups, Detrended Correspondence Analysis (DCA) axis scores (SD units), absolute abundance of diatoms (millions of diatoms per g dry sediment), sedimentation rate in  $\text{g}/\text{cm}^2 \text{ yr}$ , dry weight percent biogenic silica, and *Diporeia*, zebra, and quagga mussel density ( $\text{animals}/\text{m}^2$ ). Year is given on y-axis and represents either date estimated from  $^{210}\text{Pb}$  inventory or sampling date. *Aul.* = *Aulacoseira*, *Lg* = *large*, *Sm* = *small*.



**Figure 10.** Historical biological and geochemical changes at Lake Michigan station C5 based on sediment core analysis and benthic monitoring, *ca.* 1960-2009. The data include: downcore percent abundance of select diatom species or species groups, Detrended Correspondence Analysis (DCA) axis scores (SD units), absolute abundance of diatoms (millions of diatoms per g dry sediment), sedimentation rate in  $\text{g/cm}^2 \text{ yr}$ , dry weight percent biogenic silica, and *Diporeia*, zebra, and quagga mussel density ( $\text{animals/m}^2$ ). Year is given on y-axis and represents either date estimated from  $^{210}\text{Pb}$  inventory or sampling date. *Aul.* = *Aulacoseira*, *Lg* = large, *Sm* = small.



**Figure 11.** Historical biological and geochemical changes at Lake Michigan station H22 based on sediment core analysis and benthic monitoring, *ca.* 1960-2009. The data include: downcore percent abundance of select diatom species or species groups, Detrended Correspondence Analysis (DCA) axis scores (SD units), absolute abundance of diatoms (millions of diatoms per g dry sediment), sedimentation rate in  $\text{g/cm}^2 \text{ yr}$ , dry weight percent biogenic silica, and *Diporeia*, zebra, and quagga mussel density ( $\text{animals/m}^2$ ). Year is given on y-axis and represents either date estimated from  $^{210}\text{Pb}$  inventory or sampling date. *Aul.* = *Aulacoseira*, *Lg* = *large*, *Sm* = *small*.



**Figure 12.** Historical biological and geochemical changes at Lake Michigan station H41 based on sediment core analysis and benthic monitoring, *ca.* 1960-2009. The data include: downcore percent abundance of select diatom species or species groups, Detrended Correspondence Analysis (DCA) axis scores (SD units), absolute abundance of diatoms (millions of diatoms per g dry sediment), sedimentation rate in  $\text{g}/\text{cm}^2 \text{ yr}$ , dry weight percent biogenic silica, and *Diporeia*, zebra, and quagga mussel density ( $\text{animals}/\text{m}^2$ ; data from Lake Michigan station H31; Nalepa et al. 2005). Year is given on y-axis and represents either date estimated from  $^{210}\text{Pb}$  inventory or sampling date. *Aul.* = *Aulacoseira*, *Lg* = large, *Sm* = small.