

Change in a lake benthic community over a century: evidence for alternative community states

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Abstract Aquatic communities are one of the most studied systems where alternative states or regime shifts have been detected. We used data spanning a century of time to test whether the zoobenthic community of Lake Mendota, Wisconsin, USA, was relatively stable through time, variable, or whether there was any evidence of alternative community states. We used multivariate statistical analyses to test for community structure similarity and whether

detected differences corresponded to major changes in the local environment. Surprisingly, the benthic community in Lake Mendota was not statistically different from the mid 1960s to the present. Similarly, the benthic community was not significantly different from 1914 to the 1950s. However, between the 1950s and mid 1960s there was a dramatic change in the zoobenthic community, including the loss of key taxa and a decrease in the diversity of several major taxa. This dramatic change cannot be attributed to any single environmental factor, and is correlated with multiple factors acting simultaneously, including increased urban development, human population density, intensive agriculture, and the introduction of a

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major invasive species, Eurasian watermilfoil. The long-term similarity in the benthic community before and after the shift suggests two alternative states that switched with the confluence of multiple stressors.

Keywords Zoobenthos · Long-term change · Community analysis · Multiple community states · Lake Mendota

Introduction

Understanding patterns of variability or change in ecological communities is critically important because different communities provide different ecosystem services (Chapin et al., 1997, 2000; Carpenter et al., 2006a, 2009), as well as for conservation and assessing the resilience of natural communities (Holling, 1986; Scheffer et al., 2001; Palumbi et al., 2008). Changes in community composition and species abundance may dramatically affect the structure and functioning of ecosystems, including trophic interactions, nutrient dynamics, or responses and susceptibility to disturbance (Chapin et al., 1997, 2000; Covich et al., 1999). All communities experience some sort of natural disturbance, and component species have evolved traits and life histories that respond to and allow recovery from regular disturbances. Extreme infrequent disturbance events, however, can result in changes that alter the fundamental character of communities, especially when communities face multiple stressors or disturbance agents simultaneously (Paine et al., 1998), or when there is a lack of diversity (redundancy or complementarity) in critical functional groups (Palumbi et al., 2008).

The ability to adequately assess changes in natural communities is often hindered because studies are conducted over relatively short time periods and over small spatial scales (Magnuson, 1990). This may make it difficult to assess changes due to natural variation in community structure, changes due to particular perturbations, and changes that occur over long periods of time (decades to centuries) or abruptly, for example, when systems exhibit multiple community states (Connell & Sousa, 1983; Holling, 1986; Gunderson, 2000; Scheffer et al., 2001). Long-term and historical data can be analyzed, though appropriate historical/long-term and complementary data that can address

short-term variation are rarely available. Both are needed to differentiate between long-term change and natural spatiotemporal variation in community structure, especially for lake benthic communities.

Limnologic research has traditionally focused on processes occurring in the open-water, pelagic zone of lakes (Vadeboncoeur et al., 2002), while benthic studies are mostly conducted in lotic environments (Covich et al., 1999; Hämäläinen et al., 2003). However, lake benthic habitats can be a major contributor to whole-lake productivity (Vadeboncoeur et al., 2002, 2008) and biodiversity (Hutchinson, 1993). Benthic organisms provide important ecosystem services including mixing the sediment, nutrient cycling, and channeling energy to higher trophic levels (Covich et al., 1999; Vander Zanden & Vadeboncoeur, 2002). Zoobenthic species are sensitive to ecological and environmental change, and are used as indicators of environmental quality (Hilsenhoff, 1987). Benthic communities change seasonally, as well as among years (Hämäläinen et al., 2003; Brown et al., 2006), which makes it difficult to differentiate short-term, local-scale variation from long-term shifts in community structure (Hämäläinen et al., 2003).

We used historical data on benthic community composition from Lake Mendota covering the last century (including data summarized by Lathrop, 1992a, b; Lathrop et al., 1992), in combination with 5 years of contemporary sampling to examine short- and long-term changes in the littoral, sublittoral, and profundal zoobenthic communities. We used multivariate community analysis to test whether community composition was stable or variable, both spatially and through time. We also tested whether there was evidence of multiple community states, and the extent to which potential environmental drivers corresponded with zoobenthic community shifts.

Methods

Lake Mendota is a dimictic, eutrophic lake located in Madison, Wisconsin (43°5'54.00"N, 89°24'19.00"W), with a surface area of 39.85 km², maximum depth of 25.3 m, and an average depth of 12.7 m. Lake Mendota has been the focus of limnological studies since the late 1800 s (Brock, 1985; Carpenter et al., 2006b), and has been part of the North Temperate Lakes Long-Term Ecological Research (NTL-LTER)

program since 1995 (Carpenter et al., 2007), providing useful historic data on the lake community as well as impacts on the lake from activities in the watershed. As an urban lake, Lake Mendota has been subject to a variety of anthropogenic impacts, including eutrophication, pesticide runoff, habitat modification, and the introduction of non-native species such as Eurasian watermilfoil, *Myriophyllum spicatum* L.

From May to October the water column is stratified. A lack of mixing and high productivity results in complete oxygen depletion below the thermocline in early July (Birge & Juday, 1911; Lathrop et al., 1992). Based on thermal stratification, the profundal zone is considered >9 m depth, which represents ~65% of the lake area. The littoral zone, where aquatic macrophytes grow, extends to 3 m depth and the sublittoral zone is between >3 and 9 m depth (Lathrop et al., 1992). During the summer, much of the littoral zone is covered with macrophytes, including *M. spicatum*, *Elodea canadensis* Michx., *Ceratophyllum demersum* L., *Potamogeton crispus* L., and *P. pectinatus* L. (Nichols & Lathrop 1994).

To determine the species composition and distribution of the zoobenthic community and year-to-year variability, 306 total bottom samples were collected from May 30 to June 20 along three fixed transects (Table 1; Fig. 1) in 2002, 2003, 2004, 2006, and 2007. For each transect, samples were collected at 1 and 3 m (littoral zone), 5 and 8 m (sublittoral zone), and 15 and 20 m depth (profundal zone). Three or more samples were taken at each depth, and the data were pooled. In addition, five samples were collected in 2003–2007 in the deepest portion of the lake (deep hole). All samples were collected with an Ekman grab, with the exception of littoral and sublittoral samples in 2002, which were collected by SCUBA divers using a suction device. However, because this sampling technique did not produce data comparable to the Ekman grab, 2002 data were excluded from analyses of recent change in the benthic community, and only data from 2003 to 2007 were used. To compare recent benthic community composition with historic data, which were collected with a variety of methods, we used all data, including those collected in 2002. Five additional samples were collected in 2002, 2003, 2004, and 2006 from the rocky littoral zone to assess whether some species that were historically recorded were present, but missed by our sampling.

At each sampling location, the substrate and macrophyte coverage were determined. Samples were washed through a 500 µm mesh. All macroinvertebrates collected were fixed with 10% neutral buffered formalin, and identified to the lowest possible taxonomic level (usually species, genus or family), counted, blotted dry on absorbent paper, and weighed to the nearest 0.0001 g (total wet mass). Two species of oligochaetes, *Stylaria lacustris* (Linnaeus) and *Branchiura sowerbyi* Beddard, were identified to species. All others were categorized as oligochaetes.

To test for long-term patterns in benthic community composition, we compared all available historic information with the results of recent sampling. The zoobenthos of Lake Mendota has been sporadically sampled since 1914 (Table 1). Most available data are for the profundal zone. To minimize the effects of changes in taxonomic designations (Metzeling et al., 2002), we used a similar, common level of taxonomic resolution to analyze all historic and recent data, and synonymized historic and current names (Supplementary File 1). For some taxa, to avoid possible species confusions, we used the lowest common taxon for analysis (Supplementary File 1). We also calculated the EPT index, which is the sum of the number of Ephemeroptera, Plecoptera, and Trichoptera divided by the total abundance of all benthic organisms in the sample (Mandaville, 2002). A decrease in the EPT index is indicative of environmental stress (Plafkin et al., 1989).

We used a two-way repeated measures Analysis of Variances (rm-ANOVA) on log-transformed data to test whether the total combined density and biomass of all species in the zoobenthos differed among transects, zones, and years from 2003 to 2007 (STATISTICA ver. 6, Statsoft Inc. 2001). A post hoc Tukey test was used to assess differences among factors.

We tested for differences in community structure through time with non-parametric multivariate statistical techniques on data matrices of all species and their abundances found in the community (PRIMER 6, Version 6.1.6, Primer E-Ltd. 2006). A recent critique of these methods has found that these statistical methods can have low power if the mean to variance ratio is not constant for species within the communities studied (Warton et al., 2012), reducing the ability to detect small differences.

Table 1 Sources of benthic macroinvertebrate community data for Lake Mendota used in this study as well sampling periods and their references

Sampling period	Data available	References
<i>Littoral zone</i>		
1914–1915	Average of 150 quantitative samples (hauls) collected from ≤ 3 m depth in the spring, summer and fall of 1914 and 1915	Muttkowski (1918)
2002, 2003, 2004, 2006, 2007	106 total samples collected with an Ekman dredge from 1 and 3 m depth	This study
<i>Sublittoral zone</i>		
1951	Average of 14 samples collected with an Ekman dredge in January and February from 6 to 9 m depth	Mackenthum & Cooley (1952)
2002–2004; 2006, 2007	90 total samples collected with an Ekman dredge from 5 and 8 m depth	This study
<i>Profundal zone</i>		
1917	Average of 276 samples collected with an Ekman dredge over 1 year from >20 m depth	Juday (1921)
1939	Samples collected in summer from >20 m depth	David Frey, Indiana University (in Lathrop et al., 1992)
1951	Average of 45 samples collected with an Ekman dredge in January and February from >9 m depth	Mackenthum & Cooley (1952)
1964–1965	Average of 84 total samples collected monthly with an Ekman dredge from September 1964 to August 1965 from 12 to 24 m depth	Sapkarev, Univ. Skopje, Yugoslavia (in Lathrop et al., 1992)
2002–2004, 2006, 2007	110 total samples collected with an Ekman dredge from 15, 20, and 24 m depth	This study

A square root or fourth root transformation was used to normalize the data for analysis. The similarity of the community composition was summarized by calculating Bray–Curtis distances (BC; [Bray & Curtis, 1957](#); [Clarke, 1993](#)). BC distances are a measure of similarity, and have values ranging from 0 (identical samples) to 1. To visualize the differences among assemblages we used non-metric multi-dimensional scaling (NMDS), which calculates a set of metric coordinates for samples, most closely approximating their non-metric distances. NMDS was found to be consistently reliable in a comparative study of ordination methods for community data ([Kenkel & Orloci, 1986](#)). Complete descriptions of these tests can be found in [Clarke & Green \(1988\)](#) and [Clarke \(1993\)](#).

We tested for differences in community composition among different transects, lake zones and years with analysis of similarities (ANOSIM), a resampling technique that uses permutation/randomization methods on BC similarity matrices to identify differences among groups of samples, after which pairwise comparisons are conducted ([Clarke, 1993](#)). Large

values of the test statistic (R) indicate complete separation of groups, and small values (close to 0), little or no separation. Thus, R is a useful comparative measure of the degree of separation, and its value is at least as important as its statistical significance, which is limited by the number of available permutations ([Clarke & Warwick, 2001](#)).

Univariate diversity indices are used to reduce the data on the community's multivariate complexity into a single index. Diversity indices emphasize the species richness (total number of species present or some adjusted form) or equitability (how evenly the individuals are distributed among the different species) components of diversity to varying degrees. To demonstrate between-sample relationships obtained from the full range of diversity information extracted (evenness + richness) ([Clarke & Gorley, 2006](#)), we used PRIMER to create a similarity matrix of diversity indices (total number of taxa in each sample, Margalef's species richness, Pielou's evenness, Shannon–Wiener diversity index (Log e base), and Simpson's diversity index). ANOSIM was used with this matrix

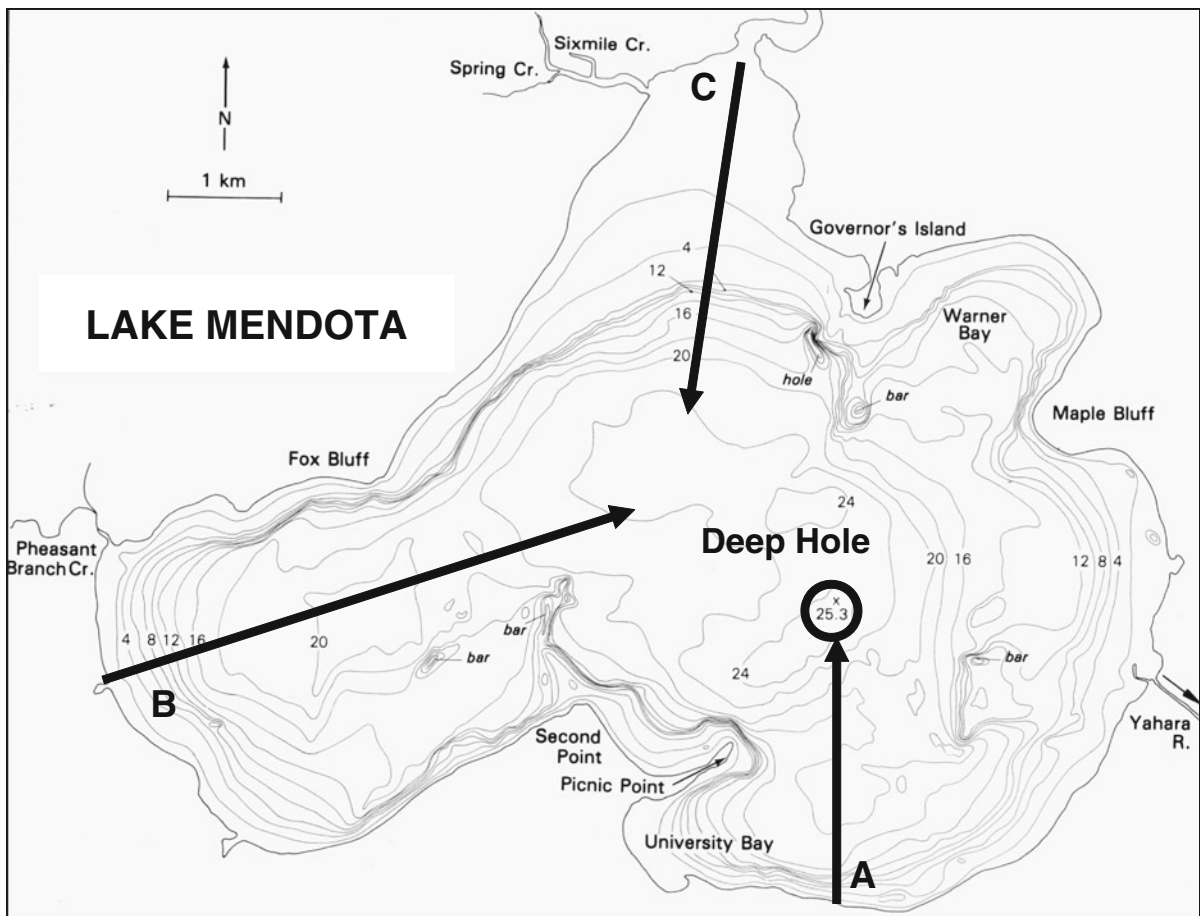


Fig. 1 Permanent transects in Lake Mendota that were sampled in 2002–2007. Coordinates of transects: *Transect A* 1 m depth: 43.07778N, 089.40543W; 20 m depth: 43.08650N, 089.40582W. *Transect B* 1 m depth: 43.10493N, 089.47915W; 20 m depth:

43.05932N, 089.27548W. *Transect C* 1 m depth: 43.13650N, 089.41724W; 20 m depth: 43.11745N, 089.41623W. *Deep hole* 24 m depth: 43.10867N, 089.40542W. Modified from Lathrop (1992b)

to test for differences in community composition among years and lake zones.

To test whether community dominance changed among years we used ANOSIM with k -dominance curves for density and biomass data. k -dominance curves are determined by ranking species in decreasing order of importance along the x axis, with their relative contribution to the total plotted on the y axis. The pairwise differences among k -dominance curves among samples were used to construct the similarity matrix for analysis. To describe the variability in the multivariate structure of benthic communities we used the multivariate dispersion (Warwick & Clarke, 1993). “Similarity profile” permutation tests (SIMPROF routine) were used to test for structure in the data (Clarke & Gorley, 2006).

To test for correlations between the biotic resemblance matrix (BC distances of square-root transformed profundal benthos density data from 1917 to 2007) and a matrix of environmental variables for the same years (Euclidian distances of log-transformed and normalized variables), the BIOENV (Bio-Environmental Analysis) algorithm in a BEST routine was used. The environmental variables that we focused on included factors known to affect benthic communities and factors that could influence the whole-lake ecosystem in general through changes in nutrient inputs or changes in light penetration. These included maximal depth of macrophyte distribution (m) (affected by light penetration), the presence of Eurasian watermilfoil (an important invasive species), population size of the city of Madison, area of

Madison (km²), and area planted in corn for Dane County (km²; data from U.S. Department of Agriculture (USDA) National Agricultural Statistics Service, <http://www.nass.usda.gov/QuickStats>). This algorithm selects environmental variables that best explain the community pattern, by maximizing a Spearman rank correlation between their respective resemblance matrices (Clarke & Ainsworth, 1993). To distinguish among years that were different in environmental variables, we used Cluster analysis followed by SUMPROF to find significant difference among clusters. All tests effects were considered significant if $P < 0.05$.

Results

Modern community structure

From 2002 to 2007 we found a total of 83 taxa (species, genera, or higher taxa) of benthic macroinvertebrates in Lake Mendota, including 19 taxa of chironomids, 12 taxa of trichoptera larvae, and 9 taxa of molluscs. The most abundant invertebrates in the lake as a whole, excluding unidentified oligochaetes, were the chironomids *Cladotanytarsus* sp. ($380 \pm 195 \text{ m}^{-2}$, mean \pm SE here and elsewhere), *Procladius* sp. ($352 \pm 42 \text{ m}^{-2}$), and *Polypedilum halterale* (Coquillett) ($295 \pm 120 \text{ m}^{-2}$), and the amphipod *Hyaella azteca* Saussure ($258 \pm 73 \text{ m}^{-2}$). The benthic community in the littoral zone had the highest diversity and wet biomass of benthic macroinvertebrates among all the lake zones (Table 2). The distribution of benthic macroinvertebrates was most heterogeneous in the littoral zone, and this variability among samples was most likely due to differences in substrate type, especially between sand and macrophytes. In contrast, the benthic community in the profundal zone was the most uniform, and had the lowest diversity (Table 2).

The total density of benthic invertebrates in Lake Mendota from 2003 to 2007 was not significantly different among transects ($P = 0.545$) or years ($P = 0.253$), but as expected, was different among lake zones ($P = 0.0004$, rm-ANOVA; Supplementary File 2). Similarly, the biomass of benthic invertebrates did not significantly differ among transects ($P = 0.094$) or years ($P = 0.705$), but did differ among lake zones ($P = 0.002$, rm-ANOVA; Supplementary File 2). The density of benthic invertebrates was three times higher

in the littoral zone than the sublittoral ($P = 0.001$) or the profundal zones ($P = 0.001$), and did not differ between the sublittoral and profundal zones ($P = 0.87$, Tukey test). The biomass of macroinvertebrates in the littoral zone was higher than in the sublittoral zone ($P = 0.02$), but not significantly different than in the profundal zone ($P = 0.588$), and the biomass in sublittoral and profundal zones did not differ ($P = 0.099$; Tukey test).

Taxon richness was not significantly different among transects ($P = 0.176$) or years ($P = 0.205$), but was different among lake zones ($P = 0.0004$, rm-ANOVA; Supplementary File 2). Richness was higher in the littoral zone than the sublittoral zone ($P = 0.004$) and the profundal zone ($P = 0.001$), but the sublittoral and profundal zones were not different ($P = 0.086$, Tukey test).

Community composition, based on the presence and density of macroinvertebrate taxa, did not differ significantly among the three transects in 2003–2007 ($R = 0.024$, $P = 0.114$; one-way ANOSIM; Fig. 2). There was a significant difference among the three lake zones ($R = 0.686$, $P = 0.001$; Fig. 2), but not among years ($R = 0.008$, $P = 0.39$; two-way ANOSIM; Fig. 2). Similar patterns were found for community composition based on the biomass rather than abundance of macroinvertebrates. There was no difference among transects ($R = 0.03$, $P = 0.088$; one-way ANOSIM). There was a significant difference among lake zones ($R = 0.67$, $P = 0.001$), but not among years ($R = -0.012$, $P = 0.615$; two-way ANOSIM). For both the benthic community composition based on density ($R = 0.88$, $P = 0.001$) and on biomass ($R = 0.85$, $P = 0.001$), the difference between the profundal zone and the littoral zone was the greatest.

We found no significant difference among similarity matrices built with diversity indices among years ($R = -0.04$, $P = 0.872$). There were, however, significant differences in diversity indices among lake zones ($R = 0.44$, $P = 0.001$; two-way ANOSIM; Fig. 2).

For community structure based on species present and their density, there was no difference in the k -dominance curves among years ($R = -0.044$, $P = 0.917$), but there was a difference among lake zones ($R = 0.367$, $P = 0.001$, two-way ANOSIM; Fig. 3). We found similar results for community structure based on biomass. There was no difference

Table 2 Taxon richness, density, wet biomass, multivariate dispersion (MD), and coefficient of variation of density (CV) of the zoobenthos of the Lake Mendota from 2002 to 2007 for each lake zone

Lake zone	2002	2003	2004	2006	2007
Littoral (<i>n</i>)	6	6	6	6	6
Taxon 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 (g m ⁻²)	14.5 ± 9.3	7.2 ± 3.3	7.0 ± 2.5	10.8 ± 4.3	11.5 ± 1.9
MD	1.536	1.184	1.592	1.549	1.239
CV (%)	127	55	60	101	59
Sublittoral (<i>n</i>)	7	6	6	6	6
Taxon 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 (g m ⁻²)	1.2 ± 1.0	4.8 ± 1.4	2.7 ± 0.3	4.7 ± 0.6	2.8 ± 0.5
MD	1.476	1.334	1.364	1.050	1.259
CV (%)	111	93	71	74	59
Profundal (<i>n</i>)	5	7	7	7	7
Taxon richness	3.4 ± 0.4	4.1 ± 0.3	3.4 ± 0.4	3.6 ± 0.3	5.0 ± 0.6
Density (m ⁻²)	3994 ± 955	2146 ± 420	2451 ± 513	1200 ± 222	2228 ± 480
Biomass (g m ⁻²)	9.0 ± 1.0	6.0 ± 1.1	7.8 ± 0.9	5.3 ± 0.9	6.7 ± 1.6
MD	0.410	0.464	0.392	0.486	0.521
CV (%)	53	52	55	49	57

For richness, density and biomass, cell values are the mean ± SE. Sample sizes (*n*) indicate the averages of three grabs from each sampling site

in the *k*-dominance curves among years ($R = 0.044$, $P = 0.421$), but there were differences among lake zones ($R = 0.408$, $P = 0.001$, two-way ANOSIM).

Littoral zone community structure through time: 1914–1915 versus 2002–2007

Using a common level of taxonomic resolution, we compared the benthic community composition (species presence and density) within the littoral zone from 1914 to 1915 (Muttkowski, 1918) with that found in 2002–2007 (Supplementary File 1). We found a major shift in community composition between 1914–1915 and 2002–2007 in the littoral zone ($R = 1.0$, $P = 0.003$, one-way ANOSIM; Fig. 3). The total number of taxa in quantitative samples in 1914–1915 (76) was similar to that found in 2002–2007 (65), as were the traditional diversity indices (Shannon–Wiener diversity index: 2.46 vs. 2.32; Simpson's diversity index: 0.83 vs. 0.82; Pielou's evenness: 0.57 vs. 0.56). However, only 38 of 103 total taxa were found in both surveys. Fifty percent of the taxa present in the early part of the 20th century (1914–1915) were not found in

our recent surveys, including the important predator *Chaoborus punctipennis* (Say), the amphipod *Gammarus fasciatus* (Say), large bodied molluscs like the clam *Sphaerium striatinum* (Lamarck), and the gastropods (e.g., *Planorbella campanulata* (Say) and *Lymnaea stagnalis* (Linnaeus)), which have not been replaced by functionally or taxonomically similar taxa. Forty-two percent of the taxa found in 2002–2007 are new to this community. Other taxa have decreased dramatically in abundance, including the snail *Ammicola limosus* (Say) and unionid bivalves (Supplementary File 1). In contrast, Muttkowski (1918) did not find the now common isopod *Asellus* sp. and other taxa that are now quite abundant. In his writings, Muttkowski expressed surprise at the lack of *Asellus* in the lake benthic community, as this species is typical of lake zoobenthos, and it was, at the time, common in the lake tributaries. The densities of other taxa, including chironomids, oligochaetes, the gastropod *Valvata tricarinata* (Say), and the planarian *Dugesia tigrina* Girard, have also dramatically increased since 1914–1915. In addition, in 2007 we found a single individual of the exotic oligochaete,

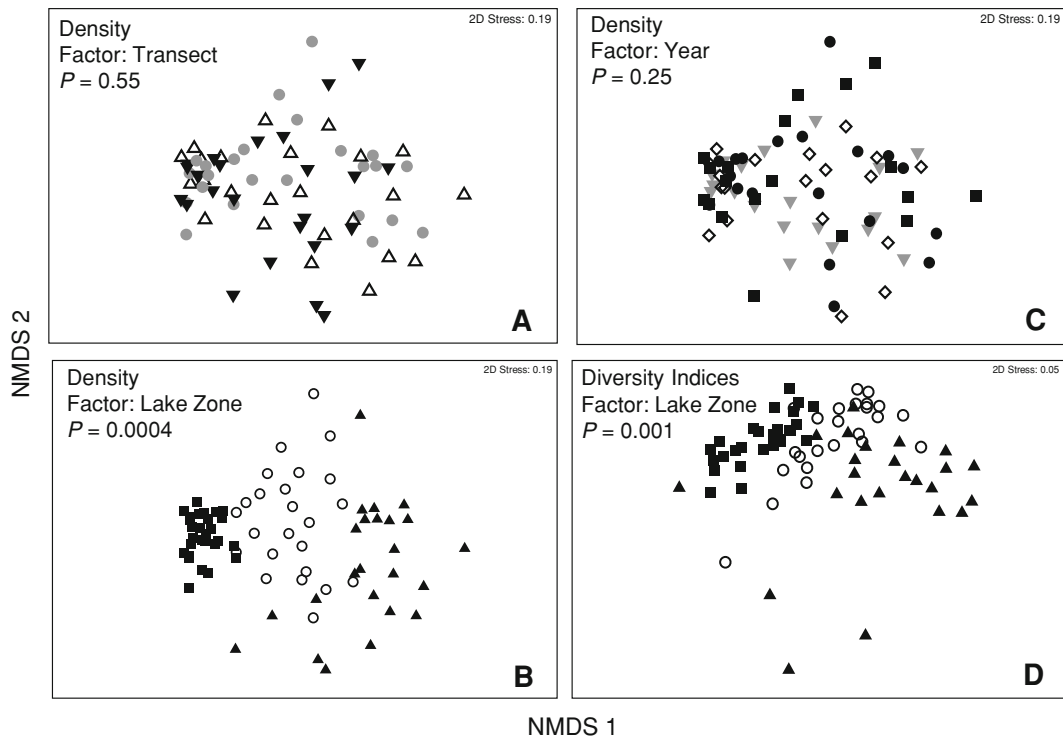


Fig. 2 NMDS ordination plots of the benthic community structure of Lake Mendota based on Bray–Curtis similarities for 2003, 2004, 2006, and 2007. Stress = 0.19. **A** There was no difference in community structure among the three transects: **A**—triangles, **B**—filled circles, **C**—filled triangles. **B** There were significant differences in community structure among the three zones: littoral filled triangles, sublittoral circles, profundal filled squares. **C** There was no difference in community structure among years: 2003 gray triangles, 2004 filled squares, 2006

rhombuses, 2007 filled circles. **D** NMDS ordination of similarity diversity indices of the benthic community (taxon densities) based on normalized Euclidian distances of diversity indices in 2003–2007. There was no significant difference among years, but there were among zones. Lake zones: littoral filled triangles, sublittoral circles, profundal filled squares. Diversity indices: total number of species in each sample, Margalef’s species richness, Pielou’s evenness, Shannon–Wiener diversity index (log), and Simpson’s index. Stress = 0.05

B. sowerbyi, which may have recently invaded, as it is often dominant where it invades (Mills et al., 1993). Excluding unidentified oligochaetes, of the five most abundant taxa in 1914–1915, only the amphipod *H. azteca* was still dominant in the littoral benthic community in 2002–2007. Other current dominants were either not found (Chironomidae, *Cladotanytarsus* sp.) or were rare in 1914–1915 (e.g., Chironomidae *Polypedilum* sp., Turbellaria *D. tigrina*, Ephemeroptera *Caenis* sp.) (Supplementary File 1). The density *k*-dominance curves were significantly different between these two time periods ($R = 0.751$, $P = 0.007$, one-way ANOSIM with density *k*-dominance curves, excluding unidentified oligochaetes). The most dramatic changes were for the Ephemeroptera, Trichoptera, and Chironomidae. Since 1914–1915, seven taxa of caddisflies, and four species of mayflies disappeared. In addition, we found 13 species of

chironomids and 5 species of caddisflies that were not reported in 1914–1915. As a result, the EPT index decreased from 1.30 in 1914–1915 to 0.53 in 2002–2007, which is usually indicative of stress.

Sublittoral zone community structure: 1951 versus 2002–2007

Although some historic studies report information about the benthic macroinvertebrates within this zone before 1951, only Mackenthum and Cooley (1952) reported data comparable to ours, limiting our power to detect shifts in this community. The sublittoral benthic community in Lake Mendota appears to have undergone a dramatic change from 1951 to 2002–2007 (high *R*-statistic), however, this difference was only marginally significant due to the low number of possible permutations and low statistical power

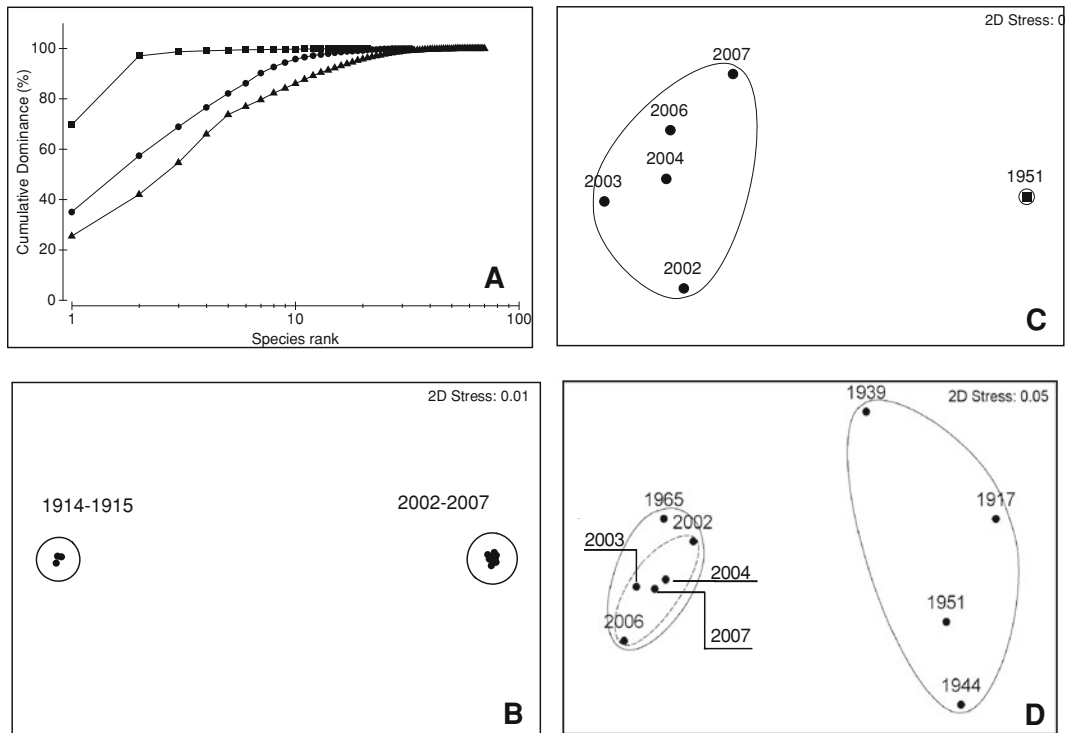


Fig. 3 Changes in the benthic community through time. **A** Cumulative dominance plot of taxon densities for each lake zone with data pooled from all years (2002, 2003, 2004, 2006, and 2007). *Triangles* littoral zone, *circles* sublittoral zone, *squares* profundal zone. **B** NMDS plot of difference in the benthic macroinvertebrate community (based on densities) for the littoral zone for 1914–1915, 2002–2004, 2006, and 2007. For each year, two depths (1 and 3 m) within this zone are plotted. Groups are distinct at a 33% similarity. Stress = 0.01. **C** NMDS

plot of difference in the benthic macroinvertebrate community (based on densities) for the sublittoral zone for 1951, 2002–2004, 2006, and 2007. Groups are distinct at a 57% similarity. Stress = 0.0. **D** NMDS plot of difference in the benthic macroinvertebrate community (based on densities) for the profundal zone for 1917, 1939, 1944, 1951, 1965, 2002–2004, 2006, and 2007. Groups are distinct at a 60% (*solid line*) and 80% (*dashed line*) similarity. Stress = 0.05. **B–D** axis X NMDS 1, axis Y NMDS 2

($R = 1.0$, $P = 0.167$, one-way ANOSIM) (Fig. 3). During the winter of 1951, the zoobenthos was dominated by *Chironomus* sp. and large fingernail clams, identified as *Pisidium idahoense* Roper (Mackenthum & Cooley, 1952), which are likely to be *S. striatinum*, identified by Juday (1921) in his 1916–1918 study. The predatory *C. punctipennis* was also common in 1951. As for the littoral zone, we found a dramatically different community at present. The large bodied molluscs have been replaced by smaller bodied taxa, such as *Pisidium variable* Prime, and *C. punctipennis* have also been lost from this community (Supplementary File 3). The dramatic reduction and subsequent disappearance of *C. punctipennis* and large bodied fingernail clams, and the appearance of small bodied pea clams (*P. variable*) in the 2000s were primarily responsible for the

differences in community composition pre- and post-1951 (Supplementary File 3). For this zone the EPT index decreased from 0.22 in 1951 to 0.01 in 2002–2007.

Profundal zone community structure: 1917–1951 versus 1965–2007

The benthic community in the profundal zone changed in concert with the other two zones sometime between 1951 and 1965 (Fig. 3). This benthic community was significantly different between 1917–1951 and 1965–2007 ($R = 0.964$, $P = 0.005$, one-way ANOSIM; Fig. 3). Community structure in this zone did not change from 1917 to 1951 (Similarity 61–77%, $P > 0.64$, SIMPROF), and then dramatically shifted sometime between 1951 and 1965, forming two

significantly distinct clusters (1917–1951 vs. 1965–2007) with 48% similarity ($P = 0.003$, SIMPROF). From 1965 to 2007 the community in this zone was not significantly different among years (Similarity 79–97%, $P > 0.50$; Fig. 3). From 1917 to 1951 the profundal zone was dominated by five taxa: *C. punctipennis*, oligochaetes, two chironomids, *Chironomus* sp. and *Procladius* sp., and fingernail clams, *S. striatinum* (Supplementary File 4). By the 1960s fingernail clams and *C. punctipennis* had both dramatically decreased in abundance and later completely disappeared from the community. The five most common taxa found in this zone from 1917 to 1951 (*C. punctipennis*, *Chironomus* sp., *Procladius* sp., *S. striatinum*, and oligochaetes), are the typical dominants in the profundal zones of glacial lakes world-wide (reviewed in Brinkhurst, 1974). In 1942–1943 the density of *C. punctipennis*, a key predator that displays nocturnal vertical migrations and can control zooplankton, reached $10,500 \text{ m}^{-2}$ (Hasler, 1945). In 1951 the density of fingernail clams, important suspension feeders, was 460 m^{-2} (Mackenthum & Cooley, 1952). By 1965, the density of both of these species had dropped by several orders of magnitude, and by the 1990s these species completely disappeared from Lake Mendota (Supplementary File 4). Fingernail clams were not found in summer or winter surveys in 1987–1989, although *C. punctipennis* was found in low densities during the winter (Lathrop, 1992a, b). Neither species was found in our 2002–2007 sampling.

Potential drivers of benthic community change

We found concordance between changes in community structure and several potential environmental factors that could cause such differences (1965–2007 vs. 1917–1951, $P = 0.001$, SIMPROF; Figs. 3D, 4C). The environmental variables that best explained the difference in zoobenthic community structure of the profundal zone over this period were the presence of Eurasian watermilfoil, population size of the city of Madison, the urbanized area of Madison, and the area planted in corn in Dane County (Spearman $\rho = 0.768$; $P = 0.018$). The best single variable that grouped the years in a manner consistent with the faunal pattern was the presence of Eurasian watermilfoil, but this factor alone was only marginally significant (Spearman $\rho = 0.804$; $P = 0.067$).

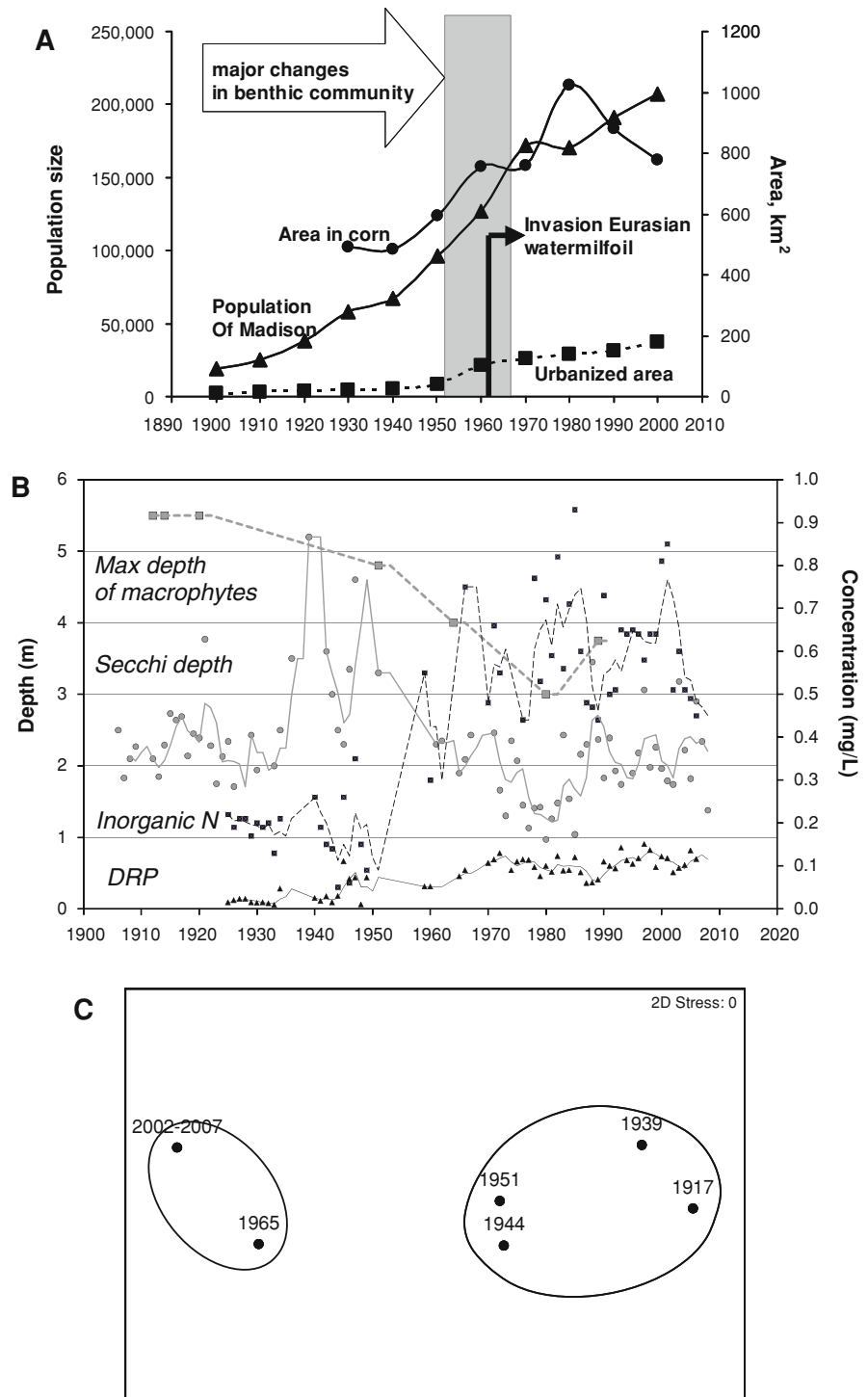
Discussion

Our results demonstrate a dramatic shift in zoobenthic community structure in Lake Mendota in the middle of the twentieth century. Despite the expected variability and patchiness, the benthic community in Lake Mendota remained stable from the mid 1960s to the present. Similarly, the benthic community was relatively stable from 1914 to 1950s. Between the 1950s and 1965 there was a dramatic change in the benthic community. Similar differences were detected in all three zones, particularly the profundal zone, which has been especially well-sampled. The differences in community structure included changes in dominant species, the extirpation of key species in the profundal zone, a 40–50% change in taxa present, a decrease in the diversity of trichopterans, ephemeropterans, and molluscs, and a decrease in the EPT index, an indicator of environmental stress (Plafkin et al., 1989), in littoral and sublittoral zones. This shift was preceded and followed by long periods of stability in community composition, much longer than the generation time of individuals within this community. In stark contrast to the large changes we found in the benthos over the past century, the zooplankton community is relatively unchanged since the 1850s (Brock, 1985; Lathrop & Carpenter, 1992).

Potential drivers of benthic community change

The shift between zoobenthic community states that occurred in the 1950s and 1960s is correlated with multiple potential environmental stressors, and is thus hard to attribute to any single factor. From 1950 to 1970, the Lake Mendota watershed saw a threefold increase in urbanized area, a 50% increase in the population of Madison, and a 71% increase in the county population (Fig. 4A). Simultaneously there was a ~50% increase in land used for intensive corn agriculture and a dramatic increase in the application of fertilizers, pesticides and herbicides. Many of these changes contributed to the eutrophication of Lake Mendota (Lathrop, 2007). This period also marked the introduction of Eurasian watermilfoil, which colonized the lake in the early 1960s, and attained maximal densities by the end of the 1960s (Nichols & Lathrop, 1994; Buchan & Padilla, 1999). We found that all of these factors were highly correlated with the shift in community structure in Lake Mendota. Because these

Fig. 4 **A** Factors affecting Lake Mendota from 1900 to the present. **B** Changes in physical and chemical parameters of Lake Mendota through time: maximum depth of macrophytes (m) (gray rectangles, dashed thick gray line, left Y axis); mean Secchi depth (m) during summer stratification (gray circles, thick gray line, left Y axis); median surface water dissolved reactive phosphorus (DRP) concentration during fall turnover (mg l^{-1} , black triangles, solid black line, right Y axis); median inorganic [N] in surface water during fall turnover (black rectangles, dashed black line, right Y axis). Trendlines: 3 year moving averages. **C** NMDS plot of changes in factors affecting Lake Mendota from 1917 to 2007 (maximal depth of macrophyte distribution, presence of Eurasian watermilfoil, population of the city of Madison, area of Madison (km^2), and area planted for corn in Dane County (km^2). Data from Lathrop et al. (1992, 1996), Lathrop (2007), LTER data (https://secure.limnology.wisc.edu/lterquery/abstract_new.jsp?id=PHYS), and USDA National Agricultural Statistics Service, <http://www.nass.usda.gov/QuickStats>). Groups are distinct at 4.02 Euclidean distances, and are significant ($P = 0.001$, SIMPROF test)



factors are also highly intercorrelated, and each is associated with changes in the lake environment, including changes in nutrient availability,

sedimentation, and light availability (Fig. 4B), no single factor could be identified as the primary driver of this change. Biological invaders in freshwater

systems have often had profound impacts on freshwater ecosystems worldwide (Karatayev et al., 1997; Eiswerth et al., 2000). However, Eurasian watermilfoil directly impacts only the littoral zone of the lake. Corresponding changes to the rest of the lake, the sublittoral and profundal zones, may suggest that although these three lake zones have different benthic communities, and physical environmental factors impact them, they are interconnected. Indeed, it may be the confluence or interaction of multiple factors acting during this period that drove the rapid and dramatic changes in the benthic macroinvertebrate community throughout this lake. Interestingly, hypolimnetic dissolved oxygen depletion rates have not changed over the past century (Brock, 1985).

Through time there have been many species introductions and manipulations of the fish assemblage in Lake Mendota. Before anthropogenic introductions, 37 fish species were believed to have occurred in the lake (Magnuson & Lathrop, 1992). Fish introductions started in the late 1800s, and by 1989, 18 non-native species had been introduced to the lake. Most fishes were introduced in the 1920s and 1940s, prior to the shift in the benthic community. Of the three fish species introduced in the late 1950's, only the shorthead redhorse persists, and no new species were introduced in the 1960s. There have also been many changes in the relative abundances of fishes in the lake, but again, known changes in fish populations (Magnuson & Lathrop, 1992) do not correspond with the dramatic shift in the zoobenthic community that we observed.

Lathrop and colleagues reported declines in some species of benthic macroinvertebrates in the profundal zone of Lake Mendota (Lathrop, 1992a, b, 2007; Lathrop et al., 1992), and suggested several possible reasons for these changes including a decline in food availability, an increase in predation by fish, use of toxic insecticides in the drainage basin, and an increase in sulfide and ammonium concentrations in the overlying hypolimnetic waters. Both phosphorus and nitrogen concentrations in the lake have increased through time with increased anthropogenic activity (Fig. 4B), and these increases roughly correspond with the shift in the benthic community. However, it is not clear which of these factors or combinations of factors may be responsible for the changes in Lake Mendota benthos, especially because each of these factors are likely to affect different species, and many

species have different, and sometimes opposite, environmental requirements. For example, the loss of both *Chaoborus* and fingernail clams is curious. Clams are quite sensitive to eutrophication and low oxygen (Holopainen & Jónasson, 1983), but phantom midges are very tolerant of low oxygen, and can be abundant in hypereutrophic lakes (Brinkhurst, 1974; Holopainen & Jónasson, 1983).

The changes in the benthic macroinvertebrate community in Lake Mendota over the past century are striking. The wholesale shift in community structure that occurred supports the notion of multiple community states for zoobenthos in this system. Gradual changes in environmental conditions, such as human-induced eutrophication, may not have had immediate effects on the community, but may have reduced system resilience, increasing the probability of a shift to a new state when impacted by a stochastic event or set of events (Paine et al., 1998, Scheffer et al., 2001, 2009). The confluence or interaction of multiple stressors may have been such a stochastic trigger for this system. Changes in dominant species with different life forms, as seen in Lake Mendota, are a common feature of systems with alternative stable states and regime shifts (Scheffer et al., 2001). We were fortunate to have historic community data for Lake Mendota to contrast with our recent studies, however, our understanding of the shifts in community composition are still limited due to the paucity of samples through time. The contrast between the relative stability of the planktonic community and the large changes in the benthic community over the past century may indicate that the benthic community is particularly sensitive to environmental change, and may provide a bellwether for future change. Frequent, regular sampling is needed to detect increases in variance and changes in recovery from small disturbances, which are apparent indicators of tipping points between system states or regimes (Scheffer et al., 2009). As such, including benthic sampling in routine lake monitoring is critical, especially if, as it appears in Lake Mendota, the planktonic community is less sensitive to environmental changes. At present we do not know the consequences of these changes in the benthic community for the lake as a whole. Interactions between the benthic and pelagic habitats, especially for the profundal zone, are likely to have changed considerably. The benthos also provides an important link in food webs (Vander

Zanden & Vadeboncoeur, 2002), thus the changes we detected could have had cascading impacts throughout the system.

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