Final Report

For Research Grant:

"POTENTIAL EFFECTS OF ZEBRA MUSSELS IN THE MADISON LAKES"

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ABSTRACT

Invasions of non-native species rank among the leading threats to aquatic ecosystems and biodiversity, and zebra mussels (*Dreissena polymorpha*) are certainly among those North American invaders with the most dramatic and potentially adverse impacts. Although lakes Mendota and Monona are not yet colonized with the zebra mussel, the establishment of high *D. polymorpha* densities in the Madison lakes could be rapid, and may happen during the next decade. The goal of this study was three-fold: 1) provide pre-invasion information on the community composition, density, biomass and production of benthic habitats in the Madison lakes; 2) predict the effect of zebra mussel invasion on benthic communities in the Madison lakes through comparisons with data to be obtained in southeastern Wisconsin lakes and an extensive long-term database from Eastern European lakes; 3) estimate the potential effect of zebra mussels on benthic and pelagic communities and associated fisheries in the Madison Lakes.

To determine the species composition and distribution of zoobenthos community, over 250 bottom samples were taken from Lake Mendota and 119 samples from Lake Monona in the summer of 2002 - 2007. During the five years of our study in we found 82 taxa of bottom macroinvertebrates (species, genera or higher taxa) in Lake Mendota, and 54 taxa in Lake Monona. Total density and biomass of benthic invertebrates in lakes Mendota and Monona was not significantly different among transects and between years, but was significantly different among littoral, sublittoral and profundal zones. We found significant changes in the biodiversity and community structure of zoobenthos of Lake Mendota over the last 100 years that occurred between 1950s and 1960s. The most dramatic change in the diversity was found in the most diverse and heterogenic littoral zone. Fifty two percent of the total diversity disappeared from the littoral benthic community since 1914-1915, while 43% of species and higher taxa, not previously recorded, were found during our study. The least diverse and most stable profundal zone lost about 40% of its diversity, including a key species *Chaoborus punctipennis*, along with the fingernail clam. A new exotic oligochaeta *Branchiura sowerbyi* was found in Lake Mendota in 2007.

The impact of *D. polymorpha*'s aggregations ("druses") on benthic community was studied in Lake Lower Nashotan. The overall effect of zebra mussels on macrobenthos was associated with the significant increase of diversity, density and biomass of native macroinvertebrates in *D. polymorpha* druses, compared to bare sediments near druses. From 27 taxa that were found both in druses and sediments, 18 taxa were found in druses only, while only 5 taxa were found exclusively in bare sediments.

To determine the distribution and abundance of *D. polymorpha* 107 samples were collected in Delavan Lake, and in Upper Nemahbin Lake. The average density (21,141 ± 6,785 m^{-2}) and biomass (1,077 ± 268 g m^{-2}) of *D. polymorpha* in Delavan Lake were extremely high and significantly differed from Upper Nemahbin Lake (average density 3,009 ± 971 m^{-2}; biomass

71 ± 19 g m^{-2}). The distribution of *D. polymorpha* by depths in these lakes was almost identical. In both lakes *Dreissena* density and biomass increased from 0.5 m, reached maximum at 3 – 5 m depth and then decreased to almost zero in profundal zone. The pattern of zebra mussel distribution found in Wisconsin lakes is very similar to *D. polymorpha* distribution across depths in European lakes.

Dreissena polymorpha potential effects on Madison lakes may include an increase in water transparency and light penetration, decreased concentrations of seston and organic matter in the water column, and increased concentrations of ammonia, nitrates and phosphates. The invasion by *D. polymorpha* will decrease phytoplankton density and chlorophyll concentrations, although unpalatable algae may increase in abundance. Increased light penetration due to the filtering activity by *D. polymorpha* will allow macrophytes and periphyton to grow deeper and cover larger portions of the lake bottom. Zooplankton density and biomass will decrease after *Dreissena* invasion. Their presence alone they will increase the total biomass of zoobenthos by at least 10-fold. We may expect at least a 2-fold increase in the density and biomass of native zoobenthos in the littoral and sulittoral zones of Madison lakes after *D. polymorpha* invasion. In addition, bottom macroinvertebrates, typical for gravel and rocky substrates, will spread deeper into the lakes, and occupy areas that are currently unsuitable for them. In contrast, burrowing species that live in sediments may be negatively affected by *Dreissena* druses. The strongest negative effect *Dreissena* colonization will have on unionids, which have already declined in their abundance in Madison lakes. The impacts of *D. polymorpha* on the fish community will depend on fish feeding mode and may include an increase in all benthic feeding fishes, even those that do not feed directly on zebra mussels, because zebra mussel invasion is associated with an increase in the biomass of native benthic invertebrates.

OBJECTIVES:

1) Provide pre-invasion information on the community composition, density, biomass and production of benthic habitats in the Madison lakes.

2) Predict the effect of zebra mussel invasion on benthic communities in the Madison lakes through comparisons with data to be obtained in southeastern Wisconsin lakes and an extensive long-term database from Eastern European lakes.

3) Estimate the potential effect of zebra mussels on benthic and pelagic communities and associated fisheries in the Madison Lakes.

INTRODUCTION

Invasions of non-native species rank among the leading threats to aquatic ecosystems and biodiversity, and zebra mussels (*Dreissena polymorpha*) are certainly among those North American invaders with the most dramatic and potentially adverse impacts. With few predators in North America, zebra mussel commonly reaches extremely high densities. Zebra mussels fit the profile of ecosystem engineers in their ability to restructure their biotic and abiotic environment (Karatayev et al., 2002, 2007a). As a result of their high densities and filter-feeding capacity, zebra mussels increase water transparency and decrease phytoplankton and zooplankton biomass, and increased light penetration can lead to increased benthic and macrophyte production (reviewed in Karatayev et al., 1997, 2002, 2007a; Vadeboncoeur et al., 2001; Mayer et al., 2002; Vanderploeg et al., 2002 et al). Zebra mussels are known to have an especially strong effect on the species composition and biomass of native benthic community. The effect of zebra mussels on the fish community is more controversial, and largely depends on the feeding type of fishes in the community (reviewed in Karatayev et al., 2007b).

Establishment of high zebra mussel densities in the Madison lakes could be rapid, perhaps during the next decade, after which the opportunity to characterize ecosystem-level changes relative to pre-invasion conditions will be lost. As such, the impending invasion provides a fleeting opportunity to collect the pre-invasion data and predict the impacts of a zebra mussel invasion in two of the most well studied lakes in the world. The Madison lakes are intensively studied as part of the North Temperate Lakes long-term ecological research (LTER) site, based at the University of Wisconsin, Center for Limnology. The LTER program provides the core limnological data on water chemistry, invertebrates and fish. Yet it is the benthic habitats will be most directly impacted by zebra mussel invasion, but are not presently featured in LTER monitoring. Our study provides important pre-invasion data on the poorly sampled benthic habitats of the Madison lakes, and is built on past efforts of the LTER program in addressing the potential impacts of zebra mussels. The comparison of acquired data with data received from other well studied lakes colonized with zebra mussels allowed us to predict the potential impacts of *Dreissena* introduction on the major aquatic communities of Madison lakes.

METHODS

Study Area

The focus of this study was zoobenthic communities of eutrophic lakes Mendota and Monona located near Madison in southern Wisconsin (Table 1).

Table 1. Morphometric parameters of lakes Mendota and Monona (modified from Lathrop et al., 1992).

Parameters	Lake Mendota	Lake Monona
Latitude	43.099	43.063
Longitude	-89.405	-89.361
Area (km^2)	39.85	13.26
< 3 m (littoral zone)	6.97 (17%)	3.39 (26%)
3 - 9 m (sublittoral zone)	6.82 (17%)	3.43 (26%)
> 9 m (profundal zone)	26.06 (65%)	6.44 (49%)
Mean depth (m)	12.8	8.2
Maximum depth (m)	25.3	22.5

From May to October the water column of the lakes is stratified. Based on the lake's thermal stratification, the profundal zone is defined as > 9 m, which represents ca. 65% of the area of Lake Mendota and 49% of Lake Monona (Lathrop et al., 1992). The littoral zone extends down to 3 m depth and sublittoral zone occupied depth between 3 and 10 m (Lathrop et al., 1992). Bottom sediments in the profundal zone are mainly silt and a mixture of silt and fine sand. The littoral zone has a variety of substrates which include rocks, gravel, sand, coarse detritus, and silt, as well as various combinations of these. During the vegetation season a substatial portion of the littoral zone is covered with various macrophytes, including: *Myriophyllum spicatum*, *Elodea canadensis*, *Ceratophyllum demersum*, *Potamogeton crispus*, and *P. pectinatus.*

Density of *Dreissena polymorpha* was studied in June 2006 in lakes Delavan (Walworth County), and Upper Nemahbin (Waukesha County). The effect of *D. polymorpha* on benthic community was studied in June 2007 in the Lower Nashatan Lake (Waukesha County).

Lake Delavan is a meso-eutrophic lake located on Jackson Creek (draining to the Lower Rock River), that has a surface area of app. 8.39 km^2, mean depth 6.4 m, and maximal depth 17.1 m. About 73% of bottom sediments of the lake is covered with mud, app. 15% - with sand and gravel, and the remaining 12% is covered by rock (A Lake Management Plan for Delavan Lake, 2002). *Dreissena polymorpha* was first found in this lake in October 1999 (Zebra Mussel Watch).

Mesotrophic Upper Nemahbin lake belongs to the Fox River basin, has a surface area of 1.15 km^2, mean depth 9.0 m, and maximal depth 18.3 m (Upper Nemahbin Lake Watershed Inventory Findings). *Dreissena polymorpha* was first found in this lake in October 1999, at the same time as in adjacent Lake Lower Nashotan (Zebra Mussel Watch). Lake Lower Nashotan belongs to the Fox River basin, and has a surface area of 0.36 km^2.

Sampling Protocol

Benthic sampling

To determine the species composition and distribution of zoobenthos community, over 250 bottom samples were taken from Lake Mendota and 119 samples from Lake Monona. All lakes were sampled during May 30 – June 20 from 3 transects (Fig. 1).

For this study we analyzed samples from Lake Mendota collected in 2002, 2003, 2004, 2006, and 2007, and from Lake Monona in 2002, 2006 and 2007. For each transect, samples were collected from 1, 3, 5, 8, 15, and 20 (or 18) m. Three or more replicate samples were taken at each depth with an AquaVac, AirVac or an Eckman dredge, depending on the depth and substrate type. In Lake Monona in 2007, only one replicate sample was collected from each depth. In addition, 6 samples were collected from the rocky littoral of Lake Mendota, at ca. 1 m depth (“extra rocky substrates”), and 5 samples were collected in the deepest portion of the lake (Deep hole).

In 2002 the AquaVac (sampling area = 0.096 m^2) designed by Vander Zanden et al. was used to sample 1 m sites, and the AirVac, an air-driven suction devise powered by a scuba air tank modified from the sampler used by Wahle and Steneck (1991) (sampling area = 0.096 m^2) was used to sample 3, 5, and most 8 m sites. Eckman dredge with sampling area 0.023 m^2 was used to sample some 8 and deeper sites. In 2003, 2004, 2006, and 2007 all samples were taken with an Eckman dredge.

All samples were washed through a 500 µm mesh. At each sampling point, the type of substrate and macrophyte coverage was described, and bottom temperature and oxygen were measured. After sampling, all macroinvertebrates were transferred to containers with 10% neutral buffered formalin and labelled. All macroinvertebrates were identified to the lowest possible level, counted and weighted to the nearest 0.0001 g after being blotted dry on absorbent paper (wet mass). For oligochaetes, only *Stylaria lacustris* and *Branchiura sowerbyi* were identified to species level.

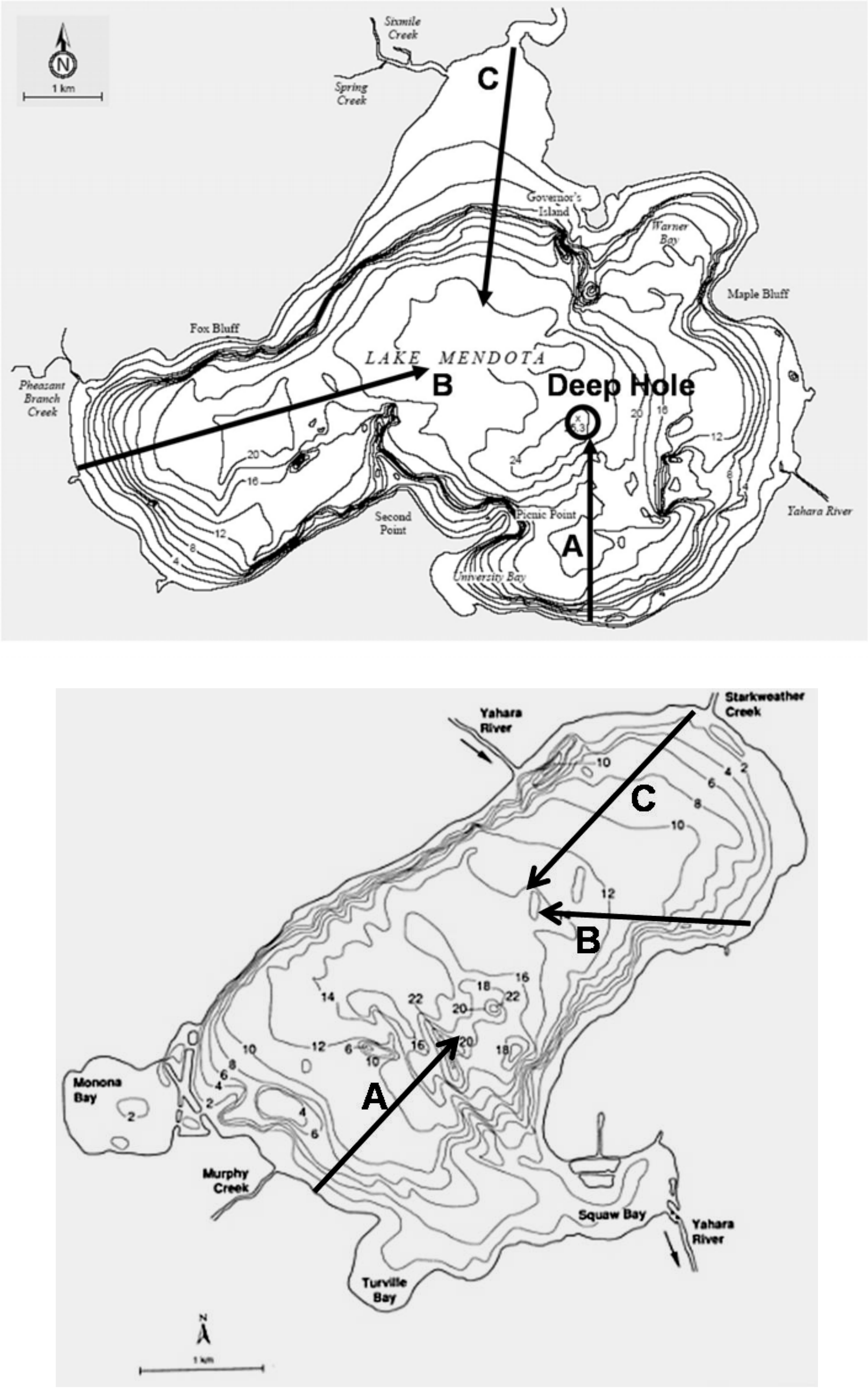


Fig. 1. Map of Lake Mendota (upper) and Lake Monona (lower) with sampling transects identified.

Dreissena polymorpha distribution

All samples used to determine the distribution and abundance of *D. polymorpha* were collected in Delavan Lake on June 13, 14 and 19, and in Upper Nemahbin Lake – on June 20, 2006. In Delavan Lake we collected samples from 3 transects that initiated on the shore and ran perpendicular to the shore toward the center of the lake. Transects were distributed around each lake based on bathymetric maps, maps of bottom sediments, and distribution of macrophytes such that they included all major habitat types within each lake and covered all regions of the lake. For each transect, 3 to 5 replicate samples were collected at 0.5, 1, 3, 5, 8 and 15 m depth (the maximum depth where *D. polymorpha* was found). Samples at 0.5 and 1 m depth were collected from 0.25 m^2 quadrat by hand. Within each quadrat, the bottom sediments down to 5 cm were collected, except for pure sand sediments when the visibility was sufficient to determine that there were no mussels within a quadrat. Deeper water benthic samples were collected with an Eckman dredge (area 0.023 m^2). In the Upper Nemahbin Lake three to five replicate samples were collected from 2 transects. Samples at 1 m depth were collected from quadrat, and samples from 3, 5, 8, and 15 m depth were collected with an Eckman dredge.

For all quadrat and dredge samples, sediments were washed through a 550 µm mesh, and within 48 hours of sampling all zebra mussels larger than 1 mm maximum dimension were counted, opened with a scalpel to remove water from the mantle cavity, and the total sample was weighed to the nearest 0.01 g after being blotted dry on absorbent paper (wet weight, soft tissue plus shell) (Burlakova et al., 2006). Due to seasonal changes in soft mass due to spawning, and the zebra mussel thin shells, total wet weight has been determined to be the most stable measure of mass for both reproductive potential and filtering impact (Karatayev, 1983).

Impact of *D. polymorpha* on benthic community

We studied the impact of *D. polymorpha* druses on benthic community in Lake Lower Nashotan on June 18, 2007. In this lake we sampled three different substrates types (sand, rocks and silt) with and without *D. polymorpha.* Thirty six samples total were collected from *D. polymorpha* druses and from bare sediments near druses including 6 replicate samples of *D. polymorpha* druses and 6 replicate samples of bare sediments (not containing *D. polymorpha*) from each of the substrates: sand, rocks, and a combination of silt and shells. Samples from sand and rocks were collected at 1 m depth, and from silt and shells - at 2.5 m depth. *Dreissena polymorpha* druses were collected with their substrates by a diver, put into zip-lock bags and brought to the surface. Benthic samples from bottom sediments were collected with a Tube dredge sampler (area 0.004 m^2). From rocky substrates we collected 6 stones (mean area ± standard deviation was 0.0045 ± 0.0022 m^2) without *D. polymorpha*, and six stones with *D. polymorpha* attached (0.0051 ± 0.0011 m^2). All organisms were carefully collected from stones, and the stone surface area was estimated.

All samples were thoroughly washed through 500 µm net and fixed with a 10% neutral buffered formalin. All organisms from all samples were identified to the lowest possible level, counted, and weighted after blotted dry on absorbent paper (total wet weight). Druses surface area was estimated as their projection on the surface; mean area of the druse was 0.0050 (±0.0015) m^2.

Long-term dynamics of Lake Mendota benthic community

Since much more historical information on benthic community is available for Lake Mendota than for Lake Monona, the analysis of the long-term dynamics of zoobenthos over the last century was conducted on Lake Mendota only. We summarized all available information on benthic community of Lake Mendota and compared this data with our results. Zoobenthos of Lake Mendota was studied repeatedly since 1914 (Table 2). Taxonomic resolution of inter-annual samples (1914–2007) was combined into a similar level to minimize the effect of changes in taxonomic knowledge since 1914, and different sample processors (Metzeling et al., 2002).

Table 2. Data used in the analysis of the long-term changes in zoobenthos of Lake Mendota.

Sampling period	Sites sampled	References
	Littoral zone	
1914 – 1915	Over 280 quantitative samples were obtained from 0-1; 1-2; 2-3; 3-5 m depth intervals in spring, summer and fall of 1914 and 1915	Muttkowski, 1918
2002, 2003, 2004, 2006, 2007	18 samples were collected each year from 1 and 3 m	This study
	Sublittoral zone	
1951	Bottom samples were taken with an Ekman dredge during January and February from 3 to 9 m	Mackenthum and Cooley, 1952
2002, 2003, 2004, 2006, 2007	18 samples were collected each year from 5 and 8 m	This study

Sampling period	Sites sampled	References
Profundal zone		
1917	Annual (average for monthly data for 5 station), deep hole	Juday, 1921
1939	Summer, deep hole	David Frey, Indiana Univ., unpublished data
1944	Summer, deep hole	Hasler, 1945
1951	Winter	Mckenthun and Cooley, 1952
1964-65	Averaged June, July, and August data for profundal (12-18m) and deep hole (>20m)	Sapkarev, Univ. Skopje, Yugoslavia, unpublished data; from Lathrop et al. 1992)
2002, 2003, 2004, 2006, 2007	23 samples were collected each year from 15, 20, and 24 m	This study

Estimation of the zoobenthos secondary production

To estimate the secondary production of zoobenthos, we used taxa-specific production/biomass ratios (P/B coefficients) from the literature (Table 3). Where possible, we selected P/B coefficient estimated for the same species (e.g. *Hyalella azteca*), genus (e.g. literature P/B coefficient for *Valvata piscinalis* was used to estimated production for *V. tricarinata*), or higher taxon (e.g. oligochaeta). Where several P/B coefficients were available, we used the average. P/B values were quite similar among studies/systems for a given taxa (Table 3). To convert the mass of invertebrates into its energetic equivalent we assumed 1 g wet mass was equivalent to 1 kcal (Banse and Mosher, 1980). To estimate benthic production for each lake zone, we multiplied the average biomass (g m^{-2}) of each species in this zone by its P/B coefficient, and summed up the non-predatory and predatory production separately.

Table 3. Taxa-specific production/biomass ratios (P/B coefficients, year^{-1}) accepted to estimate zoobenthos production in lakes Mendota and Monona.

Taxa	P/B coefficients accepted	P/B coefficients reported in the literature
Non-Predators:		
Mollusca (excluding *V.tricarinata)*	2.0	2.0, molluscs, Uchinskoe Reservoir, Russia (Sokolova, 1980)
Valvata tricarinata	2.1	2.1, *V. piscinalis,* Lake Myastro, Belarus (Gavrilov, 1985); 2.1, *V. piscinalis,* Uchinskoe Reservoir, Russia (Sokolova, 1980)
Oligochaeta	4.6	4.5, oligochaeta, Caribou River, Minnesota, USA (Krueger and Waters, 1983); 3.8, oligochaeta, Lake Myastro, Belarus (Gavrilov, 1985); 5.4, tubificidae, Lake Leman, Switzerland (Lafont, 1987); 4.9, *Limnodrilus hoffmeisteri,* Lake Leman, Switzerland (Lafont, 1987)
Ephemeroptera	5.5	5.5, *Caenis* sp., Uchinskoe Reservoir, Russia (Sokolova, 1980)
Chironomidae *Chironomus* sp. (including *C. plumosus*)	4.9	3.8, *Chironomus plumosus,* Lake Myastro, Belarus (Gavrilov, 1985); 4.3, *C. plumosus,* Uchinskoe Reservoir, Russia (Sokolova, 1980); 6.4, *C. plumosus,* Eglwys Nunydd Reservoir, UK (Potter, Learner, 1974); 4.9, *C. plumosus,* Lake Lukomskoe, Belarus (Karatayev, 1988)
Tanytarsus sp.	6.5	6.6, *Tanytarsus holochorus,* 5.2, *T. inopertus,* 7.6, *T. lugens,* Eglwys Nunydd Reservoir, UK (Potter and Learner, 1974)
Cladotanytarsus sp.	6.9	8.6, *T. mancus,* Lake Batorino, Belarus (Gavrilov, 1985); 5.2, *C. mancus,* Eglwys Nunydd Reservoir, UK (Potter and Learner, 1974)
Parachironomus sp.	5.8	5.8, *Parachironomus tener,* Eglwys Nunydd Reservoir, UK (Potter and Learner, 1974)
Glyptotendipes sp.	4.5	3.0, *G. grypekoveni,* Lake Myastro, Belarus (Gavrilov, 1985); 5.9, *G. paripes,* Eglwys Nunydd Reservoir, UK (Potter and Learner, 1974)
Microtendipes sp.	5.7	5.7, *Microtendipes* sp., Eglwys Nunydd Reservoir, UK (Potter and Learner, 1974)

Taxa	P/B coefficients accepted	P/B coefficients reported in the literature
Miscellaneous Chironimidae	5.9	5.9, Chironomidae (excluding Tanypodinae), Caribou River, Minnesota, USA (Krueger and Waters, 1983)
Amphipoda *Hyalella azteca*	4.5	4.5, *H. azteca,* Caribou River, Minnesota, USA (Krueger and Waters, 1983)
Isopoda *Asellus* sp.	4.7	4.7, *A. aquaticus,* Eglwys Nunydd Reservoir, UK (Potter and Learner, 1974)
Trichoptera	5	5.5, Trichoptera, Uchinskoe Reservoir, Russia (Sokolova, 1980); 4.0, Trichoptera, Lake Drivyaty, Belarus (Gavrilov 1970); 5.0, Trichoptera, Caribou River, Minnesota, USA (Krueger and Waters, 1983)
Lepidoptera *Nimphyla* sp.	1.6	1.6, *Acentropus niveus*, Uchinskoe Reservoir, Russia (Sokolova, 1980)
Predators:		
Ceratopogonidae	4	4.0, Ceratopogonidae, Lake Myastro, Belarus, average for 1968, 1975, 1976, 1977 (Gavrilov, 1985)
Chironomidae *Procladius* sp.	5.5	4.1, *Procladius,* Lake Myastro, Belarus, average for 1968, 1975, 1976, 1977 (Gavrilov, 1985); 6.5, *P. choreus,* Eglwys Nunydd Reservoir, UK (Potter and Learner, 1974); 6.0, *P. indet*, Kuraknovskoe Reservoir, Ukraine (Pidgayko, 1971)
Tanypodina sp.	4.5	4.5, Tanypodinae, Caribou River, Minnesota, USA (Krueger and Waters, 1983)
Turbellaria *Dugesia tigrina*	4	4, Lake Myastro, Belarus (Gavrilov, 1985)
Trichoptera *Polycentropus* sp.	3.9	3.9, *Polycentropus* sp., Caribou River, Minnesota, USA (Krueger and Waters, 1983)
Leptocerus sp.	5.0	5.5, Trichoptera, Uchinskoe Reservoir, Russia (Sokolova, 1980); 4.0, Trichoptera, Lake Drivyaty, Belarus (Gavrilov 1970); 5.0, Trichoptera, Caribou River, Minnesota, USA

Taxa	P/B coefficients accepted	P/B coefficients reported in the literature
		(Krueger and Waters, 1983)
Hirudinea		3.5, *H. stagnalis*, Eglwys Nunydd Reservoir, UK (Potter and Learner, 1974)
Helobdella stagnalis	3.5	
Miscellaneous hirudinea	2.7	2.0, *Hirudinea*, Lake Naroch, Belarus, average for 1968, 1975, 1976, 1977 (Gavrilov, 1985); 3.4, *Hirudinea,* Caribou River, Minnesota, USA (Krueger and Waters, 1983)
Odonata	3.6	3.6, Odonata, Caribou River, Minnesota, USA (Krueger and Waters, 1983)
Coleoptera		5.0, *Agabus* sp., Caribou River, Minnesota, USA (Krueger and Waters, 1983)
Haliplus sp.	5.0	

Statistical analysis

The replicate samples collected at each benthic site were pooled to minimize variation due to small scale spatial effects. We applied 2-way repeated-measures ANOVA (rm-AMOVA) on log-transformed data to test whether the total density and biomass of zoobenthos was different on sampled transects, lake zones, and among years in STATISTICA version 6 (StatSoft, Inc. 2001).

The macroinvertebrate community structure was summarized using number of taxa (i.e. richness), macroinvertebrate abundance (density as individual m^{-2} and biomass as gm^{-2}) and diversity indices. PRIMER 6 (Version 6.1.6, Primer E-Ltd. 2006) package was used to analyze changes in benthic communities. Temporal variations in macroinvertebrate community composition were assessed using Non-metric Multi-Dimensional Scaling (NMDS) that calculates a set of metric coordinates for samples, most closely approximating their nonmetric distances (Legendre and Legendre, 1998). The similarity (stability) of macroinvertebrate community composition (density and biomass) between successive samples was summarized by calculating Bray–Curtis distances (BC; Bray and Curtis, 1957; Clarke, 1993). BC is a measure of dissimilarity with values ranging from 0–1; zero denotes identical samples. Abundance data were fourth root transformed prior to analyses. Differences between assemblages at different transects, lake zones, and years were assessed by Analysis of Similarities (ANOSIM). ANOSIM is a resampling technique that uses permutation/randomization methods on Bray-Curtis similarity matrices to identify differences among groups of samples, after which, pairwise comparisons between regions can be conducted (Clarke 1993, 1999; Clarke and Warwick, 2001). ANOSIM on diversity indices was used to test for a difference in the benthic community composition of lakes in different years. For this analysis, PRIMER created a similarity matrix on several diversity indices (total number of species in each sample (S), the number of individuals in each sample (N), Margalef's species richness (d), Pielou's evenness (J'), Shannon-Wiener diversity index (H', Log e base), and Simpson (1-Lambda') diversity index). ANOSIM on density and biomass' k-dominance curves (cumulative percentage contribution of species to the abundance/biomass ranked in decreasing order of importance along the *x* axis) was used to test whether community dominance changed among years. The k-dominance curves represent the cumulative percentage contribution of species to the abundance/biomass ranked in decreasing order of importance along the *x* axis. RELATE procedure was used to analyze serial correlations between years (temporal trend). This procedure tests for hypothesis of no relation between a multivariate pattern from sets of resemblance community matrices for each lake zone, and a serial generated pattern (years). A SIMPROF test routine in PRIMER 6 software was used to test for structure in the data. To characterize diversity in benthic communities we used univariate Margalef's index of species richness, while to describe the variability in the multivariate structure of these communities we used the Relative Multivariate Dispersion. The comparative Index of Multivariate Dispersion (IMD, Warwick and Clarke 1993) was calculated as a measure of increased variability between druse and sediment communities (IMD = 0 signifies no difference, and IMD +1 indicates maximum difference). Effects were considered statistically significant at $P < 0.05$.

To predict the potential densities and biomass of zebra mussels in the Madison lakes, we used averages for each zone calculated from our samples collected with the same methods in Wisconsin and Belarus lakes. We used 6,000 bootstrap re-samples to derive 90% confidence intervals, and these intervals were used as the predicted range. To calculate the predicted average density and biomass of *D. polymorpha* population per the total area of the lake bottom, we used the predicted values for each lake zone for both lakes, and multiplied them per the relative area of the zone in each lake. To calculate the average time for the population of zebra mussels to filter the total volume of water in lakes Mendota and Monona, we used the filtration rate averaged across multiple studies (58 $\text{mLgWTM}^{-1}\text{h}^{-1}$, Karatayev et al., 1997). The time was calculated using the predicted biomass of *D. polymorpha*, the average filtration rate, and the average depth of the lake. Due to reduced filtration rate by *D. polymorpha* at night (Kondratiev, 1970), we considered that *D. polymorpha* filters 20 hrs per day.

It is important to note, however, that if the lakes are populated by *D. bugensis* instead of *D. polymorpha*, the predicted population size would be underestimated, as well as the total effect of the species on the lake ecosystems. *Dreissena bugensis* is known to populate soft sediments in profundal zone, and as a result, its population will be larger.

RESULTS AND DISCUSSION

1. Community composition, density, biomass and production of benthic habitats in lakes Mendota and Monona

Diversity and spatial variability of zoobenthos in Lakes Mendota and Monona

During five years of our study in Lake Mendota we found 82 taxa (species, genera or higher taxa) of bottom macroinvertebrates, including 30 taxa of chironomids (21 identified to species level), 12 trichoptera larvae, and 9 species of molluscs (Table 4). The most abundant invertebrates across the whole lake, excluding unidentified oligochaetes, were chironomids *Cladotanytarsus* sp. (380 ± 195 m^{-2}), *Procladius* sp. (352 ± 42 m^{-2}), *Polypedilum halterale* (295 ± 120 m^{-2}), and amphipod *Hyalella azteca* (258 ± 73 m^{-2}, mean and standard error here and elsewhere unless noted).

In Lake Monona during the three years of our study, we found 54 taxa (species, genera or higher taxa) of bottom macroinvertebrates, including 30 taxa of chironomids, 4 trichoptera larvae, and 7 species of molluscs (Table 4). Therefore, benthic diversity of Lake Monona was substantially lower than that of Lake Mendota. This difference may be due to the smaller size and lower heterogeneity of bottom substrates in Lake Monona compared to Mendota. The most abundant invertebrates in the benthic community of Lake Monona, excluding unidentified oligochaetes, were oligochaetes *Stylaria lacustris* (1,002±324 m^{-2}), chironomids *Chironomus* sp. (680 ± 122 m^{-2}), *Dicrotendipes tritomus* (407 ± 133 m^{-2}), and amphipod *Hyalella azteca* (256 ± 87 m^{-2}).

In total we found 96 taxa (species, genera or higher taxa) of bottom macroinvertebrates, including 41 taxa of chironomids (21 identified to species level), 12 trichoptera larvae, and 10 species (and higher taxa) of molluscs in both lakes.

Table 4. Benthic macroinvertebrates found in lakes Mendota and Monona in 2002-2007.

Taxon	Lake Mendota	Lake Monona
Gastropoda		
Amnicola limosus	+	+
Amnicola pupoideus	+	-
Ferrissia walker	+	-
Gyraulus circumstriatus	+	-

Taxon	Lake Mendota	Lake Monona
Gyraulus deflectus	+	+
Physella sp.	+	+
Promenetus exacuous	+	+
Pyrgulopsis lustrica	-	+
Valvata tricarinata	+	+
Pelecypoda *Pisidium* sp.	+	+
Oligochaeta *Branchiura sowerbyi*	+	-
Chaetogaster sp.	-	+
Oligochaeta sp.	+	+
Stylaria lacustris	+	+
Ephemeroptera		
Caenis sp.	+	+
Maccaffertium mexicanum integrum (=*Stenonema integrum*)	+	-
Ceratopogonidae		
Bezzia sp.	+	+
Culicoides sp.	+	+
Chironomidae		
Chironomus sp.	+	+
Cladopelma sp.	+	+
Cladotanytarsus sp.	+	+
Clinotanypus sp.	+	-
Coelotanypus tricolor	+	-
Corynoneura sp.	+	+

Taxon	Lake Mendota	Lake Monona
Cricotopus absurdus	+	-
Cricotopus politus	+	-
Cricotopus sylvestris	+	+
Cricotopus sp.	+	+
Cryptochironomus sp.	+	+
Cryptotendipes sp.	+	+
Demicryptochironomus sp.	+	+
Dicrotendipes modestus	-	+
Dicrotendipes tritomus	-	+
Dicrotendipes sp.	+	-
Einfeldia sp.	+	+
Endochironomus nigricans	-	+
Endochironomus subtendens	-	+
Endochironomus sp.	+	-
Eukiefferiells sp.	-	+
Glyptotendipes carlicola	-	+
Glyptotendipes paripes	+	+
Labrundinia sp.	+	-
Larsia sp.	+	+
Microtendipes pedellus	+	-
Parachironomus frequens	-	+
Parachironomus pararostratus	-	+
Parachironomus sp.	+	-
Paratendipes albimanus	+	+
Polypedilum halterale	+	+

Taxon	Lake Mendota	Lake Monona
Polypedilum illinoense	+	+
Procladius sp.	+	+
Psectrocladius dilatatus	-	+
Psectrocladius vernalis	-	+
Pseudochironomus sp.	+	-
Rheotanytarsus pellucidus	+	+
Stictochironomus sp.	+	+
Tanypus sp.	+	-
Tanytarsus sp.	+	+
Tribelos jucundum	-	+
Turbellaria		
Dugesia tigrina	+	+
Planaria sp.	+	-
Amphipoda		
Hyalella azteca	+	+
Isopoda		
Asellus sp.	+	+
Crustacea		
Decapoda sp.	+	-
Trichoptera		
Agraylea sp.	+	-
Leptocerus americanus	+	+
Leptocerus sp.	+	-
Molanna sp.	+	-
Neophylax sp.	+	-

Taxon	Lake Mendota	Lake Monona
Oecetis sp.	+	-
Orthotrichia sp.	+	+
Oxyethira sp.	+	+
Platycentropus sp.	+	+
Polycentropus sp.	+	-
Triaenodes sp.	+	-
Trichoptera sp.	+	-
Hirudinea		
Alboglossiphonia heteroclite	+	-
Dina sp.	-	+
Glossiphonia complanata	+	-
Helobdella elongate	+	+
Helobdella stagnalis	+	+
Hirudinea sp.	+	-
Placobdella translucens	+	-
Odonata		
Agria sp.	+	-
Amphiagrion sp.	+	-
Chromagrion sp.	+	+
Coenagrion sp.	+	-
Enallagma sp.	+	-
Ischnura sp.	+	-
Zygoptera sp.	+	-
Coleoptera		
Coleoptera sp.	+	-

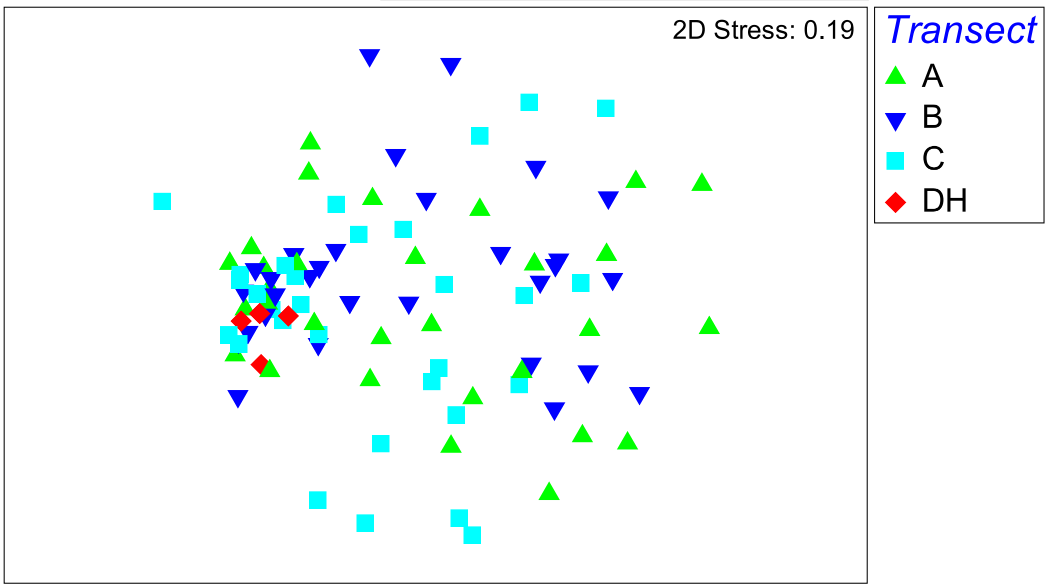
Taxon	Lake Mendota	Lake Monona
Ectopria sp.	+	-
Haliplus sp.	+	-
Stenelmis sp.	+	-
Lepidoptera		
Lepidoptera sp.	+	-
Nymphalis sp.	+	-

Benthic samples in the littoral and sublittoral zones of lakes Mendota and Monona were collected by AirVac and AquaVac, and in all following years – with Eckman grab. As a result, density and biomass of invertebrates collected were different, and we had to analyze the data for both lakes not considering 2002.

Total density and biomass of benthic invertebrates in Lake Mendota was not significantly different among transects ($0.09 < P < 0.54$) and between years ($0.25 < P < 0.71$), but was significantly different among lake zones ($0.001 < P < 0.022$, rmANOVA). The highest density in Lake Mendota was found in the littoral zone ($P < 0.002$, Tukey test), while the densities in the sublittoral and profundal zones were not significantly different ($P = 0.87$). Correspondingly, biomass of benthos was the highest in the littoral zone, and significantly different from density in the sublittoral zone ($P = 0.02$). However, due to the second peak of abundance in benthos in the profundal zone, density there was similar to the littoral zone ($P > 0.10$, Tukey test).

The total density of benthic invertebrates in Lake Monona was not different among transects ($P = 0.72$), but was significantly different between years ($P = 0.025$), and among lake zones ($P < 0.001$, rmANOVA). Total biomass was not different among transects ($P = 0.82$) and sampled years ($P = 0.077$), but was different among lake zones ($P = 0.007$). The density and biomass of benthos in Lake Monona was highest in the littoral, but was also high in the sublittoral zone ($0.65 > P > 0.08$). Benthic densities, both in littoral and sublittoral zones were higher than in the profundal zone ($P < 0.005$, Tukey test).

Benthic community composition in Lake Mendota and Monona during all five years of our study did not differ significantly among three transects sampled (Global R = -0.23 – 0.013, $0.89 > P > 0.24$, 2-way ANOSIM on density and biomass, Fig. 2). In our subsequent analyses we used these transects as replicates.



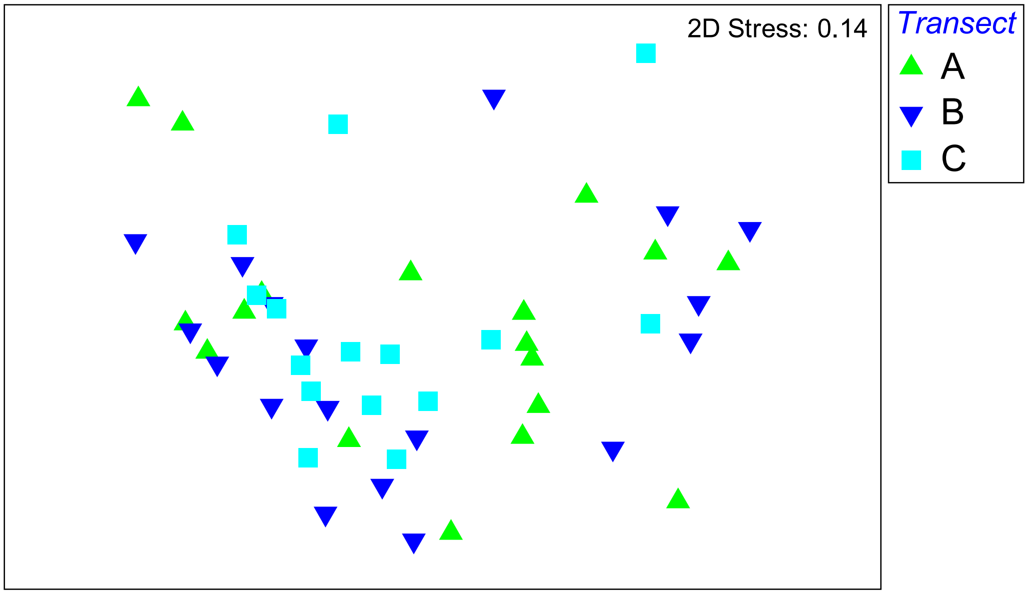
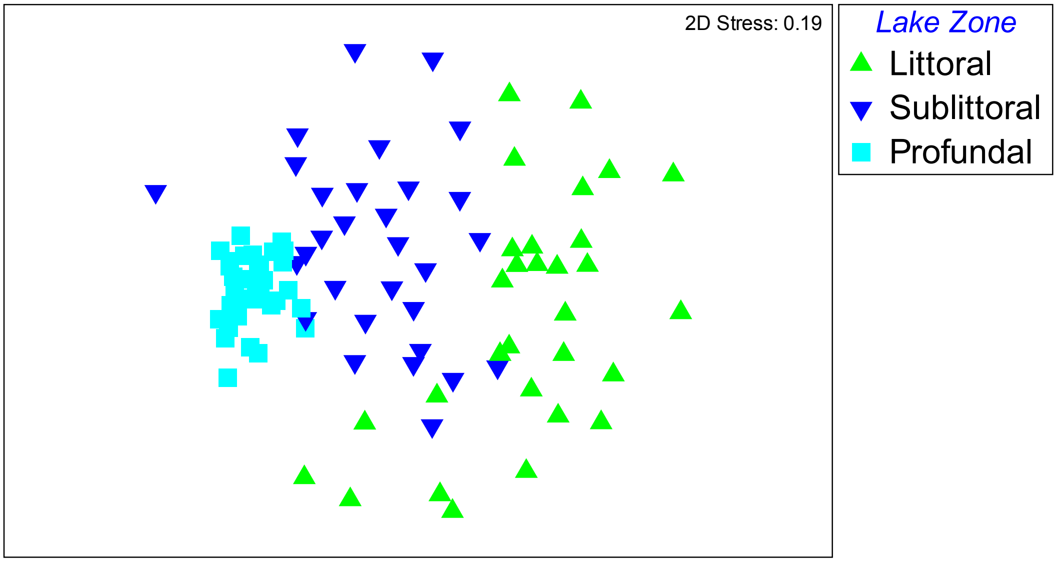


Fig. 2. Non-linear 2-dimentional MDS ordination of benthic community of Lake Mendota based on Bray-Curtis similarities of species densities (fourth root transformed) in 2002, 2003, 2004, 2006, and 2007 (upper graph) and Lake Monona in 2002, 2006 and 2007 (lower graph). Samples are marked by sampling transect: A, B, C, and the Deep hole (DH).

We found a significant difference between the community composition of different lake zones and this difference was consistent among all years of our study and in both lakes (Global R > 0.53, P = 0.001; 2-way ANOSIM on density and biomass, Fig. 3). The largest difference was found between littoral and profundal zones (R > 0.805, P = 0.001, pairwise test after ANOSIM on density and biomass).



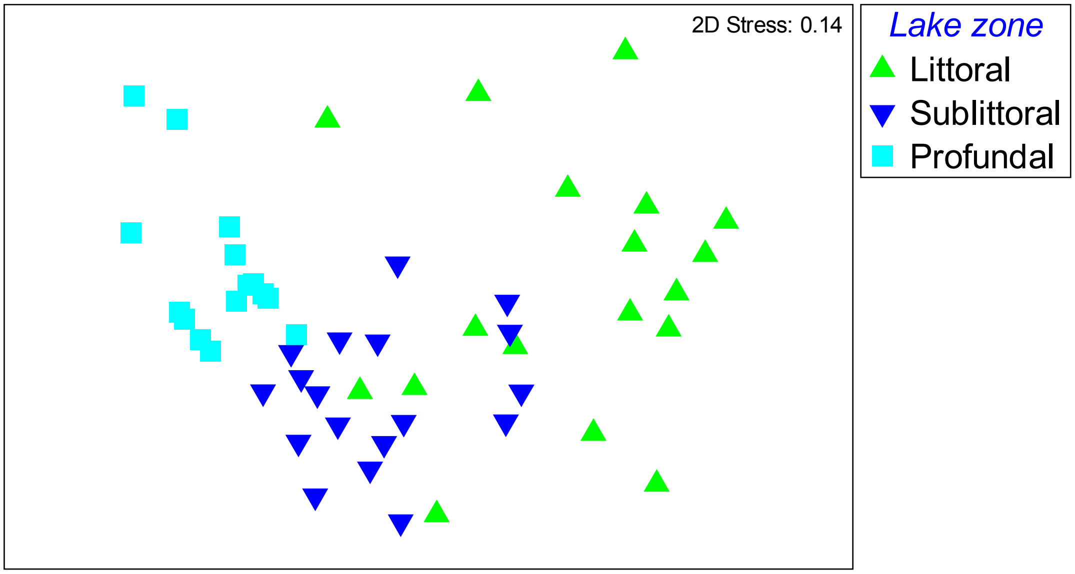


Fig. 3. Non-linear 2-dimentional MDS ordination of benthic community of Lake Mendota based on Bray-Curtis similarities of species densities (fourth root transformed) in 2002, 2003, 2004, 2006, and 2007 (upper graph) and Lake Monona in 2002, 2006-2007. Samples are marked by lake zone.

Within each zone, the spatial variability was always much higher in the littoral and/or sublittoral, compared to the profundal zone (Table 5, Table 6).

Table 5. Average species richness (number of taxa found ± standard error of the mean), density, wet biomass, multivariate dispersion index, and coefficient of variation (CV, calculated on density data) of zoobenthos of Lake Mendota in 2002 – 2007.

Lake zones	2002	2003	2004	2006	2007
Littoral:					
Species richness	19.2±3.6	16.3±3.3	15±3.1	17±2.7	17.3±2.7
Density, m^{-2}	2656±1379	3638±817	4010±977	9175±3791	11968±2883
Biomass, mg. m^{-2}	14.48±9.33	7.2±3.3	7.0±2.5	10.8±4.3	11.5±1.9
Dispersion index	1.536	1.184	1.592	1.549	1.239
CV, %	127	55	60	101	59
Sublittoral:					
Species richness	6.7±0.7	8.8±0.7	7.7±0.9	10.2±0.9	11±1.5
Density, m^{-2}	705±295	3862±1468	1758±511	1978±599	1790±431
Biomass, mg. m^{-2}	1.2±1.0	4.8±1.4	2.7±0.3	4.7±0.6	2.8±0.5
Dispersion index	1.476	1.334	1.364	1.050	1.259
CV, %	111	93	71	74	59
Profundal:					
Species richness	3.4±0.4	4.1±0.3	3.4±0.4	3.6±0.3	5±0.6
Density, m^{-2}	3994±955	2146±420	2451±513	1200±222	2228±480
Biomass, mg. m^{-2}	9.0±1.0	6.0±1.1	7.8±0.9	5.3±0.9	6.7±1.6
Dispersion index	0.410	0.464	0.392	0.486	0.521
CV, %	53	52	55	49	57

Table 6. Average species richness (mean number of taxa found ± standard error of the mean), density, wet biomass, multivariate dispersion index (calculated from data on density), and coefficient of variation (CV, calculated on density data) of zoobenthos of Lake Monona in 2002, 2006 and 2007.

Lake zones	2002	2006	2007
Littoral:			
Species richness (number of taxa found)	12.2±2.5	22.2±2.5	13.2±2.9
Density, m^{-2}	1070±196	15746±3440	15830±3708
Wet Biomass, mg. m^{-2}	0.6±0.3	14.4±2.4	13.3±5.5
Dispersion index	1.428	1.138	1.346
CV, %	78	93	57
Sublittoral:			
Species richness (number of taxa found)	8.5±1.6	9.3±2.2	6.3±1.6
Density, m^{-2}	927±290	2158±313	5881±1514
Wet Biomass, mg. m^{-2}	4.3±1.0	6.0±0.9	13.4±1.5
Dispersion index	1.060	1.242	0.774
CV, %	133	61	63
Profundal:			
Species richness (number of taxa found)	3.0±0	3.6±0.4	1.6±0.2
Density, m^{-2}	1378±338	507±177	418±152
Wet Biomass, mg. m^{-2}	6.8±1.1	2.3±0.5	2.4±1.5
Dispersion index	0.268	0.429	0.820
CV, %	95	135	81

Littoral zone

Eighty species and higher taxa of bottom macroinvertebrates were found in the littoral zone of Lake Mendota, and 51 species and higher taxa in Lake Monona. The dominant species in Lake Mendota were chironomid *Cladotanytarsus* sp., amphipod *H. azteca,* and oligochaeta *Stylaria lacustris*, comprising respectively 17, 13, and 12% of the total density of bottom invertebrates in the littoral zone. Dominant species in Lake Monona were *Stylaria lacustris*, chironomids *Dicrotendipes tritomus*, *Chironomus* sp., and amphipod *H. azteca* (31, 9, 9 and 9% respectively of the total littoral density).

In general, the benthic community of the littoral zones of both lakes was consistently the most diverse and productive among all zones studied and were characterized by the high spatial variability (Table 5, Table 7, and Table 7). This is typical for littoral benthos and is associated with high heterogeneity of environmental factors, like wave action, slope, substrate heterogeneity, and presence of macrophytes (Brinkhurst, 1974; Rasmussen, 1988; Tolonen et al., 2001; Wetherhead and James, 2001; Jonasson, 2004; Stofeels et al., 2005). In shallow areas wave activity creates conditions typical for lotic systems, preventing the accumulation of detritus. Benthic organisms found here are usually those typical for streams, while many lacustrine invertebrates could be inhibited in this area (Barton and Hynes, 1978; Tolonen et al., 2001; Wetherhead and James, 2001). Many of these organisms are infaunal organisms that are relatively small and live within bottom sediments (Karatayev and Karatayeva, 1992). They may form high densities, but being small, they usually do not create high biomass.

The total benthic diversity and biomass in the sandy littoral zone of Lake Mendota was the lowest at one meter depth, and significantly increased to the highest at 3 m depth, where macrophytes were the most abundant substrate of all the depths sampled, while the highest total densities were often found at one meter depths. Macrophyte beds increase substrate complexity, offer benthic organisms food (epiphytic algae and detritus), and refuge from predators (Tolonen et al., 2001; Wetherhead and James, 2001), often yielding the highest diversity and density of zoobenthos (Jonasson, 2004). Therefore, at 3 m depth we consistently recorded the highest diversity and biomass of zoobenthos of all depths sampled in the lake. The high spatial variability, in addition to high diversity, makes littoral benthos difficult for monitoring, as it requires extensive sampling of shores with different wind exposure and types of habitat (Tolonen et al., 2001).

Table 7. Benthic secondary production (kcal m^{-2} year^{-1}) in Lakes Mendota and Monona calculated per each lake zone.

Lake Zone	Non-predatory production	Predatory production
Lake Mendota		
Littoral	36.2	7.2
Sublittoral	9.4	4.6
Profundal	26.0	6.6
Lake Monona		
Littoral	40.4	1.7
Sublittoral	34.9	1.1
Profundal	17.6	0.9

Sublittoral zone

Although a total of 33 species and higher taxa of bottom macroinvertebrates were found in the sublittoral zone of each of the studied lakes, the taxa richness per sample in the sublittoral zone was almost twice as low as in the littoral zone (Table 5, Table 6). In Lake Mendota, chironomid larvae *Polypedilum halterale* and *Procladius* sp. dominated benthos, and were responsible for 22 and 13% of the total densities, and for 7 and 22% respectively of the total wet zoobenthos biomass in this zone. In addition, only a few other species were common here, including molluscs *Valvata tricarinata*, *Pisidium* sp., and turbelaria *Dugesia tigrina.* In Lake Monona, the dominant species in terms of both density and biomass were *Chironomus* sp., which, together with *Cladopelma* sp. and unidentified oligochaetes, were responsible for 85% of the total density (60, 9, and 16% respectively) and 89% of the total biomass (81, 2, and 6%).

The total zoobenthos density, biomass and productivity in the sublittoral zone were among the lowest in Lake Mendota, but not in Lake Monona (Table 5, Table 6, and Table 7). The variability of zoobenthos in the sublittoral zone of both lakes was similar to the littoral, but was usually higher than in the profundal zone. In the sublittoral zone the diversity and density of bottom invertebrates declined from 5 m to 8 m in both lakes. This decline was associated with a change in the bottom substrate from macrophytes to various combinations of silt and sand.

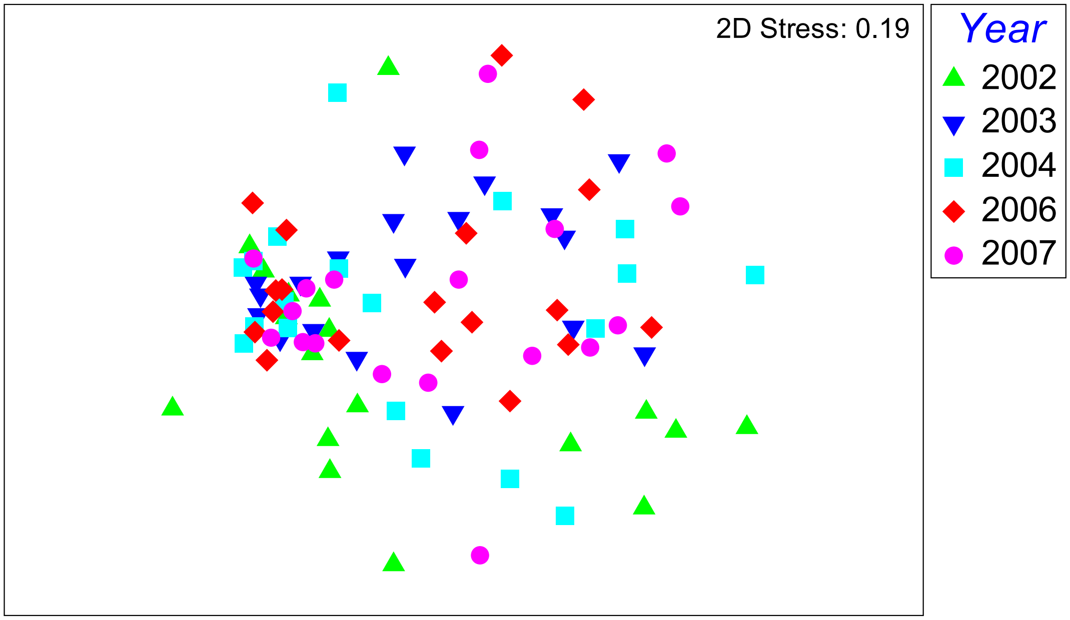
Profundal zone

In contrast to the littoral, benthos in profundal zone everywhere was more homogeneous, had the lowest diversity, and often lowest variability (Fig. 3, Table 5, and Table 6). Although a total of 20 taxa were found in this zone in Lake Mendota, and 6 in Lake Monona, only oligochaetes and chironomid larvae *Procladius* sp. and *Chironomus* sp. were common and abundant here, and average species richness was very low (app. 4 ± 1 taxa per sample in Lake Mendota, and 1.6±0.2 in Lake Monona) (Table 5, Table 6). The low benthic diversity in the profundal zone can be explained by the low substrate heterogenity, represented by deep silt sediments at low oxygen concentration. As the result, only a few species which are typically found in muddy substrates and are tolerant to low oxygen survive in the profundal zone, including chironomids (mostly *Chironomus* sp. and *Procladius* sp.), oligochaetes, and flatworm *Dugesia tigrina*. These species are typical for the profundal benthos of lakes (Brinkhurst, 1974; Wiederholm, 1980). The accumulation of sediments in the profundal zone with high organic content may create a sufficient food base to support high densities of benthic detritivores. Consequently, although benthic biodiversity in the profundal zone is much lower than in the littoral, the overall density, and especially the biomass of invertebrates in the profundal zone, may be higher than in the littoral. This resulted in the second peak of vertical distribution of benthic biomass in Lake Mendota recorded at 20 m on mud. In contrast, no such peak was recorded in Lake Monona, where benthic biomass was maximal at 3 m, peaked again on 8 m depth, but then decreased on 15 m and further on 20 m (20 m depth in Lake Monona were found only at 2 transects). Correspondingly, benthic production was high in Lake Mendota profundal, but the lowest in Lake Monona (Table 7). Low spatial variability, low biodiversity and relatively easy sampling make the profundal benthos a convenient community for long-term monitoring. As a result, profundal zoobenthos has been a subject of a long-term monitoring (Wiederholm, 1988).

Temporal variability in benthos

Lake Mendota

There was a significant difference in the community composition of Lake Mendota among sampled lake zones (density and biomass, lake zone: Global $R > 0.65$, $P = 0.001$, 2-way ANOSIM, Fig. 3). The difference among sampling years was very low (Global $0.06 \leq R \leq 0.08$, Fig. 4), and was mainly due to the year 2002, when different sampling devices were used on littoral and sublittoral zones.



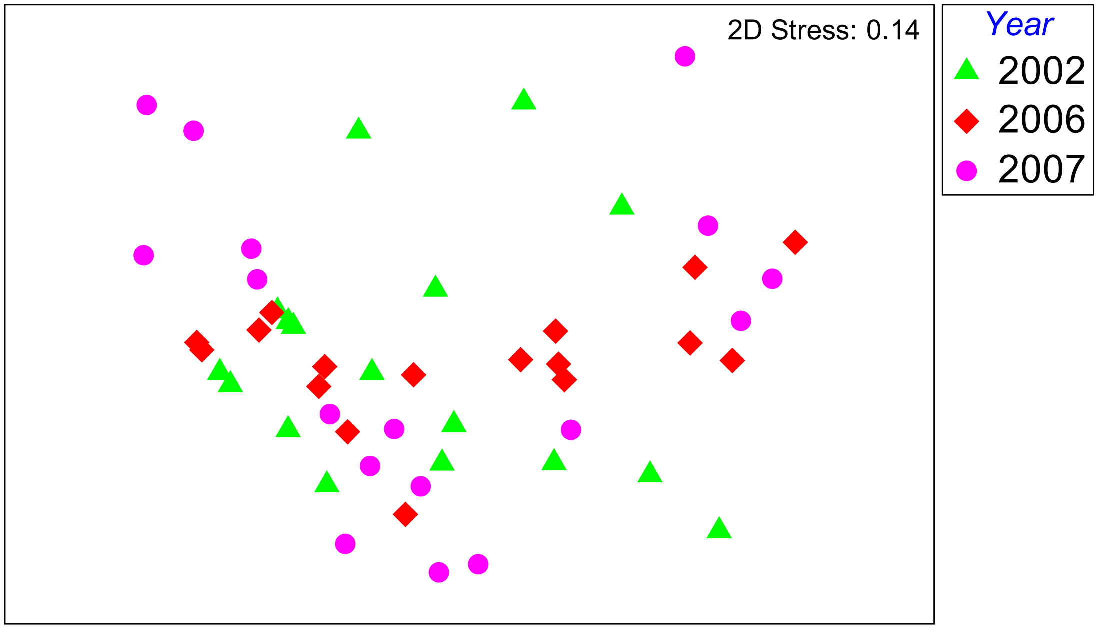


Fig. 4. Non-linear 2-dimentional MDS ordination of benthic community of Lake Mendota based on Bray-Curtis similarities of species densities (fourth root transformed) in 2002, 2003, 2004, 2006, and 2007 (upper graph), and Lake Monona (2002, 2006, 2007, lower graph). Samples are marked by sampling year.

In addition, there were no serial correlations in the benthic community similarity matrices among years calculated for the whole lake (Spearman ρ = 0.035, P = 0.07), as well as in the littoral and profundal zones (littoral zone: Spearman ρ = 0.093, P = 0.054; profundal: Spearman ρ = 0.005, P = 0.46; RELATE). Temporal correlation in the sublittoral zone was significant (mostly due to 2002 year), but not strong (Spearman ρ = 0.158, P = 0.008; without 2002: Spearman ρ = 0.041; P = 0.23).

No significant changes in the diversity of benthic community were found among sampling years (Global R = -0.017, P = 0.86, 2-way ANOSIM on diversity indices matrix), but diversity indices were significantly different among lake zones (Global R = 0.43, P = 0.001; Fig. 5).

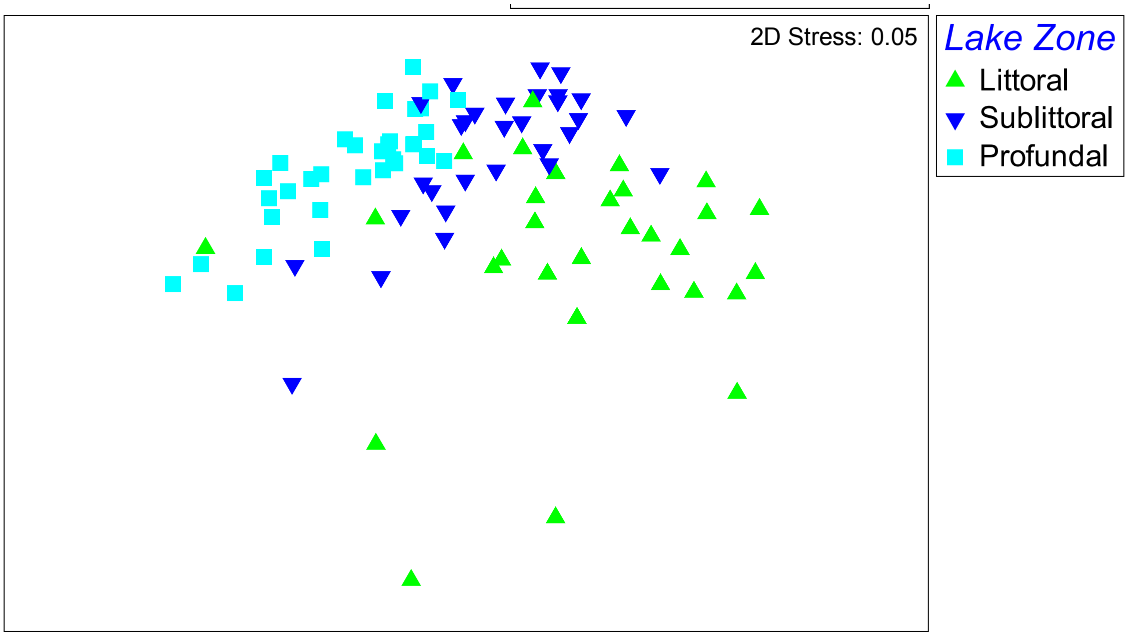


Fig. 5. Non-linear 2-dimentional MDS ordination of similarity indices of Lake Mendota benthic community based on normalized Euclidian distances of diversity indices of species densities in 2002-2007. Samples are marked by lake zones. Diversity indices used were: total number of species in each sample, the number of individuals in each sample, Margalef's species richness, Pielou's evenness, Shannon-Wiener diversity index, and Simpson's index.

To test for differences in dominant species in benthos among sampled years, we used ANOSIM on k-dominance density and biomass curves (cumulative ranked density or biomass vs. species rank). There was no difference in dominance among 2002-2007 (0.84 < P < 0.37, density and biomass), but the dominant curves were significantly different among lake zones (P = 0.01, 2-way ANOSIM on k-dominance curves, Fig. 6).

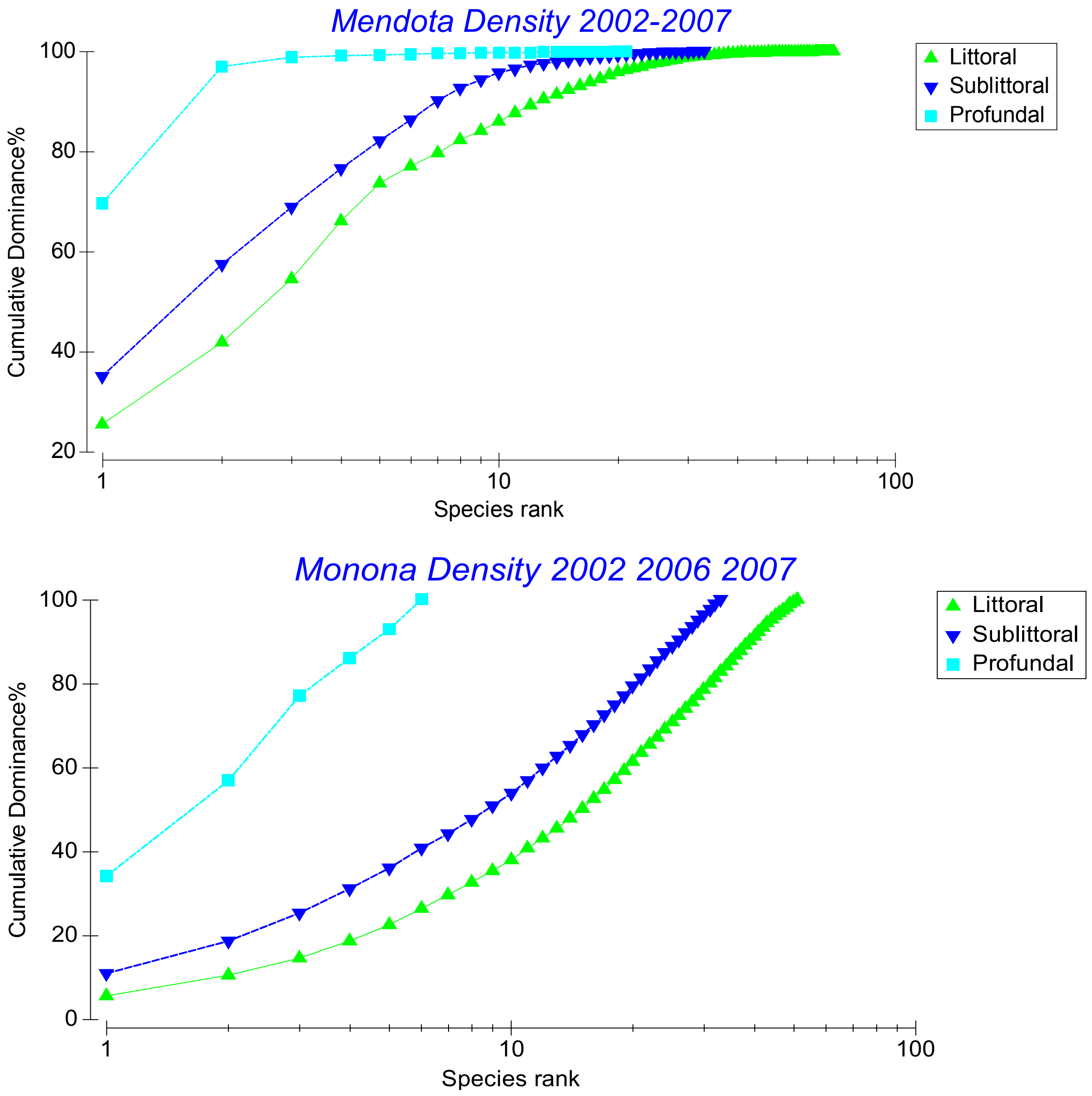


Fig. 6. k-Dominance plots for density of benthic community in each of lake zones (pooled data for Lake Mendota, upper graph, 2002-2004, 2006, 2007; Lake Monona, lower graph, 2002, 2006, 2007).

Lake Monona

We found a significant difference in community composition of Lake Monona among sampled years (density: years: Global R = 0.259, P = 0.001, lake zone: Global R = 0.605, P = 0.001; biomass: Global R = 0.245, P = 0.001, lake zone: Global R = 0.532, P = 0.001, 2-way crossed ANOSIM, Fig. 4). The largest difference was found between 2002 and 2007 (R > 0.35), and was probably due to the difference in sampling techniques used in littoral and sublittoral zones in 2002. Although there was no serial correlations in the benthic community similarity matrices among years for the whole lake (Spearman ρ = 0.051, P = 0.09), some weak but significant correlations were found when the zones were analyzed separately (littoral zone: Spearman ρ = 0.378, P = 0.001; sublittoral zone: Spearman ρ = 0.208, P = 0.02; profundal: Spearman ρ = 0.246, P = 0.02; RELATE).

We found a significant difference in benthic diversity among lake zones (Global R = 0.358, P = 0.001; Fig. 5), and some difference among sampling years (Global R = 0.112, P = 0.037, 2-way ANOSIM on diversity indices).

To test for differences in dominant species in benthos among sampled years, we used ANOSIM on k-dominance density and biomass curves (cumulative ranked density or biomass vs. species rank). Density and biomass dominant curves were significantly different among lake zones (R = 0.198, P = 0.001, 2-way ANOSIM on k-dominance curves, Fig. 6). There was a significant difference in density dominance among years (R = 0.127, P = 0.012), but only due to the significant difference between 2006 and 2007 (P = 0.009). However, there was no significant difference in dominance among sampled years by biomass (R = 0.05, P = 0.16).

Long-term changes in benthic communities of Lake Mendota

Low annual variability in benthic community during the five years of our study allowed us to use 2002-2007 years as replicates and detect dramatic changes in the benthic community of Lake Mendota within the last century. These changes were simultaneously recorded on all three zones of the lake, and include (but are not limited to) the extirpation of keystone species in the profundal zone, and the decrease in the diversity of trichopterans, ephemeropterans and molluscs in littoral and sublittoral zones. Benthic community's response was different among lake zones, in agreement with Hämäläinen et al. (2003), who suggested that, because of the littoral and pelagic zone support different communities, they are likely to show dissimilar responses to environmental variation.

Littoral

In August 1884 Forbes (1888) collected samples at ca. 3, 4-6, and 20-21 m depth. Although he did not report any quantitative data, he mentioned that in the sandy littoral he found "a great number of small white larvae of *Chironomus*, with several small amphipod crustaceans (*Allorchestes dentate*), two or three small molluscs (*Amnicola*), a few worms (*Stylaria lacustris*), a single larval ephemerid (*Caenis*), and two Entomostraca". In 1885 he sampled lake again and collected 9 samples. In addition to mentioned above species, he found *V. tricarinata* and *V. sincera*, *Sphaerium* sp., leeches and planarians. The unionids *Unio luteolus* and *Anodonta footina* were very abundant during this period (Forbes, 1888). In 2002-2007 we did not find molluscs either *V. sincera*, or *Sphaerium* sp.

In June 2006 we found live specimens of *Lasmigona complanata*, *Lampsilis siliquoidea* (former *Unio luteolus*), *Lampsilis cardium, Pyganodon grandis,* and *Strophitus undulates* (species identification was done by Lisie Kitchell, Wisconsin DNR). A special study is needed to estimate their densities. Other taxa reported by Forbes (1888) were still abundant during our study.

In 1914-1915, benthic macroinvertebrates in the littoral zone (depths 0-7m) of Lake Mendota were studied by Muttkowski (1918). During this very extensive survey (over 350 quantitative and over 400 qualitative samples), he found 106 species, including: 19 chironomids, 16 molluscs, 14 trichoptera, and 12 coleoptera species. This was the most comprehensive study of littoral benthos of Lake Mendota ever conducted. According to Muttkowski (1918), most abundant in 1914-1915 were unidentified oligochaeta, amphipoda *H. azteca,* trichoptera larvae and mollusc *A. limosa* (Table 5). He also found unionids (*Anodonta* and *Lampsilis*) at 1-2, 2-3, 3-5, and 5-7 m, with maximum density of 1.4 m^{-2} at 5-7 m. Although other authors reported some information on the zoobenthos of the littoral zone of Lake Mendota (Forbes 1888; Andrews and Hasler 1943; Mckenthun and Cooley 1952; Sapkarev 1967-68; Lathrop 1992b) they are not comparable to our study and therefore were excluded from the analysis of the long-term changes in the benthic community of the littoral zone of the lake (Fig. 7).

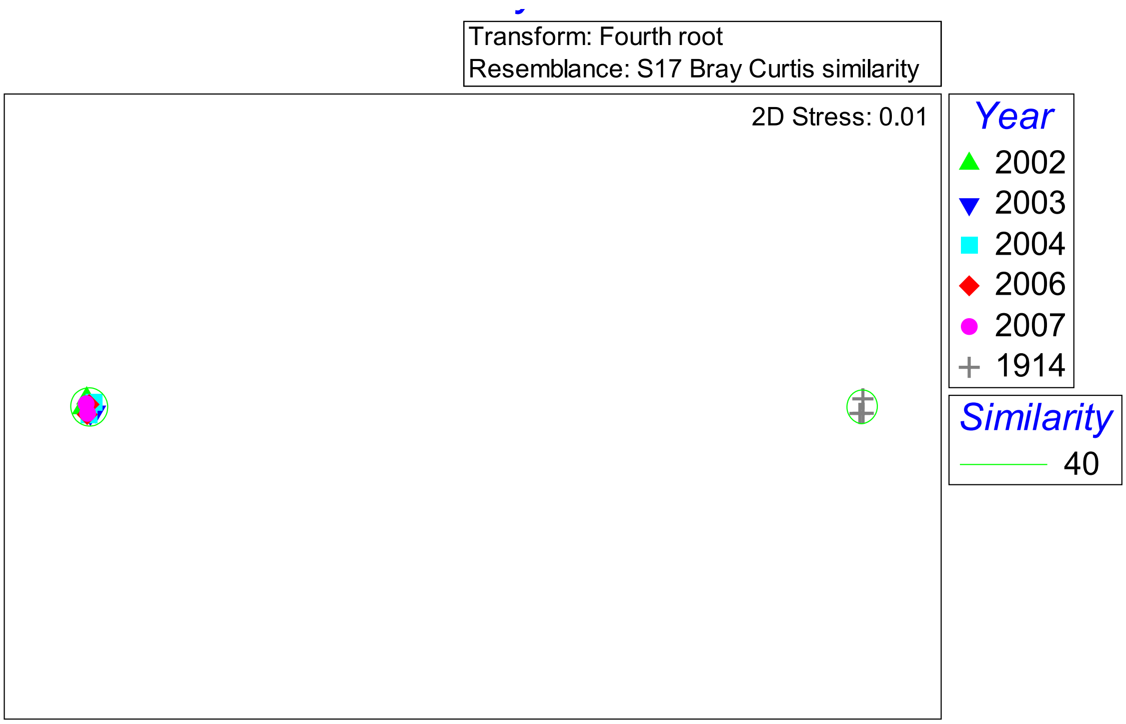


Fig. 7. Long-term changes in the zoobenthos of Lake Mendota in the littoral zone.

We found significant difference between 1914-1915 (Muttkowski, 1918) and 2002-2007 (Time: R = 1.0, P = 0.028, Depth: R = 0.46, P = 0.008, 2-way ANOSIM on density matrices, Fig. 7). There was a high temporal correlation in benthic community among 1914-1915 and 2002-

2006 (ρ = 0.79, P = 0.003, RELATE), and dominance curves were also significantly different (Global R = 0.531, P = 0.017, ANOSIM on density dominant k-plots). Changes were associated with disappearance of *Chaoborus punctipennis*, *Sphaerium occidentale*, *Gammarus fasciatus,* and others; decrease in the density of some molluscs (e.g. *Amnicola limosus,* unionids) and complete extirpation of other (e.g. *Planorbella campanulata,* and *Lymnaea stagnalis*). In addition, we found a sharp decrease in the diversity of Trichoptera and Ephemeroptera larvae. In contrast, Muttkowski (1918) did not find isopods *Asellus* sp., chironomids *Cladotanytarsus* sp., *Cladopelma* sp., gastropods *Gyraulus circumstriatus* and *G. deflectus*, trichopterans *Leptocerus americanus* and several other species that are now quite abundant. Densities of some other species including chironomids, oligochaetes, gastropods *V. tricarinata*, planarians *Dugesia tigrina,* had increased dramatically since 1914-1915. We also found an increase in diversity of chironomids larvae. In addition, a single individual of exotic oligochaeta *Branchiura sowerbyi* was found at a 5 m depth for the first time in Lake Mendota in 2007. Some of the reported differences could definitely be due to identification problems or different sampling techniques used. However dramatic changes in the benthic community are still evident. There is no doubt that numerous previously common molluscs have completely disappeared from Lake Mendota. We repeatedly found long dead shells of *Sphaerium* sp. (tentatively identified as *Sphaerium striatinum*), *Planorbella campanulata*, *Lymnaea* sp*., Elimia virginica*, *Stagnicola catascopium,* and others, and never recorded a single live individual of any of these species. After combining taxonomic resolution of 1914-1915 and our data to a similar level in order to minimize the effect of changes in taxonomic knowledge, and different sample processors (Metzeling et al., 2002), we found that 73 species and higher taxa were reported in 1914-1915 and 72 in 2002-2007. Only 35 species and higher taxa were found during both surveys. Thirty eight taxa reported by Muttkowski (1918) were not found during our study, and we found 31 taxa that were not reported in 1914-15. The most dramatic changes were found in Ephemeroptera, Trichoptera and Chironomidae. Since 1914-1915 seven taxa of caddisflies, and five species of mayflies disappeared from the benthic community of Lake Mendota. In contrast, we found 13 species of chironomids and 5 species of caddisflies that were not reported in 1914-1915. As a result, Ephemeroptera, Plecoptera, and Trichoptera (EPT) index decreased from 1.30 in 1914-1915 to 0.53 in 2002. Additionally, the complete disappearance of the previously very common *Chaoborus punctipennis* and a recent record of exotic oligochaeta *B. sowerbyi*, new for Lake Mendota, are additional clear evidences of substantial changes in the community.

Sublittoral Zone

Although several authors occasionally reported some data on the zoobenthos of the sublittoral zone of Lake Mendota (Muttkowski, 1918; Juday, 1921; Dugdale, 1965, Stewart, 1965 et al.), only Mackenthum and Cooley (1952) reported data comparable to our data. We found that benthic community in the sublittoral zone of Lake Mendota changed between 1951 and 2002-2007 (Fig. 8) (Global R = 1.0, ANOSIM), and the temporal changes were strong (ρ: 0.89, P =

0.002, RELATE). These changes were associated with the dramatic decline and disappearance in 2000s of *Chaoborus punctipennis*, *Sphaerium striatinum*, and appearance of *Pisidium* sp. in the sublittoral zone. EPT index in the sublittoral zone decreased from 0.22 in 1951 to 0.01 in 2002.

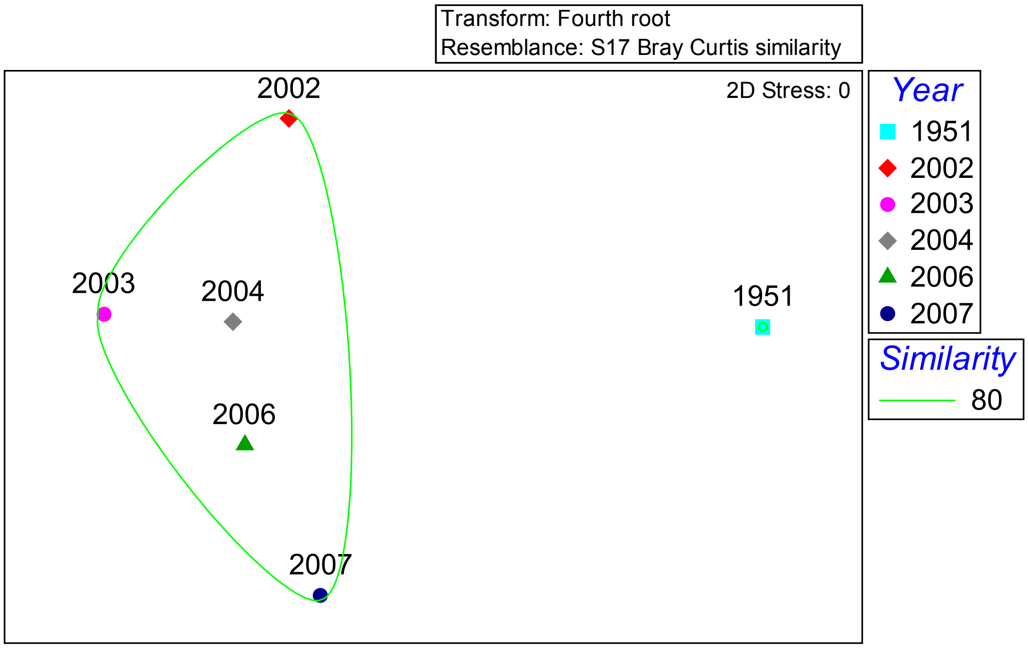


Fig. 8. Long-term changes in zoobenthos of Lake Mendota in the sublittoral zone.

In 1951 zoobenthos was dominated by *Chironomus* sp. and fingernails clams identified as *Pisidium idahoense* by Mackenthum and Cooley (1952). Other abundant taxa were unidentified oligochaetes, *Procladius* sp., and *C. punctipennis*. Chironomids larvae *Chironomus* sp., *Procladius* sp., and oligochaetes were still abundant in 2002 – 2007. However, during our study we never found even a single *C. punctipennis.* We also did not find live *P. idahoense* reported by Mackenthum and Cooley (1952), however we repeatedly found very long dead shells of *Sphaerium striatum.* Similar to *P. idahoense, S. striatum* are large clams (> 10 mm) and, probably, were the fingernails clams reported by Mackenthum and Cooley (1952). Instead, we found several peaclams *Pisidium* sp. This is a much smaller species, usually 2 – 3 mm in length with largest individual found in Lake Mendota <5 mm.

Profundal zone

We detected dramatic changes in the benthic community of the profundal zone that occurred between 1914-1965 and 2002-2007 (Global R = 0.87, P = 0.008). Communities were similar from 1917 to 1951 and from 1965 to 2007, forming two distinct clusters at 60% similarity (P = 0.001, SIMPER, Fig. 9).

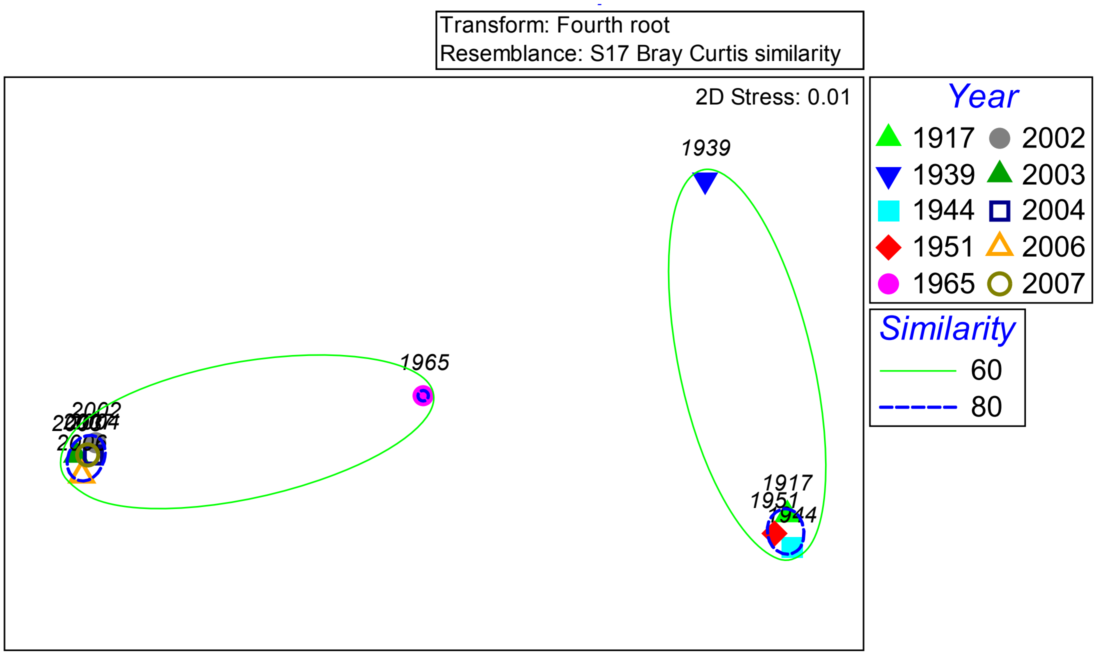


Fig. 9. Long-term changes in zoobenthos of Lake Mendota in the profundal zone

There was an evidence of significant temporal changes: Spearman ρ = 0.855 (P = 0.0005) (Fig. 9). These changes were associated with the disappearance of fingernail clams and phantom midge *C. punctipennis,* resulting in nearly a 40% decline in the species' diversity. In 1917 – 1951, profundal zoobenthos was represented by five common taxons: *C. punctipennis*, *Chironomus* sp., *Procladius* sp., fingernails clams, and unidentified oligochaets, typical for a profundal benthic community in glacial lakes (reviewed in Brinkhurst, 1974). *Chaoborus punctipennis* and *Chironomus* sp. were the dominant species. In 1942 – 1943, the density of *C. punctipennis* alone reached 10,500 m^2 (Hasler, 1945), and fingernail clams density in 1952 was 460 m^2 (Mackenthum and Cooley, 1952). By 1965, the densities of both species dropped by several orders of magnitude, and after 1987, these species completely disappeared from Lake Mendota. Fingernails clams reported by various authors from the profundal zone of Lake Mendota were identified by Juday (1921) and Mackenthum and Cooley (1952) as *Pisidium idahoense*. These are large clams, and exceeded 5 mg of dry weight of body parts (Juday, 1921), which approximately equals to 100 mg of the total wet weight (body and shell). Again we found numerous very long dead shells of large fingernails clams identified as *S. striatum* in the profundal sediments, but we never found a single live specimen. Peaclams (*Pisidium* sp.) that we occasionally recorded in this zone were much smaller and never exceeded 20 mg of the individual total wet weight.

Chaoborus was the only invertebrate predators in the profundal zone of Lake Mendota, conducting nocturnal vertical migration in the water column preying on zooplankton, while suspension feeders fingernail clams removed particulate organic matter from the water above the bottom. Different species differ in their rates and pathways by which they process resources, as well as in their effects on the abiotic environment and interaction with other species. Therefore, changes in species composition may alter ecosystem processes through changes in the functional traits of biota (Chapin et al., 1997). Both fingernail clams and phantom midges provided an important link between benthic and pelagic components of the ecosystem. Moreover, due to their unique ecological role and former high density in Lake Mendota (over 10,000 m^2), *C. punctipennis* could be considered a "keystone" species, and its disappearance might cause dramatic changes in the entire ecosystem.

Possible reasons for changes in benthic community

It is evident that over the last hundred years the benthic community of Lake Mendota had experienced dramatic disturbance that peaked in 1950s and 1960s and affected all three zones of the lake. Substantial changes in the zoobenthos of Lake Mendota were previously reported by Lathrop (1992a, 1992b, 2007). This author suggested and discussed several possible reasons for the changes including (1) decline in food availability, (2) increase in fish (especially carp) predation, (3) use of toxic insecticides in the drainage basin, and (4) changes in the profundal sediment environment (Lathrop, 1992a, 1992b). However, it is not clear which of these reasons or a combination of them are responsible for the changes in Lake Mendota zoobenthos, especially because of these changes have affected species with different, sometimes opposite, environment requirements (like fingernails clams and chaoborids). While clams are quite sensitive to eutrophication, phantom midges are very tolerant to low oxygen and often flourished even in hypereutrophic lakes (Brinkhurst, 1974; Holopainen and Jonasson 1983, Vezhnovets et al., 1992). Holopainen and Jonasson (1983) also reported a sharp decline in the density of *Pisidium* in the profundal zone of the Lake Esrom, Denmark. This decline was due to oxygen deficiency caused by eutrophication that resulted in heavy mortality and halted the growth of several *Pisidium* species. Therefore, because eutrophication has increased dramatically in Lake Mendota in late 1940s – 1970s (Lathrop, 2007), it may be responsible for the decline in fingernails clams and possibly some other molluscs, but cannot explain the disappearance of chaoborids.

Recommendation for monitoring

Ideally, extensive surveys conducted on multiple stations (dozens or even hundreds), repeated frequently (e.g. every two weeks), may largely compensate for both spatial and temporal variability and produce data reliable enough for revealing the effect of disturbance. However, due to resource limitation, long-term monitoring could be achieved either by frequent sampling of few or even one station, or by an extensive survey with a much larger time interval (e. g. once a year). Both methods are common (e. g. Wiederholm, 1988; Haberman et al., 2000; Hämäläinen et al., 2003), and both methods have their pros and cons. The first method may be effective for a long-term monitoring conducted on same sampling stations to avoid spatial variability, and will compensate seasonal variability, while the second method may be more effective to compare current data with historical data, when detail information on previously sampled sites (e.g. exact locations, depth, substrate type) is unknown.

We found that one extensive benthic survey per year was a sufficient method to detect disturbance over a long period of time, supporting Scarsbrook' (2002) suggestion that an annual time scale is appropriate to determine benthic macroinvertebrate community stability. Due to the low diversity and homogeneous substrate, which results in a spatial variability much lower than in the littoral zone, profundal benthos is very convenient for monitoring. In contrast, high spatial variability and high diversity make littoral benthos difficult to monitor, as it requires extensive sampling of all types of habitats (Tolonen et al., 2001). Although due to the lack of oxyphilic species and in general low diversity, profundal benthos could not be sensitive enough to reveal the effect of disturbance on community, it is evident that in the case of Lake Mendota, disturbance was strong enough to dramatically change the whole community of benthic invertebrates including the profundal zone.

2. *Dreissena polymorpha* in Wisconsin lakes: effect on benthic community

Large aggregations of zebra mussels create 3-D habitats, altering the surface of the substrate and providing shelter and food for other benthic invertebrates (reviewed in Karatayev et al., 1997, 2002, 2005; Ward and Ricciardi, 2007). *Dreissena* local effect is usually limited to the littoral zone of lakes, as zebra mussels usually avoid deep mud of the profundal zone. Although, both European and North American studies agree that *D. polymorpha* has positive effects on certain species (e.g., amphipods, isopods, leeches, turbellarians, some oligochaetes and chironomids), and negative impacts on others, the overall effect on species richness may be different, depending on the substrate type and native benthic community structure (reviewed in Karatayev et al., 1997; Ward and Ricciardi, 2007). The overall biomass of native invertebrates is usually higher in *Dreissena* druses; however, the overall density of invertebrates may be lower in zebra mussel aggregations than in bare sediments nearby (reviewed in Karatayev et al., 1997). To predict the potential impacts of zebra mussel invasion on benthic communities of Madison lakes we studied species composition of native macroinvertebrates within *Dreissena* druses and in nearby sediments in Lake Lower Nashatan. This lake has a large littoral zone with substrates, similarly to the Madison lakes, and therefore is a convenient model for prediction the possible impacts of *Dreissena* on lakes Mendota and Monona.

We found a total of 47 total species and higher taxa of macroinvertebrates in druses collected from all substrates (excluding *Dreissena*) and 30 taxa in all bare sediments near druses. Twenty seven taxa were found both in druses and sediments; five were found in sediments only and 18 in druses only. Across all substrates studied, the total benthic diversity was consistently higher in *Dreissena* druses than in nearby sediments (Table 8).

Table 8. Species composition, density (m^{-2}), wet biomass ($g\ m^{-2}$), coefficient of variation (CV), and diversity indices of native (excluding *Dreissena polymorpha*) macroinvertebrates in *Dreissena* druses and bare sediments nearby in Lake Lower Nashatan. Cell values are means ± SE. Diversity indices (calculated on densities) include relative multivariate dispersion (MVDISP), multivariate dispersion index (MVDISP), and Margalef's species richness for each community.

Parameters	Rocks		Silt, shells		Sand	
	Sediments	*Dreissena* druses	Sediments	*Dreissena* druses	Sediments	*Dreissena* druses
Total species	18	30	9	32	20	33
Species per sample	10.2±1.2	18.8±1.2	2.7±0.8	16.5±1.2	8.3±0.8	19.8±1.0
Density m^{-2}	10,254±159	21,764±212	833±21	18,165±156	5,708±100	22,928±229
CV (density), %	7	5	7	5	8	6
Biomass, gm^{-2}	7.23±0.15	30.31±0.31	2.71±0.13	33.03±0.30	14.76±0.51	26.06±0.23
CV (biomass), %	9	6	14	5	15	5
MVDISP	1.166	0.484	1.790	0.721	1.398	0.441
IMD, sediments *vs.* druse communities		0.884		1.0		0.982
Margalef's species richness	1.841	2.903	1.190	3.161	2.197	3.187

The diversity of native benthic invertebrates per sample was also significantly higher ($p<0.0006$, t-tests) in druses than in sediments. Communities in bare sediments were also characterized by much larger variability between samples (IMD > 0.88 for druses *vs.* sediment communities). The total density and biomass of benthic community were significantly higher in *Dreissena* druses compared to bare sediments ($0.0001 < P < 0.03$, t-tests, Table 8). Almost all taxa were much more abundant in druses than in bare sediments (Table 9). We found particularly large differences for gastropods, leaches, caddisflies, mayflies, and chironomids. Only several species of Chironomids (e.g. *Pseudochironomus* sp., *Stictochironomus* sp., *Demicryptochironomus* sp., *Nilotanypus* sp.) and burrowing mayflies *Hexagenia* sp. were more abundant in sediments than in *Dreissena* druses.

Table 9. Density (m^{-2}) of macroinvertebrates (excluding *Dreissena polymorpha*) in Lake Lower Nashatan, Wisconsin.

Taxon	Rocks		Sand		Silt, shells	
	Sediments	Druses	Sediments	Druses	Sediments	Druses
Turbellaria						
Dugesia tigrina	149	472	n. r.	388	n. r.	840
Planaria sp.	n. r.	n. r.	n. r.	n. r.	n. r.	29
Turbellaria total	**149**	**472**	n. r.	388	n. r.	**869**
Gastropoda						
Amnicola limosus	73	n. r.	n. r.	32	n. r.	27
Ferrissia walkeri	n. r.	n. r.	n. r.	55	n. r.	n. r.
Fossaria sp.	n. r.	101	42	n. r.	n. r.	n. r.
Gyraulus circumstriatus	111	734	83	500	n. r.	184
Planorbella campanulata	n. r.	30	n. r.	n. r.	n. r.	n. r.
Physella sp.	n. r.	677	n. r.	564	n. r.	966
Gastropoda total	**184**	**1542**	**125**	**1150**	n. r.	**1177**
Bivalvia						
Pisidium sp.	n. r.	54	n. r.	34	42	66
Bivalvia Total	n. r.	54	n. r.	34	**42**	**66**
Oligochaeta						
Stylaria lacustris	n. r.	88	n. r.	23	n. r.	27
Stylaria lacustris	n. r.	88	n. r.	23	n. r.	27

Taxon	Rocks		Sand		Silt, shells	
	Sediments	Druses	Sediments	Druses	Sediments	Druses
Oligochaeta sp.	458	261	83	1022	n. r.	570
Oligochaeta total	**458**	**348**	**83**	**1045**	n. r.	**597**
Hirudinea						
Helobdella fusca	171	347	42	98	n. r.	39
Hirudinea total	171	347	42	98	n. r.	**39**
Amphipoda						
Hyalella azteca	502	2324	n. r.	1447	n. r.	2668
Ceratopogonidae						
Culicoides sp.	n. r.	n. r.	333	307	n. r.	31
Chironomidae						
Chironomus sp.	n. r.	n. r.	125	61	167	27
Demicryptochironomus sp.	n. r.	n. r.	83	n. r.	42	n. r.
Dicrotendipes modestus	n. r.	334	n. r.	376	n. r.	n. r.
Dicrotendipes tritomus	1664	643	42	659	n. r.	1569
Endochironomus subtendens	106	47	n. r.	n. r.	n. r.	n. r.
Larsia sp.	293	557	n. r.	312	n. r.	158
Microtendipes gr. *chloris*	n. r.	n. r.	n. r.	n. r.	n. r.	n. r.
Microtendipes pedellus	1159	4242	1375	6770	n. r.	2148
Nilothauma sp.	n. r.	n. r.	42	n. r.	n. r.	n. r.
Nilothauma sp.	n. r.	n. r.	n. r.	n. r.	n. r.	27

Taxon	Rocks		Sand		Silt, shells	
	Sediments	Druses	Sediments	Druses	Sediments	Druses
Polypedilum halterale	1033	1336	125	1723	125	690
Polypedilum illinoense	n. r.	n. r.	n. r.	n. r.	n. r.	86
Procladius sp.	n. r.	n. r.	83	129	n. r.	29
Pseudochironomus sp.	2080	1210	1583	1287	n. r.	347
Tanytarsus sp.	1819	4671	917	3526	83	2417
Tribelos jucundus	258	1875	n. r.	1534	208	3197
Chironomidae Total	**8412**	**15071**	**4708**	**16457**	**625**	**10697**
Coleoptera *Stenelmis* sp.	n. r.	28	n. r.	85	n. r.	26
Ephemeroptera *Caenis* sp.	n. r.	696	125	1001	42	1257
Choroterpes sp.	80	194	n. r.	222	n. r.	n. r.
Hexagenia sp.	n. r.	n. r.	167	30	83	n. r.
Maccaffertium mexicanum integrum	170	304	n. r.	122	n. r.	163
Ephemeroptera total	**250**	**1194**	**292**	**1376**	**125**	**1419**
Megaloptera *Sialis* sp.	n. r.	55	42	214	42	152
Odonata *Argia* sp.	n. r.	55	42	214	42	152
Chromagrion sp.	n. r.	n. r.	n. r.	n. r.	n. r.	60
Epitheca princeps princeps	n. r.	n. r.	n. r.	n. r.	n. r.	56

Taxon	Rocks		Sand		Silt, shells	
	Sediments	Druses	Sediments	Druses	Sediments	Druses
Odonata total	**n. r.**	**47**	**n. r.**	**203**	**n. r.**	**283**
Trichoptera	n. r.	n. r.	n. r.		n. r.	n. r.
Anabolia sp.				34		
Cyrnellus sp.	n. r.	n. r.	n. r.	n. r.	n. r.	27
Goera sp.	n. r.	194	n. r.	n. r.	n. r.	n. r.
Mystacides sp.	n. r.	n. r.	n. r.	n. r.	n. r.	26
Orthotrichia sp.	n. r.	n. r.	n. r.	n. r.	n. r.	87
Nyctiophylax sp.	90	28	n. r.	31	n. r.	n. r.
Trichoptera total	**90**	**222**	**n. r.**	**65**	**n. r.**	**141**

Communities formed in druses were more similar to each other than to the sediments nearby (Fig. 10, Fig. 11). The clusters of communities formed in druses were significantly different (P = 0.001, SIMPROF test) from those found in bare sediments. The community of benthic invertebrates formed on rocks was most similar to the druse community; they joined at a 52% similarity (Fig. 10). Communities formed on sand, silt and shells, and rocks, were all significantly different (P = 0.001, SIMPROF test, Fig. 10). Therefore the presence of *Dreissena* druses significantly changed benthic communities (Global R = 0.69, P = 0.001, Two-way ANOVA of Similarities), and communities were also significantly different, depending on the substrate (Global R = 0.54, P = 0.001).

The effect of zebra mussels on macrobenthos was associated with a significant increase of diversity, density, and biomass of native macroinvertebrates in druses, when compared to bare sediments. In spite of the increase of the local diversity of native macroinvertebrates within druses, however, the total diversity of macroinvertebrates in the whole waterbody will not increase, and may even decrease due to the local extirpation of unionid species. Therefore, the local effect of *D. polymorpha* on native invertebrates is dependent on a spatial scale.

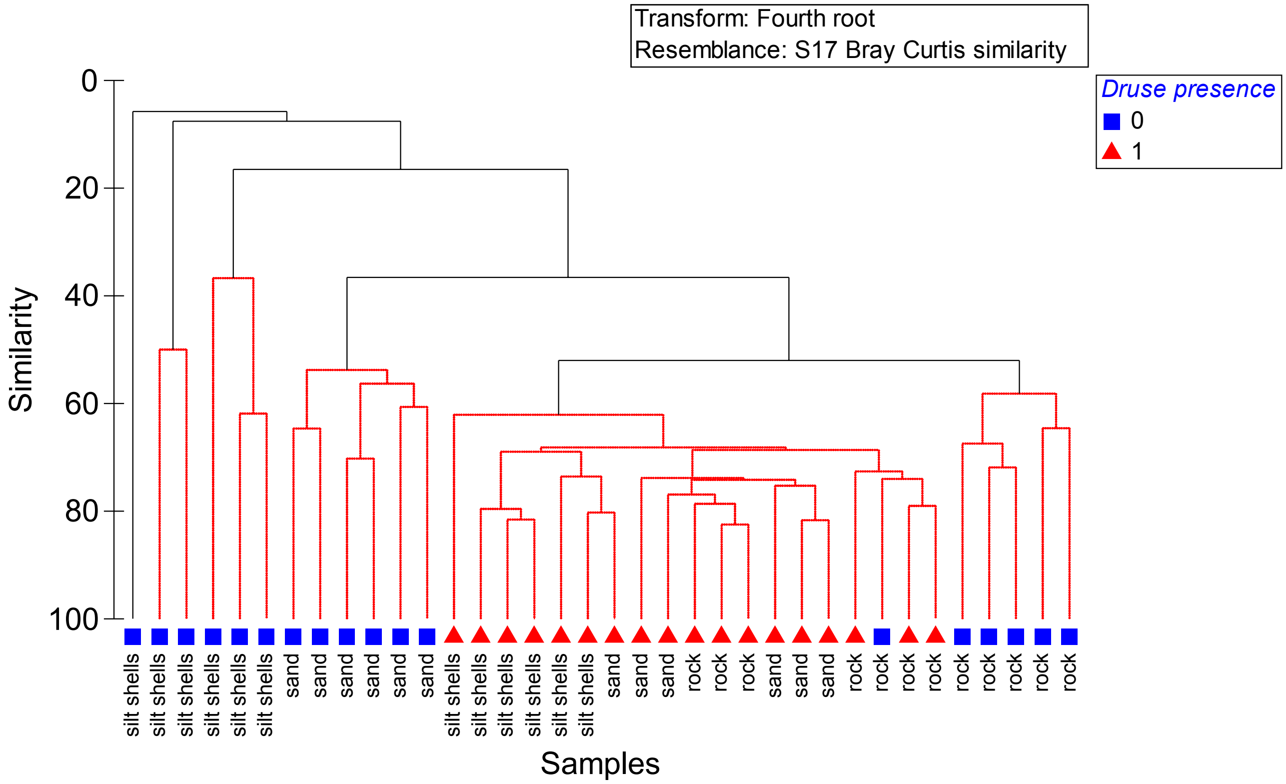


Fig. 10. Cluster analysis (group average) of benthic samples from Lower Nashatan Lake. The samples were collected in *Dreissena polymorpha* druses (samples marked with triangles), and in the sediments near druses (squares). Bray-Curtis similarity matrix used for this plot was built on fourth-root transformed density data for each taxa indentified in each sample. The groups joined by solid lines are significant at P < 0.05 (SIMPROF test), dashed lines – not significant.

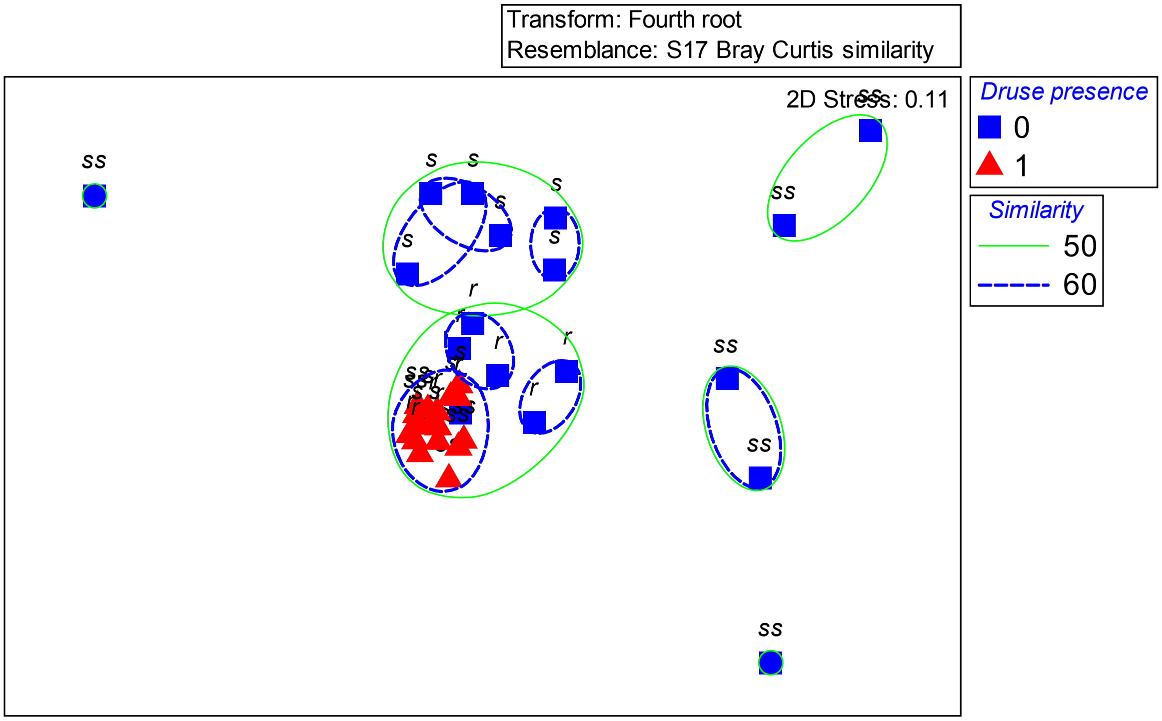


Fig. 11. Non-metric MDS plot of benthic samples from Lake Lower Nashatan. The samples were collected in *Dreissena polymorpha* druses (triangles), and in sediments near druses (squares). Bray-Curtis similarity matrix used for this plot was built on fourth-root transformed density data for each taxa indentified in each sample. Sediments from which druses and samples were collected labeled as following: *ss* – silt and shells, *r* – rocks, *s* – sand.

3. *Dreissena polymorpha* in Wisconsin lakes: density and distribution

In June of 2006 *Dreissena polymorpha* density was sampled in lakes Delavan and Upper Nemahbin. In total, 107 samples were collected from various substrata throughout the lake. The average density (21,141 ± 6,785 m^{-2}, n = 69) and biomass (1,077 ± 268 g m^{-2}) of *D. polymorpha* in Delavan Lake were extremely high and significantly different from the Upper Nemahbin Lake (average density 3,009 ± 971 m^{-2}; biomass 71 ± 19 g m^{-2}, n = 38; biomass: $P < 0.011$; density: marginally significant, $P < 0.064$). The large difference in the zebra mussel density we found among the two studied lakes strongly suggests that it is very difficult to accurately predict the potential density of *Dreissena*, and further studies are needed to develop an accurate prediction. We suggest that more Wisconsin lakes colonized with zebra mussels should be studied in order to reveal the factors that determine *Dreissena* densities in a lake, including lake morphometry, substrate distribution, and trophic type. Such study will allow the developing of a fine-tuned model which will be able to predict the potential *Dreissena* population density in any given lake based on its environmental conditions.

Distribution of *Dreissena polymorpha* by depth

Although there was a large significant difference in the population density of zebra mussels among lakes studied, the depth distribution pattern in these lakes was almost identical (Fig. 12, Fig. 13). In both lakes *D. polymorpha* density and biomass increased from 0.5 m, reached maximum at 3 – 5 m depth and then decreased to almost zero in profundal zone. The pattern of zebra mussel depth distribution found in Wisconsin lakes is very similar to *D. polymorpha* distribution across depths in European lakes (reviewed Karatayev et al., 1998; Fig. 14).

The minimum depth where zebra mussels are found in lakes is usually from 0.1-0.5 m, depending on local water level fluctuations and the probability of freezing (Stanczykowska, 1976; Lyakhnovich et al., 1994). The abundance of suitable substrate for attachment also affects depth distributions of zebra mussels. Many European studies have found that in lakes zebra mussels usually have a maximum density at depths from 3 to 5 m (reviewed in Karatayev et al., 1998; Burlakova et al., 2006). In the profundal zone of lakes, zebra mussels are usually limited by a lack of suitable substrate for attachment and low oxygen. For example, the depth distribution of *D. polymorpha* in lakes Myastro and Naroch in Belarus is very similar to Wisconsin lakes (Fig. 14, modified from Burlakova et al., 2006). This remarkable similarity of the zebra mussel depth distribution in various lakes has a strong predicting power which allow us to suggest that in Madison lakes, *D. polymorpha* density will increase from very shallow depths, reaching a maximum in the lower littoral – upper sublittoral zone, and then sharply decreasing in the profundal zone.

Distribution of *Dreissena polymorpha* by substrate

Most authors agree that the main factor that affects the distribution and abundance of *D. polymorpha* within a waterbody is the availability of suitable substrates for attachment (reviewed in Karatayev et al., 1998). In most lakes rocks, shells, and sometimes sand can be the most suitable substrate for zebra mussel attachment and the formation of stable colonies. Both European and North American studies have shown that zebra mussels can be extremely abundant on submerged macrophytes. However, because the longevity of macrophytes is usually shorter than the life span of zebra mussels, when macrophyte stems die back, *D. polymorpha* fall to the bottom and usually die, especially when the lake bottom under the macrophytes is covered by mud with little oxygenation (reviewed in Karatayev et al., 1998). Therefore, zebra mussels on macrophytes are usually much younger and smaller than on other substrates. As a result, although the highest densities of zebra mussels were commonly found on submerged macrophytes, the highest biomass was often recorder on rocks and other substrates, which are more stable than macrophytes. Again, both European and North American data agree that the poorest substrate for zebra mussel attachment is silt. Any *Dreissena polymorpha* that are occasionally found here usually use small, hard substrates like plant fragments, wood, shells, stones debris, etc. for initial attachment and then subsequently attach to each other, forming druses (Hunter and Bailey, 1992; Lyakhnovich et al., 1994).

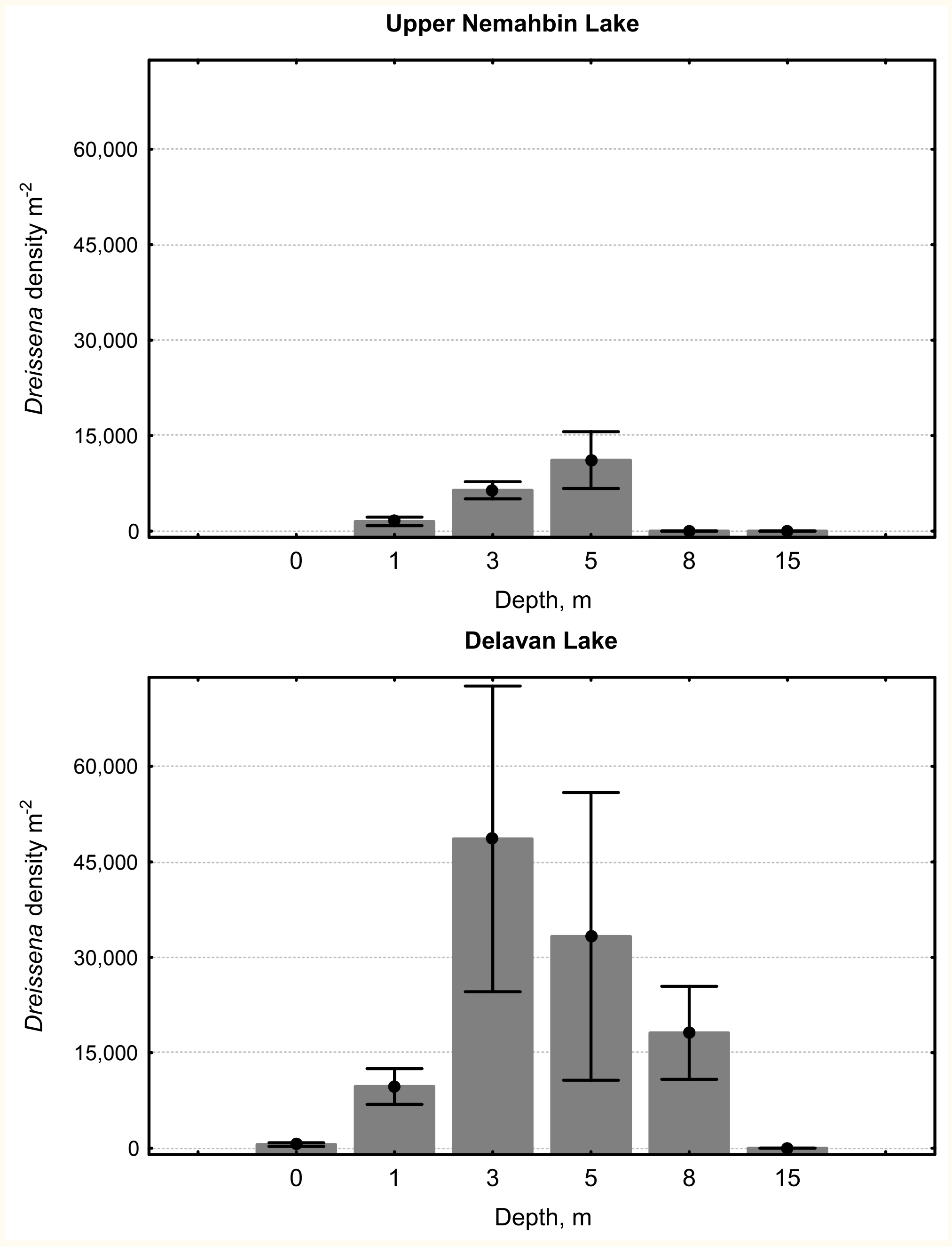


Fig. 12. Density of *Dreissena polymorpha* in Upper Nemahbin (upper graph) and Delavan (lower) lakes by depth. Means ± standard error.

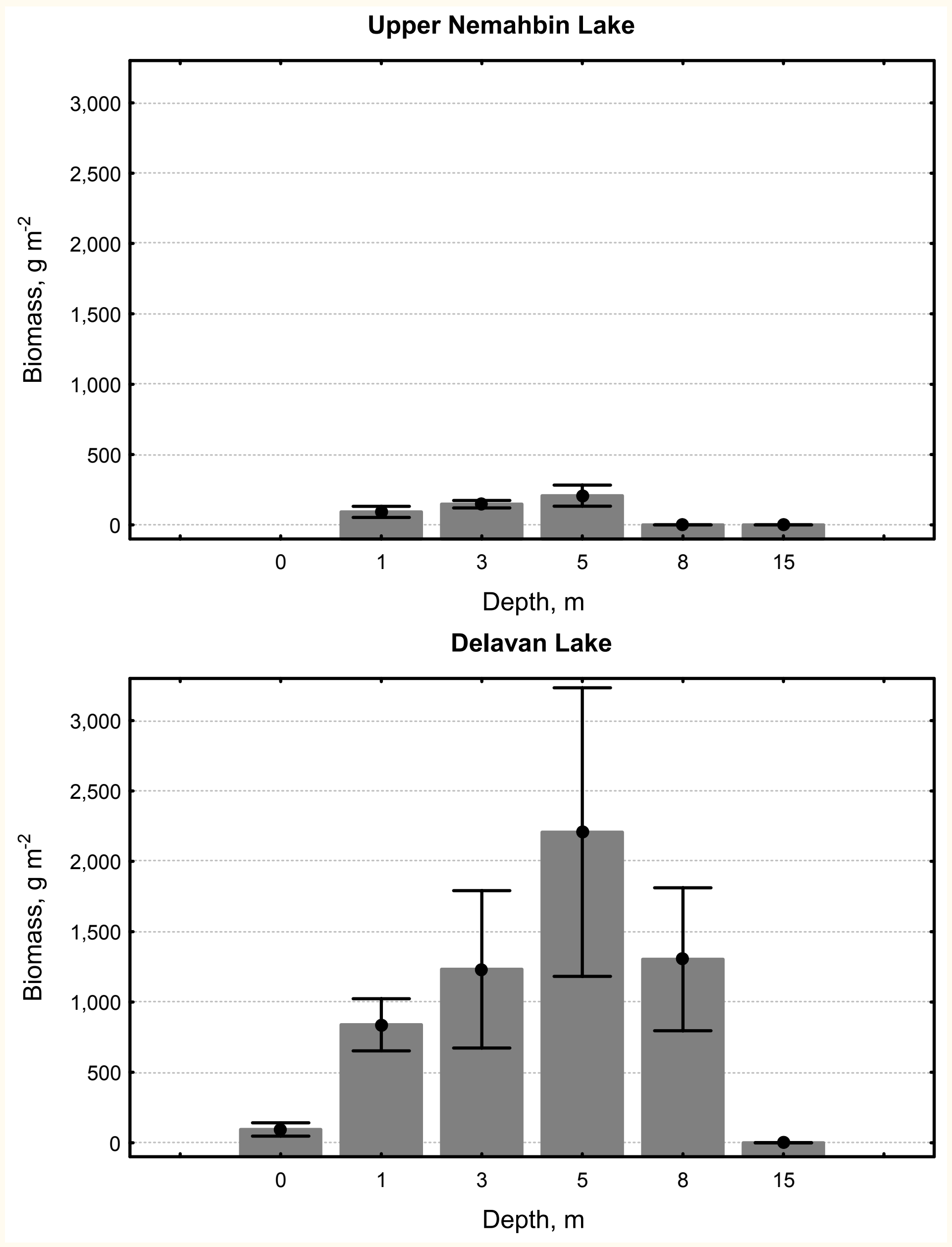


Fig. 13. Biomass of *Dreissena polymorpha* in Upper Nemahbin (upper graph) and Delavan (lower) lakes by depth. Means ± standard error.

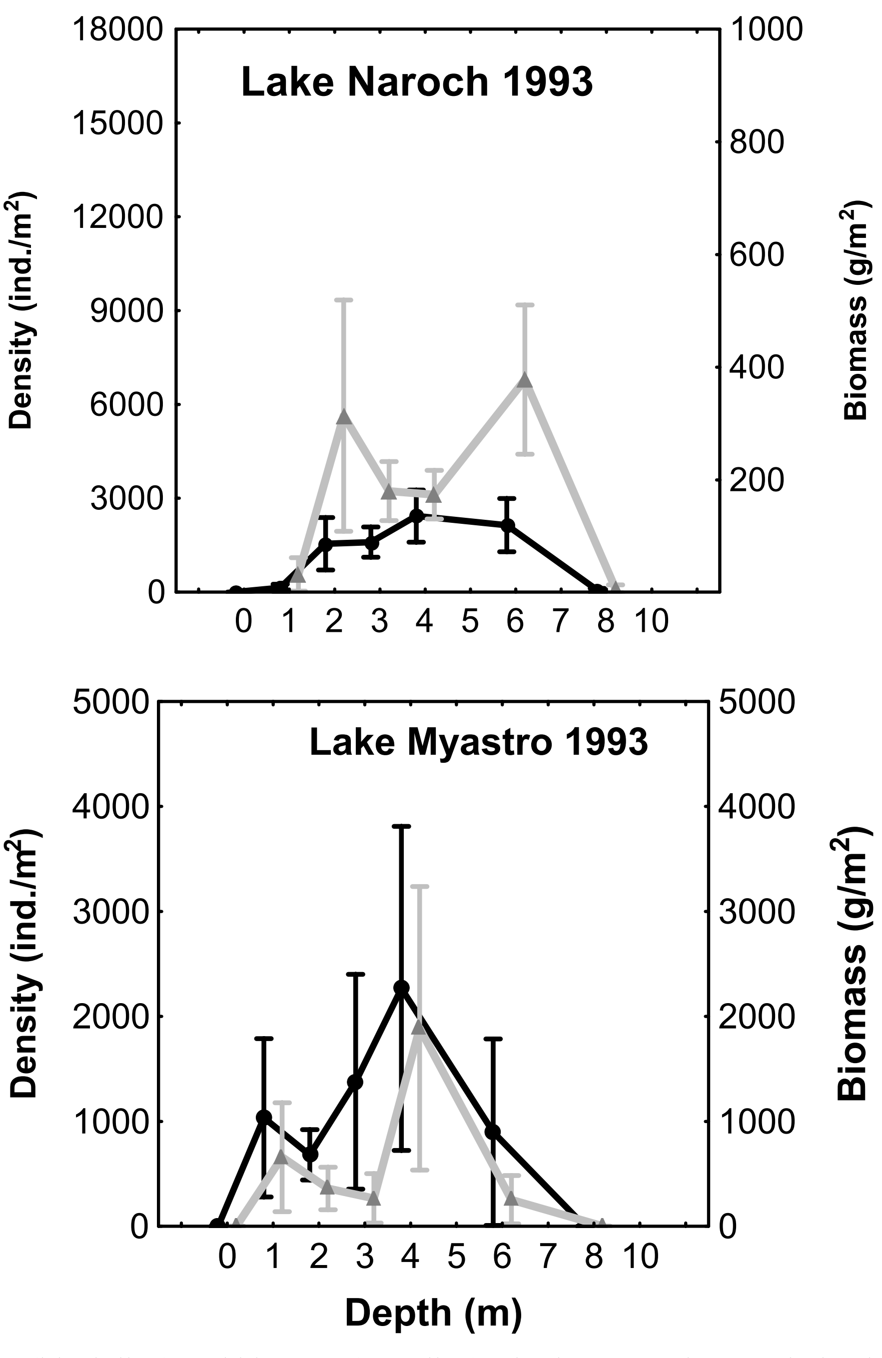


Fig. 14. Density (black line) and biomass (gray line) of zebra mussels at each depth sampled in lakes Naroch and Myastro, Belarus in 1993 (modified from Burlakova et al., 2007). Means ± standard error.

Similarly to other studies (reviewed in Karatayev et al., 1998), we found that the zebra mussel density and biomass varied substantially among substrates in Wisconsin lakes (Table 10). It was surprising to find, however, a significant difference in *D. polymorpha* density among lakes, even when the same substrates were compared. The average density of zebra mussels on macrophytes in Delavan Lake was seven times higher than in the Upper Nemahbin Lake, and biomass was 15 times higher. We suggest that the difference was due to the difference in the macrophyte species that were used as substrates for zebra mussel attachment. In Delavan Lake, macrophytes were represented almost exclusively by *Myriophilum*, while in Upper Nemahbin Lake macrophytes in the sampled areas were dominated by *Vallisneria* and *Chara*. Therefore, we can suggest that *D. polymorpha* may form different densities on different macrophytes. This difference should be taken into account while predicting the potential densities of *Dreissena* on macrophytes, and requires further investigations.

The highest zebra mussel densities in both lakes were found on macrophytes (320,000 m^{-2} in Delavan Lake and 27,556 m^{-2} in Upper Nemahbin Lake). The highest biomass in Delavan Lake was found on dead zebra mussel shells (12,444 g m^{-2}), while in Upper Nemahbin Lake the maximum biomass (449 g m^{-2}) was found on macrophytes.

Table 10. Zebra mussel density (N, m^{-2}, mean ± SE, median in parentheses), wet biomass (B, g m^{-2}), and percent of samples with mussels (P, %) across different substrates in Wisconsin and European lakes. n.r. – not recorded.

Lake		Rocks	Sand	Shells	Macrophytes	Mud with fragments	Mud
Delavan,	N	23,688±7,201	n.r.	22,133±12,035	81,914±32961	2,520±1,073	30+28
WI:		(11,200)	n.r.	(13,556)	(14,676)	(978)	(0)
	B	1,740±487	n.r.	4,338±2,384	2171±707	167±65	2±2
		(904)		(2,200)	(1,007)	(76)	(0)
	P	100		100	100	77	8
Upper	N	n.r.	n.r.	n.r.	6,716±1823	n.r.	9±9
Nemahbin,					(4,000)		(0)
WI:	B				158±30		0.2±0.2
					113		(0)
	P				100		1
Lukom-	N	n.r.	267±90	n.r.	3,706±989	n.r.	140±57
skoye,			(48)		(1,064)		(0)
Belarus	B		55±16		434±88		69±27
			(15)		188		(0)
	P		69				41
Naroch,	N	2,045±307	208±33	1,714±740	3,603±406		40±25
Belarus		(1,800)	(0)	(1,200)	(1,952)		(0)
	B	713±134	55±9	444±178	300±28		7±4
		(508)	(0)	338	(170)		(0)
	P	100	42	100	97		7

Lake		Rocks	Sand	Shells	Macrophytes	Mud with fragments	Mud
Myastro, Belarus	N	1,046±515 (304)	658±164 332	786±23 (928)	1,626±467 (720)		91±91 (0)
	B	616±359 (208)	249±93 (51)	448±315 (158)	334±155 (40)		56±56 (0)
	P	100	71	100	82		5

4. Potential effect of *Dreissena polymorpha* on benthic and pelagic communities and associated fisheries in Madison Lakes

Zebra mussels are very effective ecosystem engineers, altering both the ecosystem structure and function (Karatayev et al., 1997, 2002, 2005; Vanderploeg et al., 2002; Mayer et al., 2002; Mills et al., 2003 et al). Thus, their impacts are more likely to follow from the novel ecological niche they occupy in invaded ecosystems. As suspension feeders that attach to hard substrates, *D. polymorpha* are functionally different from most benthic freshwater invertebrates. By forming large populations, *D. polymorpha* act as powerful biofilters (reviewed in Karatayev et al., 1997, 2002, 2005; Vanderploeg et al., 2002; Mayer et al., 2002 et al). By filtering large volumes of water, *D. polymorpha* transfer energy and material from the water column to the benthos, providing a strong direct link between planktonic and benthic components of the ecosystem (benthic-pelagic coupling), and inducing major changes in the ecosystems invaded (reviewed in Morton, 1997; Karatayev et al., 1997, 2002, 2005; Johannsson et al., 2000; Vanderploeg et al., 2002; Mayer et al., 2002; Mills et al., 2003; Burlakova et al., 2005). The effects of invasion can be local, mostly affecting the benthos, especially in those areas where mussels settle, or system-wide, when the invasion influences large areas or entire water bodies through both direct and indirect effects of the mussels on physical, chemical and biological properties of the environment (Karatayev et al., 2002).

Based on our data from distribution of *D. polymorpha* in Wisconsin lakes, and our previous data from similar European lakes, we predict that in lakes Mendota and Monona *D. polymorpha* will create substantial densities in littoral and sublittoral zones, with the maximum at 3 – 5 m (Fig. 12, Fig. 13, Fig. 14, Table 10). It is very unlikely that *D. polymorpha* will spread deep into the profundal zones of both lakes, especially bellow the thermocline. Although, due to the large variability of *D. polymorpha* distribution even on similar substrates (Table 10), it is difficult to accurately predict population densities that zebra mussel may create in Madison lakes, we may suggest that the average *D. polymorpha* density and wet biomass in Lake Mendota may be app. 2,400 m^{-2} and 155 g m^{-2}, and in Lake Monona: 3,500 m^{-2} and 230 g m^{-2} respectively (Table 11).

Another, perhaps more accurate way to predict *D. polymorpha* densities in a lake is to use the median densities on different types of substrates and the area under each type of the substrate. We were able to find this type of data for Lake Mendota. Reed-Anderson et al. (2000) calculated that 1,100 ha of the lake bottom (27.6% of the total area) will be suitable for *D. polymorpha* attachment, of which 90% are represented by "firm" substrate (e.g. rock, sand, gravel, sandy mud), and the rest – by macrophytes. However, due to the extremely high densities of *D. polymorpha* in Delavan Lake, the distribution of densities by substrate type were highly skewed and were very different from averages (Table 10); we used median densities of *D. polymorpha*. The predicted range of *D. polymorpha* density for the whole lake was 192 – 1,770 m^{-2}, biomass: 45 – 237 g m^{-2} (average: 927 m^{-2}, and 128 g m^{-2} respectively, 90% confidence interval derived from 6,000 bootstrap resampling). These values were lower than those predicted based on the average densities for lake zones. However, the averages for biomass, predicted by both methods, were very similar (Table 11). Although most researchers use density (numbers of mussels per area) as the only population parameter, the impacts of *Dreissena* are more likely to be tied to biomass than numbers of mussels. Biomass and density are often decoupled because of differences in size frequency distributions among populations (Young et al., 1996). As a population parameter, biomass is a better indicator of ecological effects and population reproductive capacity, and it dampens transient fluctuations among year classes of mussel (Burlakova et al., 2006).

Table 11. Average densities (N, m^{-2}) and biomass (B, g m^{-2}) of *Dreissena polymorpha* in Wisconsin and European lakes and predicted *D. polymorpha* densities in Madison lakes. The predicted range based on the 90% confidence interval derived from 6,000 bootstrap resampling (mean in parentheses).

Lake		Lake zones			Average for the whole lake
		Littoral (< 3m)	Sublittoral (3 – 9 m)	Profundal (> 9 m)	
Delavan, WI	N B	28,821±12,485 953±290	25,337±11,838 1,770±576	0 0	15,452 772
Upper Nemahbin, WI:	N B	3,268±834 108±23	4,612±2,025 89±36	0 0	No data
Lukomskoye, Belarus	N B	1,042±395 296±96	804±288 265±100	2±2 0.1±0.1	750 124
Naroch, Belarus (average for 1997)	N B	880±167 165±31	2,723±658 330±108	0 0	922 99
Myastro, Belarus (1993, 1995)	N B	785±270 457±184	95±2 59±59	n.r. n.r.	645 288

Lake		Lake zones			Average for the whole lake
		Littoral (< 3m)	Sublittoral (3 – 9 m)	Profundal (> 9 m)	
		Predicted density and biomass for Madison lakes			
Mendota	N	926-17,626 (7,016)	1,282-15,240 (6,715)	0.0 – 1.0 (0.35)	381-5,692 (2,377)
	B	194-626 (396)	125-1,097 (502)	0 - 0.05 (0.02)	141-210 (155)
Monona	N				568-8,449 (3,531)
	B				212-316 (230)

The predicted densities will allow the *D. polymorpha* population to filter a volume equivalent to that of the lake in summer time in 53 - 78 days in Lake Mendota, and in 22 - 33 days in Lake Monona. This filtration rate is quite similar to filtration rates reported for other lakes colonized with *D. polymorpha* (Table 12). Therefore, we can use data obtained on other waterbodies colonized with *D. polymorpha* to predict their effect on Madison lakes (Table 13).

Table 12. Estimated time for *Dreissena polymorpha* to filter the volume of water equivalent to that of the waterbody in North American and European waterbodies and prediction for Madison lakes.

Waterbody	Surface area (km^2)	Time (days)	References
Pyalovskoe Reservoir, Russia	6.9	20	Mikheev, 1967
Uchinskoe Reservoir, Russia, 1967	19.3	45	Lvova, 1977
Lake Ijsselmeer, The Netherlands, 1985	n. r.	11	Reeders et al., 1989
Lake Ijsselmeer, The Netherlands, 1985	n. r.	18	Reeders et al.,,1989
Lake Lukomskoe, Belarus, 1978	36.7	56	Karatayev, 1983
1990	36.7	45	Karatayev and Burlakova, 1995a
Lake Naroch, Belarus, 1993	79.6	123	Karatayev and Burlakova,

			1995b
Lake Myastro, Belarus, 1993	13.1	17	Karatayev and Burlakova, 1995b
Lake Batorino, Belarus, 1993	6.3	54	Karatayev and Burlakova, 1995b
Long Point Bay, Lake Erie, USA	78	17	Petrie and Knapton, 1999
Predicted for Madison lakes			
Lake Mendota	40.0	53 - 78	This study, prediction based on the densities for lake zones
	40.0	47 - 248	This study, prediction based on the densities for substrate types
Lake Monona	13.3	22 - 33	This study

Table 13. Predicted effect of *Dreissena polymorpha* on Madison lakes

Parameter	Predicted change with *D. polymorpha*
Transparency, and light penetration	At least 1.5-fold increase
Seston	At least 1.5-fold decrease
Organic matter in the water	Decrease. Increase of organic matter mineralization
BOD	Decrease
Ammonia, nitrates and phosphates	Increase
Deposition of detritus on the bottom	Increase
Phytoplankton	Decrease density and primary production. Different species may have different respond
Macrophytes, benthic algae, periphyton	Increase density, overgrowth rate, and primary production
Zooplankton	Decrease density and production. Different species may have different respond
Zoobenthos including *D. polymorpha*	Increase at least 10-fold due to the presence of *D.*

Parameter	Predicted change with *D. polymorpha*
	polymorpha
Zoobenthos excluding *D. polymorpha*	Increase at least 2-fold. Littoral species will spread deeper into the lakes. Different species may have different respond
Fishes	Increase in the quantity of benthivorous fish. Different species may have different respond

Abiotic parameters. The effect of the filtering activity of *D. polymorpha* on the abiotic parameters in the Madison lakes will include an increase in the water transparency and light penetration, a decrease in the concentrations of seston and organic matter, a decrease in the biochemical oxygen demand of water (BOD), and an increase in the concentrations of ammonia, nitrates and phosphates (reviewed in Karatayev et al., 1997, 2005; Mayer et al., 2000; Idrisi et al., 2001; Vanderploeg et al., 2002). On the other hand, the deposition of large amounts of detritus on the bottom can increase siltation (reviewed in Karatayev et al., 1997; Zhukova, 2001), thus decreasing substrates available for further attachment of new *Dreissena* recruits (Lvova, 1977).

Phytoplankton. *Dreissena polymorpha* invasion will result in a decreased phytoplankton density and chlorophyll concentrations (reviewed in Karatayev et al., 1997, 2002, 2005; Idrisi et al., 2001; Vanderploeg et al., 2002). At the highest predicted densities (Table 11) a zebra mussel population could remove an amount of phytoplankton equivalent to the mean standing stock in Lake Mendota (Reed-Andersen et al., 2000). Potential bloom conditions exist in Lake Mendota at chlorophyll concentrations exceeding 50 μL^{-1}. According to the authors, moderate densities of zebra mussels (500-1000 m^{-2}) could remove enough phytoplankton to reduce the occurrence of chlorophyll concentrations exceeding 50 μL^{-1}, and at densities over 2,000 m^{-2} chlorophyll concentrations will be above that level less than 1% of the time (Reed-Andersen et al., 2000). This effect, however, will depend upon the epilimnetic circulation period: it will be maximal for a homogeneously mixed lake, but will be reduced at lower mixing, especially during extended calm periods (Reed-Andersen et al., 2000). That can lead to periods of both increased water clarity and severe midlake blooms.

The clearance rates of zebra mussels also depend on the composition of phytoplankton (Ten Winkler and Davids, 1982; Berg et al., 1996), and the overall grazing effect on planktonic communities may therefore be different in different lakes (Raikow et al., 2004). Impacts can also result from selective grazing and from changes in nutrient concentrations. Unpalatable algae (e.g. cyanobacteria) may increase in abundance due to enhanced rejection, and nutrient regeneration and input by *Dreissena* may selectively favor some phytoplankton groups (Arnott and Vanni, 1996; Vanderploeg et al., 2001; but see Dionisio Pires et al., 2005).

Macrophytes, benthic algae, and periphyton. Increased light penetration due to the filtering activity by *D. polymorpha* will allow macrophytes and periphyton to grow deeper and cover larger portions of the lake bottom (reviewed in Karatayev et al., 1997, 2002, 2005; Mayer et al., 2002; Vanderploeg et al., 2002). This creates a positive feedback because the macrophyte beds are an excellent substrate for attachment for zebra mussels.

Zooplankton. Zooplankton density and biomass usually decrease after *Dreissena* invasion (reviewed in Karatayev et al., 1997; Johannsson et al., 2000; Kryuchkova and Derengovskaya, 2000; Wong et al., 2003). This decline may be due to competition for food (phytoplankton and bioseston in general), direct filtering of small crustaceans and rotifers, or to more complex interactions, such as increased predation of zooplankton by fish larvae. In many lakes, the introduction of zebra mussels is associated with an increase in benthivorous fishes, whose larvae feed on zooplankton, including *Dreissena* larvae (reviewed in Molloy et al., 1997).

Zoobenthos. *Dreissena* will have dramatic impacts on zoobenthos of Madison lakes (see the section above). Just by their presence alone they will increase the total biomass of bottom community by at least 10-fold. Most of native benthic organisms will be positively affected by the shelter and food provided by *Dreissena* druses and will increase in their abundance. We may expect at least 2-fold increase in the density and biomass of native zoobenthos in the littoral and sublittoral zones of the Madison lakes after *Dreissena* invasion. In addition, bottom macroinvertebrates typically found on gravel and rocky substrates (e.g. amphipods, leaches, trichopterans, etc.) will spread deeper into the lakes and occupy areas that currently unsuitable for them. In contrast, burrowing species that live in the sediment, may be negatively affected by *Dreissena* druses. The strongest negative effect *Dreissena* colonization will have on Unionidae, which have already declined in their abundance in Madison lakes.

Zebra mussel invasion may cause dramatic changes in secondary production, although data on this aspect of *Dreissena* impact are very limited. Zoobenthic production after *Dreissena* invasion was studied in Lake Erie in 1993 (Johannsson et al., 2000). The authors found that benthic production was almost exclusively dominated by *Dreissena*, which accounted for > 90% of the annual production. Even though pelagic production dominated over non-dreissenid benthic production, the total benthic production including dreissenids was over 10 times higher than pelagic. In 1993, authors estimated that the benthic chain could potentially support more fish biomass than the pelagic food web in all basins, even if dreissenids were excluded from the calculations (Johannsson et al., 2000). Unfortunately, the lack of benthic production estimates for the lake prior to the colonization prevented the authors from direct comparisons of production before and after invasion.

The impact of zebra mussels on food webs and the energy flow through trophic levels have been studied in Lake Lukomskoe, Belarus (glacial lake with surface area 36.7 km^2) (Karatayev and Burlakova, 1995a). After the zebra mussel invasion, macrophyte production in this lake had increased from 51 to 166 kcal m^{-2}, and phytoplankton production decreased from

2545 to 625 kcal m^{-2}. Although the total secondary production declined twofold (from 95 to 44 kcal m^{-2}), the contribution of benthic invertebrates to whole-ecosystem secondary production dramatically increased from 3 to 77% of the total. Fish production more than doubled. The conversion of primary production to higher trophic levels increased for nonpredatory invertebrates from 3.7% (before zebra mussels invasion) to 5.5% (after invasion), and for fish from 0.15% (before invasion) to 1% (after invasion) of the total primary production. *Dreissena* became an important consumer of primary productivity, as well as an important conduit of energy flow to higher trophic levels (Karatayev et al., 2002).

Similar changes could be expected in Lake Mendota after the introduction of zebra mussels, including a decrease in the primary production (Reed-Anderson et al., 2000), an increase in the input of benthic community to the total secondary production and a general dominance of benthic foodwebs.

Fishes. We cannot assume, however, that this increase in the input of benthic community to the total secondary production will directly increase the conversion of primary production to higher trophic levers (fish).

The impacts of zebra mussels on the fish community may be direct or indirect, and to a large extent depend on the feeding mode of the fishes (Karatayev et al. 2002). *Dreissena polymorpha* may be associated with an increase in all benthic feeding fishes, even those that do not feed on zebra mussels, because a zebra mussel invasion is associated with an increase in the biomass of native benthic invertebrates (reviewed in Karatayev et al. 1997, 2002, Molloy et al. 1997). Thirty-eight species of fish have been reported to feed on adult *D. polymorpha,* including 27 species in Europe and 14 species in North America (reviewed in Molloy et al. 1997, Table 14).

Out of 57 fish species found in Lake Mendota, only 17 are considered major species, including 4 predator fish species (largemouth bass, smallmouth bass, walleye, and northern pike), 6 panfish species (yellow perch, bluegill, black crappie, white crappie, white bass and yellow bass), 6 bottom-feeding and/or rough fish species (common carp, freshwater drum, 3 bullhead species, and white sucker), and cisco (Lathrop et al. 1992). We may predict that a *Dreissena* colonization of the Madison lakes will have the strongest positive effect on bottom-feeding fishes, and especially freshwater drum. Although some panfish species are also known to consume zebra mussel (Table 14), *Dreissena* comprise a smaller proportion of their diet compared to bottom-feeding fishes, and therefore we suggest that panfish species will be less affected by zebra mussel colonization than bottom-feeding fishes. Increases in benthivorous fishes may pose a strong negative feedback on the mussel populations. In Europe, fish may consume > 80% of zebra mussel production (Lvova, 1977; Yablonskaya, 1985). However, there is no evidence of a long-term decline of mussel populations due to the effects of predation (reviewed in Molloy et al., 1997). Piscivorous fish may be positively affected by *Dreissena* because of an increase in the benthic feeding fish, but due to the change in fish dietary habits throughout their life, equivocal conclusions can be drawn only when the adults are taken into account (Karatayev et al., 2002, 2007).

Cisco, being largely planktivorous, could be negatively affected by the introduction of *Dreissena* because the mussels will decrease phytoplankton and zooplankton abundance, or due to the increase of predation on fish larvae as a result of increased water transparency (Lozano et al., 2001). Alternatively, several positive indirect effects have been suggested that could mitigate the negative effect of *Dreissena* on planktivorous fish. The larvae of *Dreissena* are readily consumed by many species of fish and can comprise over 70% of the zooplankton density during the summer (reviewed in Molloy et al., 1997). The increase in transparency and light penetration associated with an invasion may positively affect visually feeding fish (Mayer et al., 2001; Mills et al., 2003). Expansion of aquatic vegetation into deeper waters due to the increase in light penetration provides both refuge from piscivores and increased sites for production of invertebrate prey (MacIsaac 1996). However, to date there is no strong evidence supporting a negative impact of *Dreissena* on planktivorous fish (Trometer and Bush, 1999; Mayer et al., 2000).

Table 14. List of fishes, known to feed on *Dreissena polymorpha* in North America (modified from Molloy et al. 1997).

##	Common name
1	Shortnose sturgeon
2	Lake sturgeon
3	Freshwater drum
4	White sucker
5	Lake whitefish
6	Common carp
7	Brown bullhead
8	Redbreast sunfish
9	Pumpkinseed
10	White perch
11	White bass
12	Greater redhorse
13	Round goby
14	Yellow perch

CONCLUSIONS

1. During the five years of our study, we found 82 taxa (species, genera or higher taxa) of bottom macroinvertebrates in Lake Mendota, and 54 taxa in Lake Monona. Total density and biomass of benthic invertebrates in lakes Mendota and Monona were not significantly different among transects and between years, but were different among littoral, sublittoral and profundal zones. The highest diversity, density, biomass and production of benthos in both lakes were found in the littoral zone.

2. We found significant changes in the biodiversity and community structure in the zoobenthos of Lake Mendota over the last 100 years. These changes were simultaneously recorded in all three zones of the lake and most likely occurred between the 1950s and 1960s. The most dramatic change in diversity was found in the most diverse and heterogenic littoral zone. Fifty two percent of the total diversity (38 species and higher taxa) disappeared from the littoral benthic community since 1914-1915, while 43% of species and higher taxa previously not recorded were found during our study. The least diverse and most stable profundal zone lost about 40% of its diversity, including a key species *Chaoborus punctipennis*, along with a fingernail clam. A new exotic species oligochaeta *Branchiura sowerbi* was found in Lake Mendota in 2007.

3. *Dreissena polymorpha* density was sampled in lakes Delavan and Upper Nemahbin. In total, 107 samples were collected from various substrates throughout the lake. The average density (21,141 ± 6,785 m^{-2}) and biomass (1,077 ± 268 g m^{-2}) of *D. polymorpha* in Delavan Lake were extremely high and significantly different than in Upper Nemahbin Lake (average density 3,009 ± 971 m^{-2}; biomass 71 ± 19 g m^{-2}). The large difference in the zebra mussel density we found among the two studied lakes strongly suggests that it is very difficult to accurately predict the potential density of *Dreissena*, and further studies are needed to develop an accurate prediction. We propose that more Wisconsin lakes colonized with zebra mussels should be studied in order to reveal the factors that determine *Dreissena* densities in a lake, including lake morphometry, substrate distribution, and trophic type. Such a study will allow the developing of a model that will be able to predict the potential *Dreissena* population density in any given lake based on its environmental conditions.

4. We predict that in lakes Mendota and Monona, *D. polymorpha* will create substantial densities in the littoral and sublittoral zones, with the maximum at 3 – 5 m, but may not spread deep into the profundal zone of both lakes, especially below the thermocline. The average density of *D. polymorpha* is predicted to be between 192 and 1,770 m^{-2}, and an average wet biomass between 45 and 237 g m^{-2} for Lake Mendota, and density between 568 and 8,449 m^{-2} and biomass between 212 and 316 g m^{-2} for Lake Monona. These densities will allow the *D. polymorpha* population to filter the volume equivalent to that

of the waterbody in the summertime in 47 - 248 days in Lake Mendota, and in 22 - 33 days in Lake Monona. This filtration rate is similar to rates reported for other lakes colonized with *D. polymorpha*.

5. Based on our study of Wisconsin lakes colonized with *Dreissena* and European data, we predict that impacts of the zebra mussel on benthic communities of Madison lakes may include significant increases in the local species' diversity, density, and biomass of macroinvertebrates in *Dreissena* aggregations. Just by their presence alone, they will increase the total biomass of the bottom community at least 10-fold. We may expect at least a 2-fold increase in the density and biomass of native zoobenthos in the littoral and sulittoral zones of the Madison lakes after the *Dreissena* invasion. In addition, bottom macroinvertebrates typically found on gravel and rocky substrates (e.g. amphipods, isopods, trichopterans, leaches), will spread deeper into the lakes and occupy areas that are currently unsuitable for them. In contrast, burrowing species that live in soft sediments may be negatively affected by *Dreissena* druses.

6. The *Dreissena* colonization will have the strongest negative effect on native bivalves family Unionidae, which have already declined in their abundance in the Madison lakes. We found five species of unionids in Lake Mendota, but a special study is needed to estimate their current (pre-invasion) densities.

7. *Dreissena polymorpha* potential effect on the Madison lakes may include an increase in water transparency and light penetration, decreased concentrations of seston and organic matter, density of phytoplankton and zooplankton. Increased light penetration will allow macrophytes and periphyton to grow deeper and cover larger portions of the lake bottom. The impacts of zebra mussels on the fish community will depend on their feeding mode, and may include an increase in the bottom-feeding fishes, especially freshwater drum. Planktivorous cisco could be negatively affected by the introduction of *Dreissena.*

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