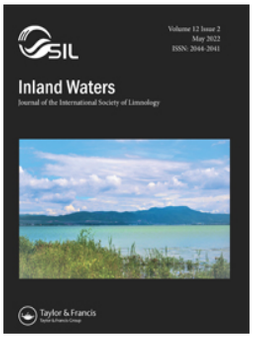

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Early changes in the benthic community of a eutrophic lake following zebra mussel (*Dreissena polymorpha*) invasion

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ABSTRACT

In the context-dependent world of biological invasions, biologists understand few general patterns of spread and impact. One possible exception is the zebra mussel (*Dreissena polymorpha*), an invader that routinely restructures food webs through an ecosystem engineering process termed "benthification." By efficiently consuming phytoplankton, zebra mussels can increase light penetration and nutrient concentrations in the benthos of a lake, thereby stimulating growth of benthic periphyton (phytobenthos) and macroinvertebrates (zoobenthos). Few studies monitor the response of these benthic communities to invasion. We documented early changes in phytobenthos and zoobenthos as zebra mussels invaded eutrophic Lake Mendota (Wisconsin, USA). From 2015 to 2018, the number of zebra mussel individuals reached densities >30 000 m^{-2} on hard substrates and 3000 m^{-2} in macrophyte beds. Community data showed classic signs of benthification, including 300% increases in (non-zebra mussel) zoobenthos and phytobenthos abundance on average across a depth gradient, including significant increases at depths where zebra mussels did colonize. Deep macrophyte biomass increased 900%, but water clarity showed no significant rapid increase. We speculate that nutrient enrichment may be more strongly responsible than increased light penetration for the benthic response of Lake Mendota. Continued integration of benthic production and processes into our study of lake ecosystems will be critical to understanding whole ecosystem function, especially as zebra mussels continue to "benthify" lakes within their invaded range.

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Introduction

Biological invasions are often described as highly context-dependent and frustratingly idiosyncratic events (Williamson 1999, Simberloff 2004, Ricciardi et al. 2013, Buckley 2017). As such, invasion biologists have struggled to develop general rules for predicting which species will invade where, when, and with what impacts (Kolar and Lodge 2001, Moyle and Marchetti 2006, Keller and Drake 2009, Buckley and Catford 2016). However, for a select few invasive species, biologists have compiled enough individual case studies, long-term datasets, and cross-system meta-analyses to begin to understand a species in its invaded range.

The zebra mussel (*Dreissena polymorpha*) is one such species (Nalepa and Schlosser 1993, Karatayev et al. 1997, Mayer et al. 2013). One of the most notorious invasive species in Europe and North America (Karatayev et al. 2002, 2007, Nalepa and Schloesser 2013), the zebra mussel arrived in the Laurentian Great Lakes in the late 1980s via transatlantic shipping vessels (Carlton 2008). The zebra mussel has spread steadily to countless inland lakes and rivers across North America (Karatayev et al. 2011, 2015, Benson 2013), allowing repeated study of its population biology and ecosystem impacts. A centuries-long invasion history throughout Western Europe (Karatayev et al. 2011, 2015) and the conspicuous advance of the North American invasion front have allowed biologists to begin to understand, at least in general terms, the biology, spread, and impacts of this species outside its native range (Karatayev et al. 1997, Ward and Ricciardi 2007, Higgins and Vander Zanden 2010).

Biologists have termed the process of ecosystem engineering by which zebra mussels impact their newly invaded ecosystems "benthification" (Karatayev et al. 2002, Mills et al. 2003, Mayer et al. 2013), a shift in

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the flow of energy away from pelagic–profundal pathways toward benthic–littoral pathways within a food web (Mayer et al. 2013). Zebra mussels drive this shift by filter-feeding phytoplankton, thereby shunting conventionally pelagic resources into mussel biomass and benthic deposition of nutrient-rich pseudofeces (Hecky et al. 2004). By consuming phytoplankton, mussels can increase light penetration to the benthos (Karatayev et al. 1997, 2002, Higgins and Vander Zanden 2010), stimulating production of light-limited benthic algae and macrophytes (Hecky et al. 2004, Zhu et al. 2006). This illumination and nutrient-enrichment of the benthos is complemented by the creation of complex new microhabitats within the dense druses of zebra mussel shells, which promote benthic invertebrates, particularly scrapers and detritivores (Burlakova et al. 2005, 2012, Ward and Ricciardi 2007), and filamentous algae (Hecky et al. 2004). Other documented effects of zebra mussel invasion include increased foraging success (Mayer et al. 2001) and abundance (Strayer et al. 2004) of littoral-feeding fishes as well as the promotion of toxic cyanobacterial taxa such as *Microcystis*, particularly in low-phosphorus systems (Raikow et al. 2004, Knoll et al. 2008, Sarnelle et al. 2012).

In October 2015, researchers at the University of Wisconsin–Madison detected zebra mussels (individuals m^{-2}) in Lake Mendota, a eutrophic inland lake in southcentral Wisconsin, USA, at densities of $\sim$1 m^{-2}. UW-Madison has conducted routine physical, chemical, and biological monitoring on Lake Mendota since 1994 as part of the North Temperate Lakes Long Term Ecological Research (NTL-LTER) program, albeit with a strong bias toward pelagic monitoring and relatively few surveys of the benthic communities. Researchers have sampled the benthic macroinvertebrate community of Lake Mendota, referred to hereafter as the zoobenthos, in only 12 of the previous 100 years prior to our study, and often only in the profundal zone (Karatayev et al. 2013). The epibenthic periphyton community of Lake Mendota, referred to hereafter as the phytobenthos, has received almost no attention. This pelagic bias is not uncommon in limnology, despite the benthos contributing a large proportion of whole-lake production in many shallow and medium-depth lakes (Vadeboncoeur et al. 2002, Vander Zanden and Vadeboncoeur 2020). The phytobenthos is especially understudied in lentic systems and along depth gradients (Cantonati and Lowe 2014).

Here, we present detailed accounts of the zoobenthos and phytobenthos communities along a depth gradient of Lake Mendota and track community responses to an incipient, invasive zebra mussel population. Despite decades of North American zebra mussel literature and a general understanding of benthification and its drivers, relatively few studies track the response of the phytobenthos to invasion (except see Lowe and Pillsbury 1995, Pillsbury et al. 2002, Cecala et al. 2008, Stević et al. 2013), particularly beyond the littoral zone (except see Makarevich et al. 2008). Even fewer study the responses of zoobenthos and phytobenthos communities together over time in one ecosystem (Higgins and Vander Zanden 2010). We address this knowledge gap by placing our detailed assessment of these 2 benthic communities into the context of ongoing NTL-LTER macrophyte and water clarity sampling, obtaining a rare, integrated perspective of the initial stages of benthification and its drivers in Lake Mendota.

Study site

Lake Mendota is a eutrophic, dimictic, drainage lake in south-central Wisconsin (USA). It has a predominantly black gyttja (hereafter referred to as "muck") substrate, especially in the profundal, with sand common in the littoral and sublittoral, rock present at shallow (1–3 m) depths, and seasonal macrophyte growth within the epilimnion (Fig. 1). It has a surface area of 3961 ha, a maximum depth of 25.3 m, and a mean depth of 12.8 m.

Methods

Zebra mussel sampling

We sampled adult zebra mussels twice a summer (early Jun and late Aug) from 2016 to 2018 at 5 depths (1, 3, 5, 8, and 10 m) along 3 transects running perpendicular to shore (A–C, Fig. 1). This sampling follows the design of a previous zoobenthos survey (Karatayev et al. 2013) in Lake Mendota. Dominant substrates at transect A were rock at 1 m depth, sand at 3 and 5 m, and muck at 8 and 10 m. At transects B and C, sand was the dominant substrate at 1 and 3 m depth, and muck was dominant at 5, 8, and 10 m. Substantial macrophyte coverage was absent at all sites in June and occurred mostly at 1, 3, and 5 m sites at transects A and C in August. Because most sites lacked hard substrate (e.g., rocks, logs) suitable for zebra mussel byssal thread attachment, we also sampled 5 additional rocky 1 m depth sites to study the population on optimal habitat. Depending on mussel density, scuba divers removed all adult mussels from a 1 m^{-2} (high mussel density) or 0.0625 m^{-2} (low mussel density) quadrat at each site in triplicate and transported samples in resealable plastic bags. In the laboratory we recorded mean zebra mussel density (individuals m^{-2}) as an average of all 3 replicates at each site. We modeled biomass (g m^{-2} wet weight)

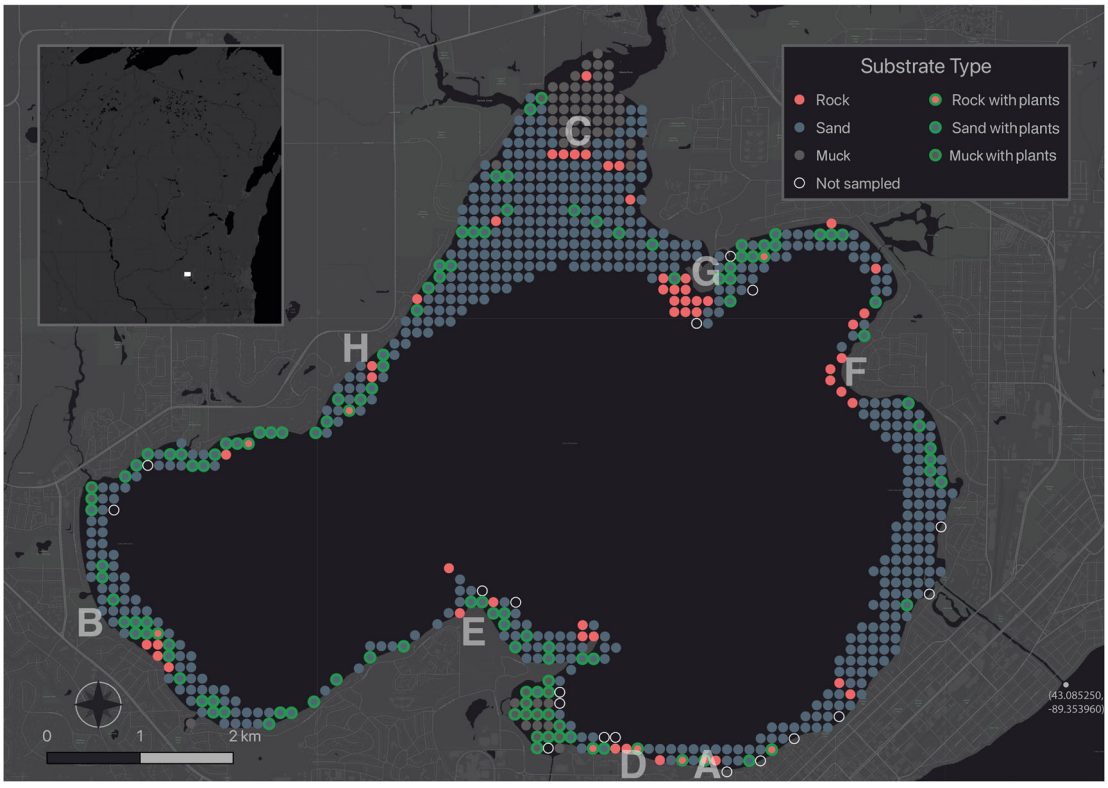

Figure 1. Lake Mendota (Wisconsin, USA) showing dominant substrate type (depths <6 m). Green rings = sites with significant seasonal macrophyte growth. Depths >6 m are assumed to be muck. Letters A–C indicate approximate shoreline origin of transects. Transects extended perpendicular to shore from 1 to 10 m depth. Along each transect we sampled adult zebra mussels at 1, 3, 5, 8, and 10 m depth sites; veliger (i.e., larval) zebra mussels at 10 m depth sites; and zoobenthos and phytobenthos communities at 1, 3, 5, 8, and 10 m depth sites. Letters D–H indicate approximate shoreline location of additional rocky 1 m depth sampling sites where we sampled adult zebra mussels only. We obtained substrate data from the aquatic plant management program administered by the Wisconsin Department of Natural Resources. Department staff and agency partners collected data on Lake Mendota using a grid-based point-intercept survey method.

based on mussel length using a subsample of measured and weighed individuals (Supplemental Fig. S1; for detailed enumeration and biomass modeling methods, see additional Supplemental Material). We also sampled larval veliger zebra mussels (see Supplemental Material for full methods), although this life stage was not a main component of our analyses.

Zoobenthos sampling

We sampled non-zebra mussel zoobenthos twice a summer (early Jun and late Aug) from 2016 to 2018 at the same 5 depths (1, 3, 5, 8, and 10 m) along the same 3 transects running perpendicular to shore (A–C, Fig. 1). We collected triplicate samples from each site using a 0.1075 m^{-2} circular quadrat and an airlift method because of difficulty closing Eckman samplers on the hard substrates of rock and zebra mussel druses. Using a modified scuba tank, we released compressed air into the center of a length of PVC pipe, creating enough backpressure to lift sediment and zoobenthos into a 500 µm mesh bag, which we transported to the surface in a resealable plastic bag.

We live-picked all zoobenthos samples within 24 h of collection without magnification after washing samples through a 500 µm sieve to remove sediment. If not processed immediately, we stored samples in the dark at 4 °C. We removed zebra mussels and planktonic taxa from the samples. We fixed samples in neutral-buffered formalin for 10–14 days to preserve wet weight biomass, rinsed in deionized water, and stored in a 75:5:10 EtOH-glycerin-deionized water solution. Dr. Kurt Schmude identified samples at the University of Wisconsin–Superior, most often to genus level. After identification, we blotted samples on absorbent tissue and recorded wet weight biomass for each taxonomic group to the nearest 0.1 mg on a high-resolution scale. Some chironomid individuals required mounting and microscopy for identification. We grouped these chironomid individuals by general size (i.e., small, medium, large) within each sample and weighed groups before mounting. After mounting and identification, we divided total

weights for each size group of these chironomids and assigned weights to each taxon according to their relative abundance in that group. We recorded all (non-zebra mussel) zoobenthos taxa as density (individuals m^{-2}) and biomass ($g\ m^{-2}$) averaged across replicates at each site. We adapted these zoobenthos methods from Environmental Protection Agency Standard Operating Procedures LG406 and LG407 for benthic invertebrate field collection and laboratory analysis (Environmental Protection Agency 2015a, 2015b).

Phytobenthos sampling

We also sampled phytobenthos twice a summer (early Jun and late Aug) from 2016 to 2018 at the same 5 depths (1, 3, 5, 8, and 10 m) along the same 3 transects running perpendicular to shore (A–C, Fig. 1). All 3 types of benthic sampling (adult zebra mussels, zoobenthos, and phytobenthos) were collected within a 2-week span in each of these 2 summer sampling periods. We collected triplicate samples at each site. Scuba divers retrieved one fist-sized rock at rock-dominated sites or a petri dish full of undisturbed sediment at sand- and muck-dominated sites and transported samples to the surface in a resealable plastic bag. We separated phytobenthos from inorganic material by adding ~1 L of deionized water, homogenizing the sample, allowing inorganic material to settle, and decanting the suspended phytobenthos and other coarse organic matter such as bits of plant material (adapted from Lowe and LaLiberte 2017). We kept samples dark and refrigerated until completely processed to prevent cell division after collection. For enumeration of cells, we preserved a 30 mL suspension of cells with several drops of neutral-buffered 50% glutaraldehyde in a sealed plastic bag. For confirmation of diatom taxa identifications made during the enumeration of these wet samples, we also mounted diatom cells on microscope slides (van der Werff 1953). A single taxonomist enumerated all wet samples at 400× magnification (Wehr et al. 2015) and confirmed all diatom taxonomy at 1000× magnification (Patrick and Reimer 1966) to the finest possible taxonomic resolution. We standardized enumerated samples as cell densities on the benthic surface (cells mm^{-2}).

Macrophyte sampling

The NTL-LTER routine monitoring program of Lake Mendota sampled macrophyte biomass at several sites within the littoral zone of Lake Mendota annually in late July or early August. NTL-LTER biologists deployed a weighted, double-sided rake from all 4 sides of a boat at 7 depths (1.0, 1.5, 2.0, 2.5, 3.0, 3.5, and 4.0 m) along several transects (~7 depending on year) running perpendicular to shore in the littoral zone. Biologists collected macrophytes from the rake, squeezed out excess water, and recorded rough biomass (g) estimates on a field scale. We accessed NTL-LTER macrophyte data and sampling methods from the NTL-LTER data portal (Magnuson et al. 2020).

Water clarity measurement

The NTL-LTER program measured water clarity using a 20 cm diameter Secchi disk on the shaded side of the boat in the deepest part of the lake as an indicator of whole-lake water clarity, assuming a well-mixed epilimnion. Measurement frequency each year was fortnightly during the spring and summer, every 6 weeks during the fall, and typically once during the ice-covered season. We accessed NTL-LTER water clarity data and methods from the NTL-LTER data portal (Magnuson et al. 2021a).

Zoobenthos analysis

We analyzed total zoobenthos biomass (both excluding and including zebra mussel biomass) and analyzed community changes without zebra mussels. For total zoobenthos biomass, we organized our 3 years, 5 depths, and 3 transects of data into a multilevel split-plot model with a randomized complete block design at the whole-plot level (Elphick et al. 2007). Depth (our subplot) was nested within year (our whole plot) and blocked by transect. This design provided the most power to investigate changes in zoobenthos density over time while controlling for different depths and transects of the lake. However, this design incorrectly assumed no interaction between transect and depth. We know an interaction between transect and depth is likely because our different transects had substantially different substrates at certain depths (Fig. 1), which may have influenced the benthic community and its responses to invasion (e.g., rocks at 1 m depth on transect A, but sand at 1 m depth on transects B and C). Because our transects were not replicated, we cannot quantify this interaction; therefore, it becomes built into the error term of the model, thereby inflating the model's error term and reducing our power. One way to correct for this inflation of our error term would be to increase the traditional α value of 0.05 in significance testing. Because we cannot quantify the inflated error, justifying any exact adjustment to our α value is difficult. Only one model resulted in a "borderline" p value (0.050) for which an adjustment to our α value might

impact an interpretation of its statistical significance. Because we know our α value should be above 0.05, we are comfortable accepting our $p = 0.050$ model result as significant without attempting to justify any exact adjusted α value.

Because our June sampling yielded consistently higher zoobenthos biomass than our August sampling, we subset our data by month and analyzed a June model and an August model separately. We averaged replicates within each Transect × Depth × Year combination before modeling. We tested for change in zoobenthos biomass based on the significance of the time term of our model with an analysis of variance (ANOVA) approach, both by including and excluding zebra mussel biomass in log-transformed zoobenthos biomass ($g\ m^{-2}$) data. We used the same multilevel model structure to analyze changes in diversity (Shannon index), richness (number of taxa), and evenness (Pielou index) over time. These indices were based on density (individuals m^{-2}), not biomass, and included data averaged across months.

To investigate shifts in community composition, we used nonmetric multidimensional scaling (NMDS) analysis on zoobenthos biomass data using the *metaMDS()* function from the *vegan* package (Oksanen et al. 2019) in R 3.6.2 (R Development Core Team 2017). We used a custom level of taxonomic resolution to compare relevantly scaled differences within each major taxonomic group (typically genus, but subfamily for many Chironomidae; Supplemental Table S1). We chose a number of dimensions ($k = 4$) for the NMDS using the *dimcheckMDS()* function in *vegan* (maximum iterations value = 100) to ensure a stress value well below 0.20 (Kruskal 1964). Based on the structure of our data, the *metaMDS()* function selected a Wisconsin double-standardization of our biomass data and analyzed sample dissimilarity as Bray-Curtis distances. We interpreted community shifts over time visually using ellipses drawn over the NMDS plot from standard deviations of samples with a 0.6 confidence limit. To highlight taxonomic "winners" and "losers" of the invasion, we used point-biserial correlation coefficients generated by the *multipatt()* function in *vegan* to identify indicator taxa highly associated with one particular year over the others (i.e., 2016 indicator taxa would be losers while 2018 indicator taxa would be winners).

Phytobenthos analysis

Phytobenthos density did not show the same monthly differences as the zoobenthos data, so we pooled June and August phytobenthos data into one analysis. In addition to benthic taxa, our sampling recovered many pelagic phytoplankton taxa that had fallen out of the water column and into the benthos. We removed those pelagic taxa from our analyses. We applied the same multilevel modeling approach from our zoobenthos analysis to our log-transformed phytobenthos data and chose a square root transformation and Wisconsin double standardization of phytobenthos density for NMDS analysis ($k = 3$).

Macrophyte analysis

We averaged macrophyte biomass data across replicates and transects and grouped data by shallow (1–2.5 m) and deep (3–4 m) sites for data from 2000 to 2018 to account for the likelihood of depth-dependent light limitation (Wetzel 2001, Zhu et al. 2006). We analyzed long-term trends using generalized additive models of depth-grouped and log-transformed macrophyte biomass data from 2000 to 2018 and short-term changes over the course of the zebra mussel invasion with a linear regression of depth-grouped and log-transformed biomass data from 2015 (when zebra mussels were first detected) to 2018.

Water clarity analysis

We analyzed water clarity differences in pre- (2010–2014) and post-invasion (2015–2020) periods by fitting a generalized additive model of Secchi depth (m) to the day of the year using cyclic cubic regression smoothers with the *mgcv* package in R 3.6.2 (Wood 2015) following methods from Walsh et al. (2018). We limited pre-invasion data to 2010–2014 to capture the period after *Bythotrephes longimanus* invaded and negatively impacted water clarity but before zebra mussels were detected. We analyzed interannual trends by summarizing and visualizing summer (Jun–Aug) Secchi depth measurements for each year as means and standard deviations. All analyses were performed in R 3.6.2 (R Development Core Team 2017). Figures were produced in R and QGIS 3.4.12 (QGIS Development Team 2019).

Results

Zebra mussels

Mean zebra mussel densities rose from ~10 m^{-2} in June 2016 to ~30 000 m^{-2} by June 2018 at shallow, rocky sites (Supplemental Fig. S2). In terms of biomass, these densities represent several grams and several thousand

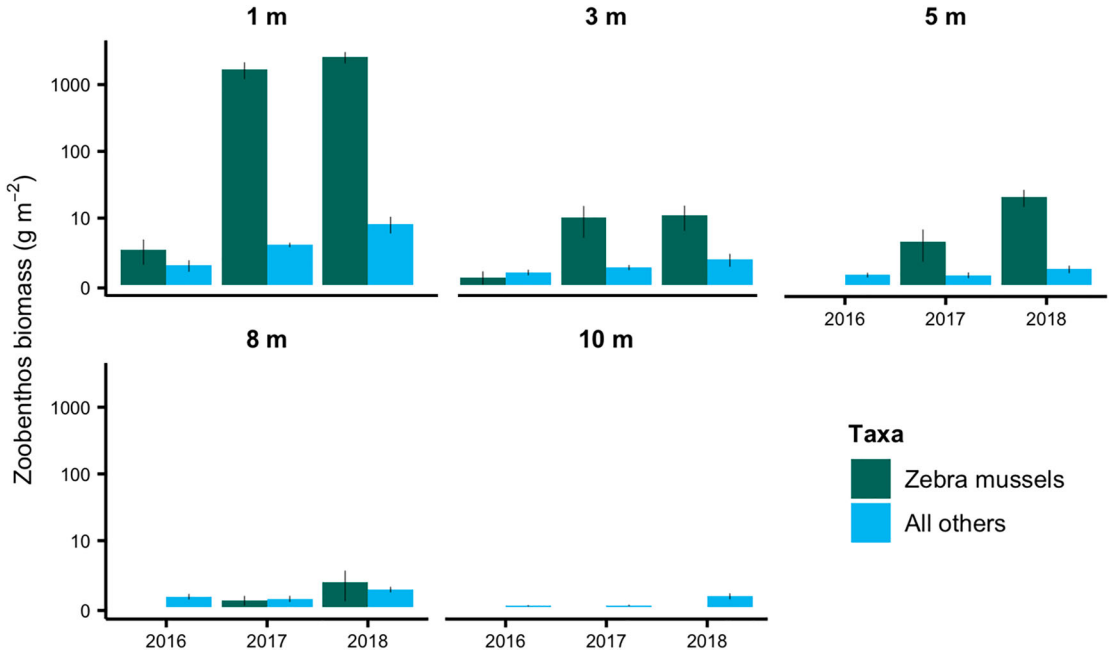

Figure 2. Mean biomass (g m^{-2}) of adult zebra mussels vs. all other zoobenthos taxa through time (2016–2018), presented on a log y-axis. Data are averaged across 2 months of sampling (Jun and Aug) in each year at 3 transects (A–C, Fig. 1). Panels represent 5 depths (1, 3, 5, 8, and 10 m) at which we sampled the benthic community along each transect. Because June sampling yielded consistently higher biomass than August sampling, we modeled the months separately. Both models indicate significant increases in non-zebra mussel zoobenthos biomass from 2016 to 2018 (Jun: +278% g wet weight, $p = 0.050$; Aug: +388% g wet weight, $p = 0.031$) with no significant interaction between depth and year (Jun: $p = 0.500$, Aug: $p = 0.767$).

grams of wet weight, respectively (Fig. 2). Mussels were absent in June 2016 at sites without abundant rocky substrate (all sites on transects B and C, and all sites on transect A except 1 m depth). Mussels could not directly attach their byssal threads to the sand or muck at these non-rocky sites, and therefore colonization was limited to errant hard objects such as stray stones, logs, or anthropogenic litter. As a result, most non-rocky sites only accumulated patches of mussels averaging ~10 m^{-2} in density. Some non-rocky sites, however, supported dense, seasonal macrophyte beds in late summer. Small mussels effectively attached to macrophyte stalks, allowing non-rocky sites with macrophyte beds to support mussel densities up to ~3000 m^{-2} by 2018. No mussels were found at 10 m depth along any transect throughout our study.

Size structure of the population varied by month, with roughly unimodal distributions in June transforming into roughly bimodal distributions in August each year due to the midsummer settlement of young-of-year mussels (Supplemental Fig. S3). Areas with significant macrophyte growth supported mostly small individuals (<5 mm length). Peak veliger densities increased 1900% from 2016 to 2017 (~100 to ~2000 m^{-3}) and remained relatively stable from 2017 to 2019 (Supplemental Fig. S4). Veligers were detectable in the water column from mid-June to mid-October. Adult and veliger zebra mussel data are archived and open-source with the Environmental Data Initiative (Spear et al. 2020c, Spear and Vander Zanden 2020).

Table 1. ANOVA results from multilevel models of zoobenthos data; *indicates statistical significance at the α = 0.05 level. Inflated model error described in the methods section suggests we may reasonably consider a *p*-value of 0.050 as significant. NS indicates no significant change. Changes in biomass were assessed excluding (w/o ZM) and including (with ZM) zebra mussel biomass from total biomass. Changes in diversity, richness, and evenness were assessed without zebra mussels.

Dependent variable	Year *p*-value	Depth *p*-value	Year: Depth interaction *p*-value	Percent change 2016–2018
Biomass w/o ZM (June)	0.050*	<0.001*	0.425	+278%
Biomass w/o ZM (August)	0.031*	<0.001*	0.767	+388%
Biomass with ZM (June)	0.001*	<0.001*	0.420	+1130%
Biomass with ZM (August)	<0.001*	<0.001*	0.767	+2416%
Diversity (Shannon index)	0.013*	<0.001*	0.678	−5%
Richness (# of taxa)	0.378	<0.001*	0.372	NS
Evenness (Pielou index)	0.100	<0.001*	0.934	NS

Zoobenthos

Total (non-zebra mussel) zoobenthos biomass increased significantly over the course of the zebra mussel invasion (Jun: $p = 0.050$, Aug: $p = 0.031$; Table 1, Fig. 2). Depth and year did not significantly interact in either multilevel model (Jun: $p = 0.50$, Aug: $p = 0.77$), indicating that changes in zoobenthos density increased over time even at depths where intense zebra mussel colonization did not occur (e.g., 8 and 10 m). Biomass increased ~4-fold from 2016 to 2018 (Table 1, Fig. 3a), driven largely by changes in Amphipoda (*Hyalella azteca*), Diptera (especially *Chaoborus* spp. and *Chironomus* spp.), and Gastropoda (Fig. 3a). Isopoda and Trichoptera also contributed to overall increases at 1 m depth, where density and biomass increased most profoundly. When including zebra mussels in total zoobenthos, biomass increased ~20-fold from 2016 to 2018 (Table 1).

Overall, no strong temporal trends were found in indices of diversity, richness, and evenness over the course of the invasion (Table 1). Shannon diversity had a significant year term in our multilevel model ($p = 0.01$), but that change was not directional (i.e., diversity increased from 2016 to 2017 but decreased from 2017 to 2018). NMDS analysis ($k = 4$, 2D stress = 0.15) revealed no strong temporal shifts in community composition (Fig. 4a). Point-biserial correlation coefficient analysis revealed that several abundant winner taxa were highly associated with 2018 (the year of

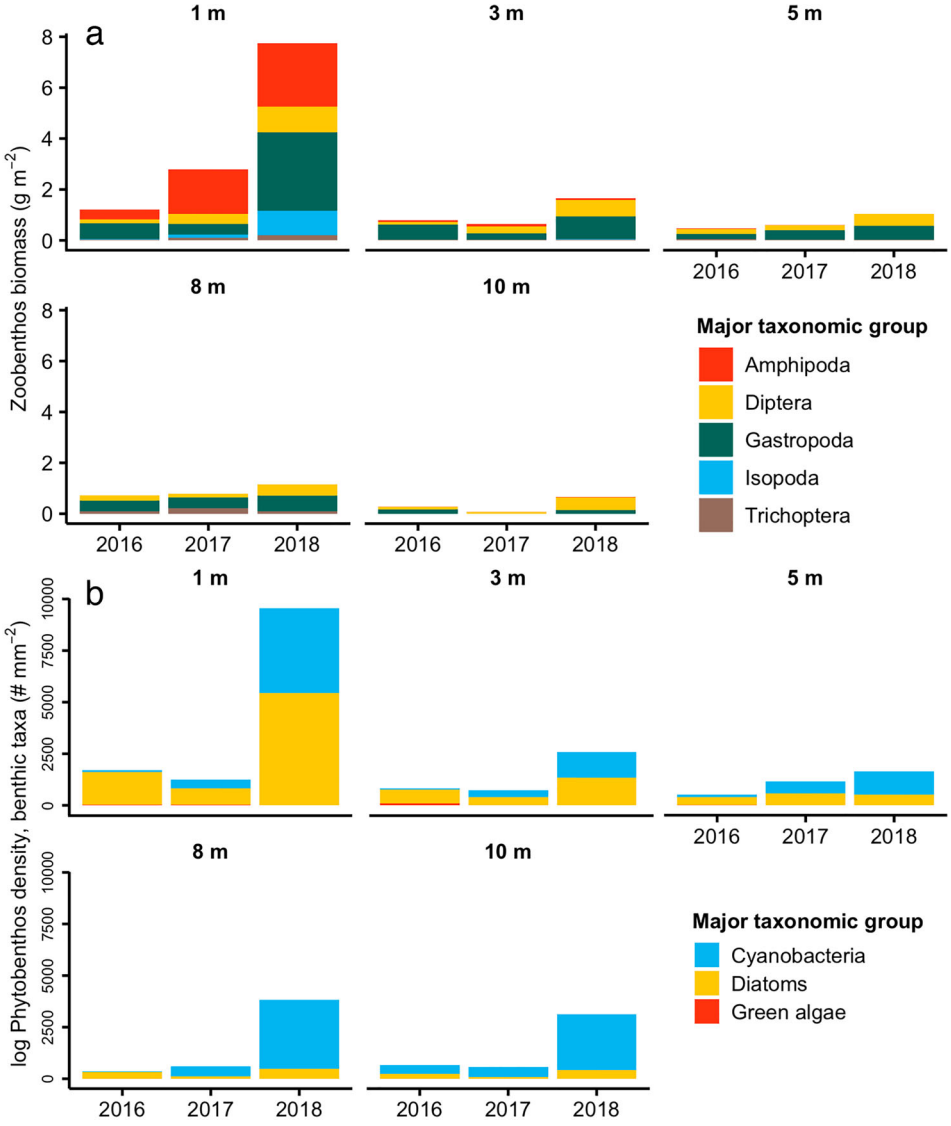

Figure 3. Changes in (a) mean (non-zebra mussel) zoobenthos biomass (g m^{-2} wet weight) and (b) mean log-transformed phytobenthos density (# of cells mm^{-2}) of select major taxonomic groups that showed strong trends through time (2016–2018). Data are averaged across 2 months of sampling (Jun and Aug) in each year at 3 transects (A–C, Fig. 1). Panels represent the 5 depths (1, 3, 5, 8, and 10 m) at which we sampled the benthic community along each transect.

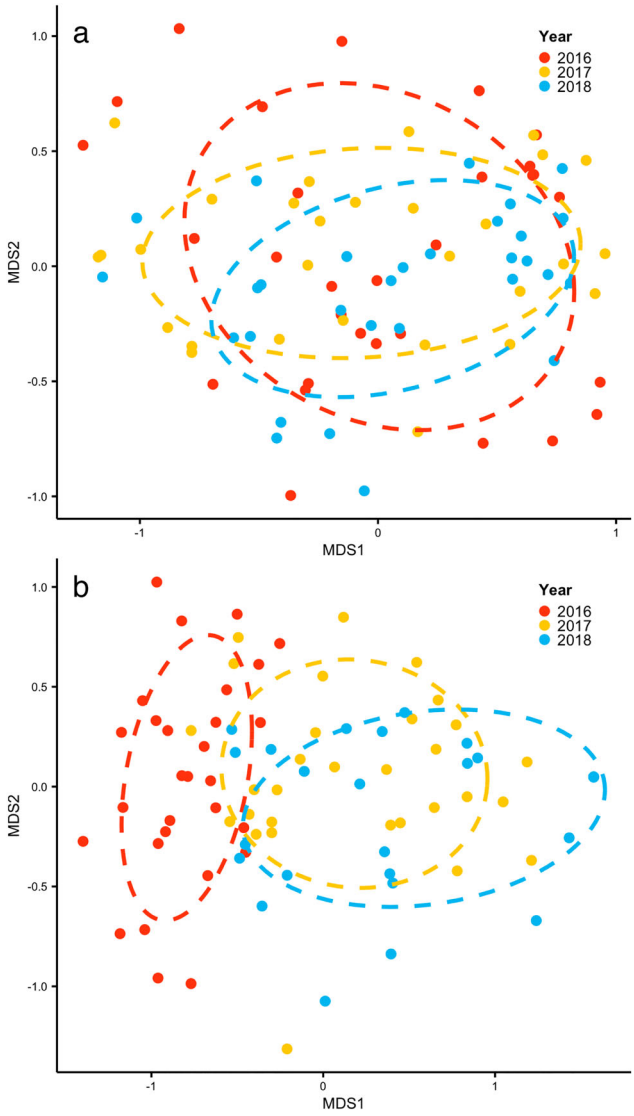

Figure 4. Bray-Curtis nonmetric multidimensional scaling (NMDS) analysis of (a) zoobenthos (excluding zebra mussels, $k = 4$, 2D stress = 0.15, Wisconsin double standardization) and (b) phytobenthos ($k = 3$, 2D stress = 0.15, square root transformation and Wisconsin double standardization) classified by year. Standard deviation ellipses at a 0.06 confidence level demonstrate a visible shift in community composition for phytobenthos but no strong shift for zoobenthos.

highest zebra mussel density) including 2 snails (*Lyogyrus granum* [$r_{pb} = 0.388$] and *Valvata tricarinata* [$r_{pb} = 0.349$]), 3 chironomids (*Chironomus* spp. [$r_{pb} = 0.388$], *Polypedilum* spp. [$r_{pb} = 0.328$], and *Dicrotendipes* spp. [$r_{pb} = 0.228$]), and the phantom midge (*Chaoborus* spp. [$r_{pb} = 0.337$]). By 2018, zebra mussels dominated total zoobenthos biomass at 1, 3, and 5 m depths, representing >99% of total zoobenthos biomass at 1 m (Fig. 2). Zoobenthos biomass and density data are archived and open-source with the Environmental Data Initiative (Spear et al. 2020b).

Table 2. ANOVA results from multilevel models of phytobenthos data. Statistical significance at the α = 0.05 level is indicated by *. NS indicates no significant change.

Dependent variable	Year *p*-value	Depth *p*-value	Year:Depth interaction *p*-value	Percent change 2016–2018
Density	<0.001*	0.106	0.442	+336%
Diversity (Shannon index)	<0.001*	0.007	0.661	−56%
Richness (# of taxa)	<0.001*	0.001*	0.999	−48%
Evenness (Pielou index)	0.158	0.743	0.866	NS

Phytobenthos

Phytobenthos density (cells mm^{-2}) increased significantly over the course of the zebra mussel invasion ($p < 0.001$; Table 2, Fig. 3b). Depth and year did not significantly interact in the multilevel model ($p = 0.442$), indicating that changes in density increased over time even at depths where intense zebra mussel colonization did not occur (e.g., 8 and 10 m). Density increased ~4-fold from 2016 to 2018 (Table 2, Fig. 3b), the majority of which occurred between 2017 and 2018, with little change between 2016 and 2017. Overall increases in density were largely driven by cyanobacteria, particularly a thin, filamentous species belonging to the *Jaaginema-Schizothrix* genus complex. We saw depth-structured, species-specific changes in benthic diatom densities, with noted increases in epiphytic and chain-forming taxa. Green algae decreased, becoming undetectable by 2018.

Overall, strong decreases (~50%) in indices of diversity and richness were found, but no strong trends in evenness (Table 2). Decreases in overall diversity and richness were caused by the loss of several diatom and green algal taxa (17–13 and 7–0 taxa, respectively) from 2016 to 2018. NMDS analysis ($k = 3$, 2D stress = 0.15) revealed a moderate shift in overall community composition (Fig. 4b). Point-biserial correlation coefficient analysis revealed 2 winner taxa highly associated with 2018, including the *Jaaginema-Schizothrix* cyanobacterial taxa ($r_{pb} = 0.389$) and one diatom, *Staurosira* spp. ($r_{pb} = 0.047$). Phytobenthos abundance data are archived and open-source with the Environmental Data Initiative (Spear et al. 2020a).

Macrophytes

Long-term (2000–2018) analysis of macrophytes revealed relatively stable biomass at depths of 1–2.5 m (i.e., shallow; with the exception of a sharp dip in 2008) and regular fluctuations in biomass at 3–4 m (i.e., deep) with a period of ~6 years and an

amplitude of ~0.5 order of magnitude (Fig. 5a). Short-term (2015–2018) linear regression analysis showed no significant change in shallow biomass ($p = 0.86$, $R^2 = 0.0001$) but a significant increase in deep biomass ($p < 0.002$, $R^2 = 0.24$) over the course of the zebra mussel invasion (Fig. 5b). Data include 27 different macrophyte taxa with no trends in richness from 2015 to 2018.

Water clarity

Our analysis of water clarity suggests no significant, rapid post-invasion change in seasonal or interannual indicators of water clarity, as measured by Secchi depth (m) near the lake center. Post-invasion (2015–2020) water clarity might have been slightly higher in the fall and slightly lower in the spring, but modeled seasonal averages were close for pre- and post-invasion data (Fig. 6a). Interannually, mean summer water clarity did not increase over the course of the invasion (2015–2018). Summer means and maxima in 2019 and 2020 were relatively high, although so were the standard deviations associated with those means. The 2019 and 2020 summer water clarity means were within the range of historic values (Fig. 6b).

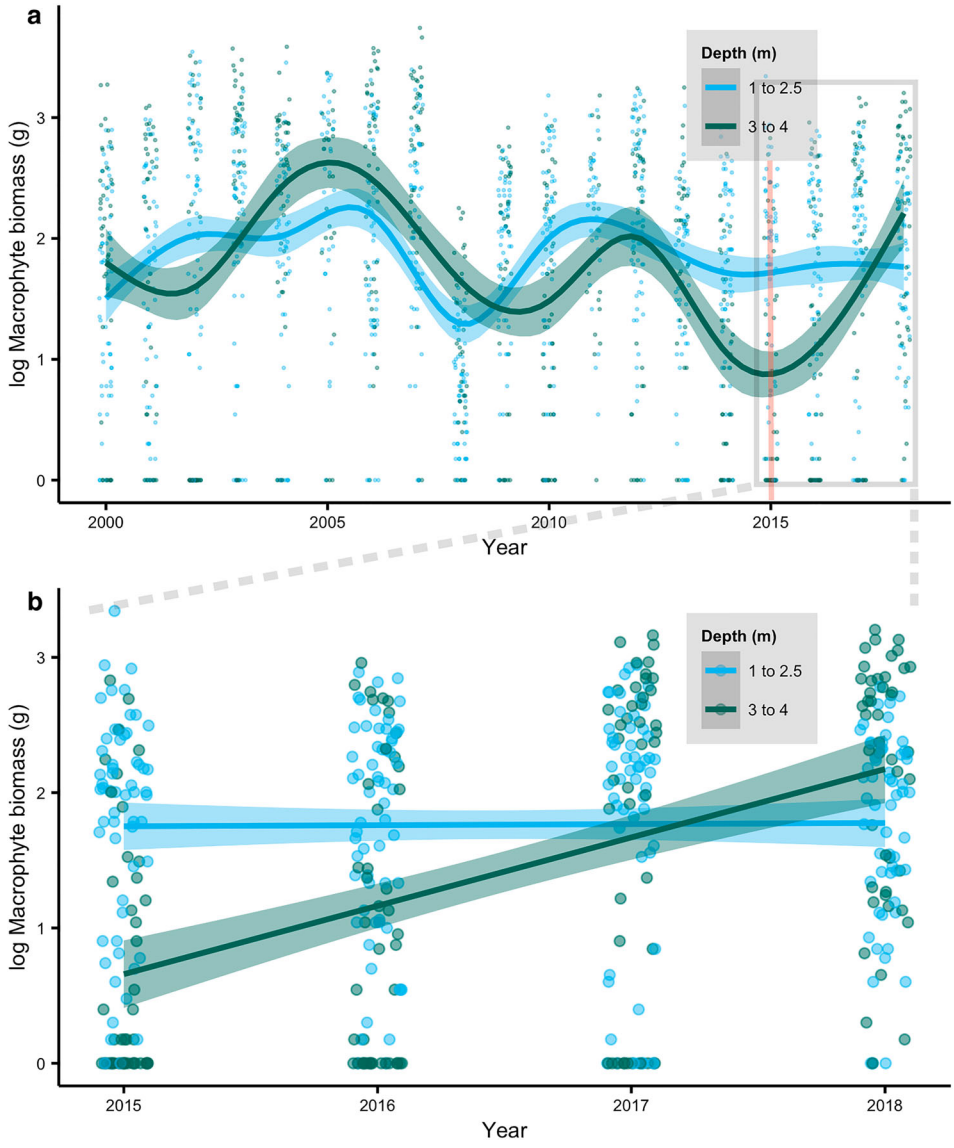

Figure 5. Littoral macrophyte biomass change from (a) 2000–2018 and (b) 2015–2018. Points are individual sampling events and trend lines are (a) generalized additive models and (b) linear models with 95% confidence intervals (shaded area). Vertical line indicates first detection of zebra mussels in 2015. Short-term trends (b) reveal a significant increase of macrophyte biomass at deeper depths ($p < 0.001$, $R^2 = 0.24$) following the invasion of zebra mussels but no significant change at shallower depths ($p = 0.86$, $R^2 < 0.01$).

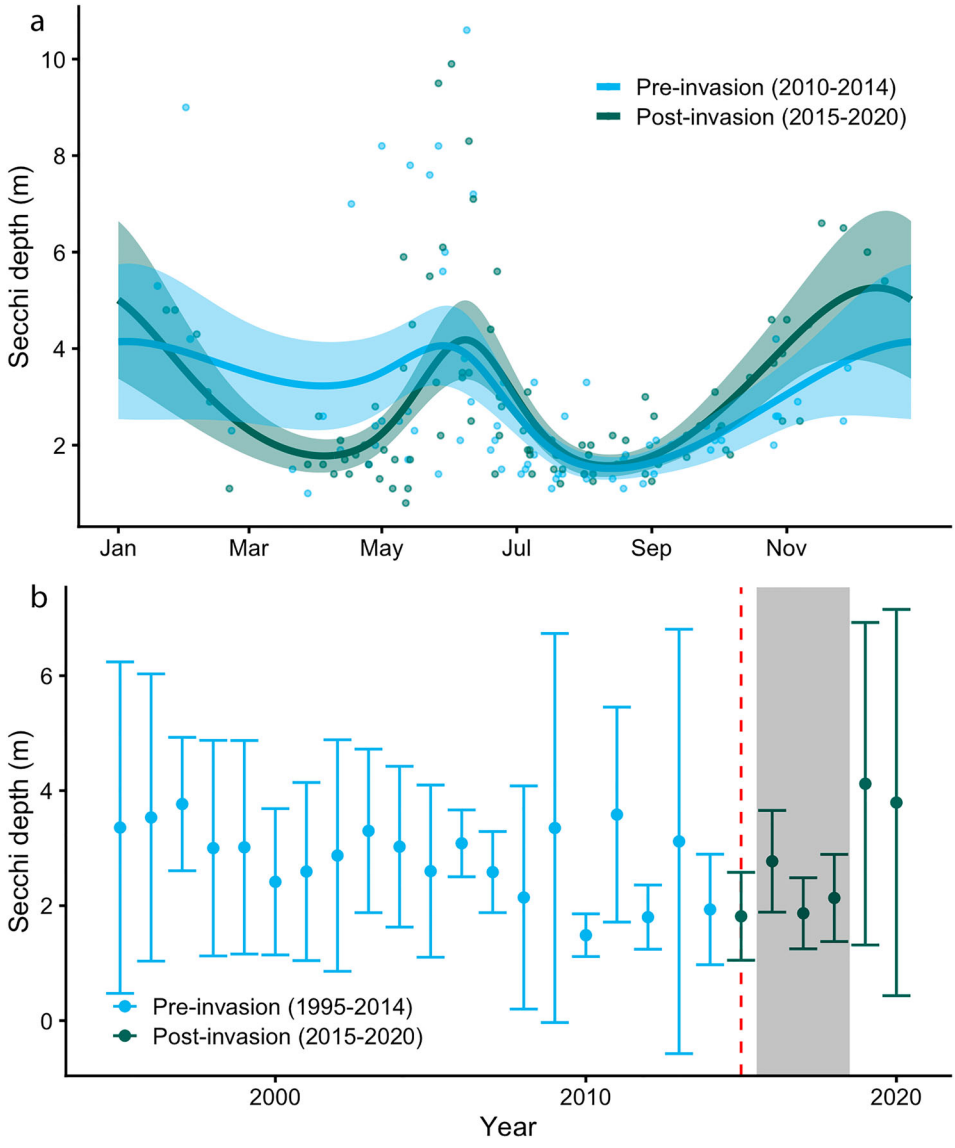

Figure 6. Water clarity, as measured in Secchi depth (m) for Lake Mendota through time. Top panel (a) depicts observations (circles), modeled seasonal trends (lines), and 95% confidence intervals (shaded areas) for pre-invasion (2010–2014) and post-invasion (2015–2020) periods using a generalized additive model. Bottom panel (b) depicts summer (Jun–Aug) means (circles) and standard deviations (error bars) for Secchi depth measurements from 1995 to 2020. Dotted vertical line indicates 2015, the year of first zebra mussel detection in Lake Mendota. Shaded gray area indicates the sampling period for observed zebra mussel, zoobenthos, and phytobenthos change in this study (2016–2018).

Discussion

Zebra mussels explode, but bulk of biomass restricted to rocky areas

Consistent with the long, documented history of zebra mussel invasion in Europe and North America (Burlakova et al. 2006, Strayer et al. 2019), the Lake Mendota zebra mussel population exhibited a 2-year timeline from detection to a maximum density of ~30 000 m^{-2} on hard substrate. Where sandy and mucky sites supported seasonal macrophyte beds, zebra mussels attached to macrophyte stalks at densities ~3000 m^{-2} by August 2018. Sandy and mucky areas without macrophytes did not significantly contribute to the lake-wide zebra mussel population, despite making up the majority of total lake area.

Lake-wide areal estimates of macrophyte coverage (142 ha) exceeded that of rocky substrate (122 ha; Fig. 7a) in late summer (Hauxwell et al. 2010, Mikulyuk et al. 2010). However, macrophytes are only seasonally available for zebra mussel attachment, generally not appearing until August and senescing each fall (Burlakova et al. 2006), and thus only supported young-of-year mussels. Macrophyte-attached mussels therefore

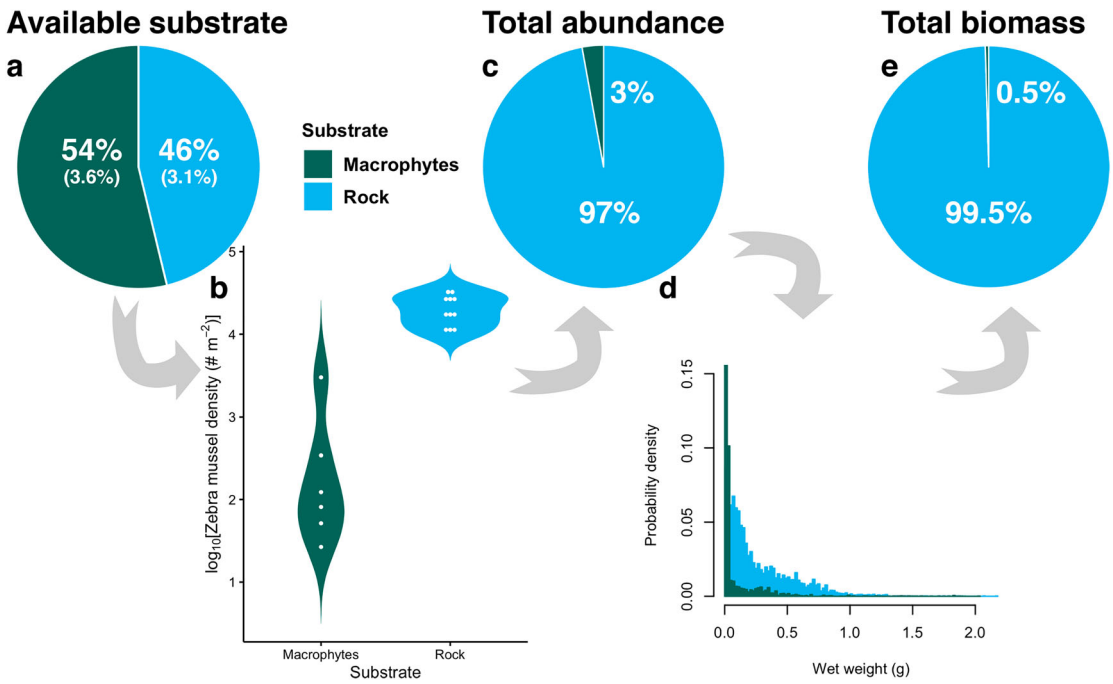

Figure 7. Breakdown of rock- and macrophyte-dominated areas of benthic Lake Mendota and how differences in the demography of zebra mussels attached to each substrate type structure the relative contribution of those areas to lake-wide zebra mussel abundance and biomass in 2018. (a) Rock- and macrophyte-dominated area make up relatively equal percentages of total suitable-habitat area and (in parentheses) total lake area. (b) However, zebra mussel abundances are consistently higher on rocks compared to macrophytes. (c) As such, macrophyte-attached mussels make up only 3% of total lake-wide population abundance. (d) Macrophyte areas also only support small individuals while rocky areas support a more full-size structure. (e) Therefore, despite having a higher percentage of lake-wide area, macrophytes support only 0.5% of total lake-wide population biomass while rocks support 99.5%.

exhibited much lower densities and much smaller body sizes than rock-attached mussels (Fig. 7b and d) and contributed little to the lake-wide zebra mussel population, comprising only 3% of total abundance and 0.5% of total wet weight biomass (Supplemental Fig. S5c and S5e). Because individual filter-feeding rates increase exponentially with biomass (Karatayev et al. 1997), the average body size of a zebra mussel colony affects its ability to clear the water column. Therefore, rocky-bottom areas, which support dense colonies of large-bodied mussels (>30 000 m^{-2}; ~3000 g m^{-2}), likely drive the majority of consumptive ecosystem impacts in Lake Mendota. Our zoobenthos, phytobenthos, and macrophyte analyses suggest that this relatively small area of lake bottom, representing only 3.1% of total lake area, still supported a zebra mussel population capable of strongly impacting the benthos, at least to the maximum depth of study (10 m).

Strong ecosystem impacts from a habitat-limited population are possible because extreme local densities of zebra mussels have a prodigious ability to filter feed phytoplankton. In well-mixed epilimnions such as that of Lake Mendota, lake-wide pelagic primary production is available for consumption even when a population is restricted to a small, nearshore area (Reed-Andersen et al. 2000). To roughly estimate the lake-wide size and filtration capacity of the Lake Mendota zebra mussel population, we extrapolated local zebra mussel densities from 2018 (Supplemental Fig. S2) to lake-wide areal estimates of suitable habitat (Fig. 1 and 7; see Supplemental Material for full methods). The 2018 population size likely exceeded 25 billion individuals and 7 million kg of wet weight biomass, representing a lake-wide density of 670 m^{-2} (180 g m^{-2}) or 2010 m^{-2} (520 g m^{-2}) within the summer epilimnion. These density estimates are within the range required to impact water clarity according to modeling of Lake Mendota (Reed-Andersen et al. 2000) and observations from other eutrophic lakes (Reeders and Bij De Vaate 1990).

Assuming a well-mixed epilimnion, a population of this size is capable of filtering the volume of Lake Mendota's epilimnion (~286 million m^{-3}; Reed-Andersen et al. 2000) in <45 days, or the entire lake volume (~480 million m^{-3}) in <75 days. Although true filtration rates depend on lake circulation patterns, circulation rates, and phytoplankton densities (Reed-Andersen et al. 2000), our estimates of population abundance, biomass, and filtration rate are consistent with predictions for Lake Mendota made prior to zebra mussel invasion (Karatayev and Burlakova 2008).

Zoobenthos increase across most taxa and depths

Overall biomass of zoobenthos increased ~300% excluding zebra mussels and ~1900% including zebra mussels. Increases of this magnitude are broadly consistent with zebra mussel benthification in other systems (Ward and Ricciardi 2007, Higgins and Vander Zanden 2010, Ozersky et al 2011). Notably, zoobenthos biomass significantly increased even where intense zebra mussel colonization did not occur (e.g., 8 and 10 m depth), although the most prolific increases occurred at shallow sites (1 m depth) where zebra mussels were most common.

Many North American case studies see profundal biomass decrease following invasion (Karatayev et al. 2002, Ward and Ricciardi 2007, Higgins and Vander Zanden 2010). These decreases in other systems are typically driven by losses of the burrowing amphipod *Diporeia* (Ricciardi et al. 1997, Lozano et al. 2001, Nalepa et al. 2009) and the filter-feeding clam *Sphaeriidae* (Lozano et al. 2001). *Diporeia* were absent in profundal Lake Mendota even prior to zebra mussel invasion and thus did not contribute to profundal decline. *Sphaeriidae* were extremely abundant in the profundal zone of Lake Mendota in the first half of the 20th century but declined dramatically by the 1960s (Karatayev et al. 2013) and showed no trends in biomass from 2016 to 2018. In fact, no zoobenthos taxa seemed to be big losers of the zebra mussel invasion, despite strong positive responses for a few winner taxa. Mesocosm experiments by Stewart et al. (1998) that lacked the 2 common losers *Diporeia* and *Sphaeriidae* prior to experimental zebra mussel addition also showed no decrease in any zoobenthos taxa. One possible contributing factor to the lack of profundal losers might be the seasonally anoxic hypolimnion of Lake Mendota, which may not have supported a pre-invasion zoobenthos diverse enough to incur a conspicuous post-invasion impact (i.e., not a lot to lose).

The Lake Mendota zoobenthos was dominated by detritivores in 2016, a community structure strengthened post-invasion by strong increases in detritivores such as amphipods (*H. azteca*) and chironomids (*Chironomus* spp., *Dicrotendipes* spp., *Polypedilum* spp.) as well as grazing/scraping snails (*L. granum*, *V. tricarinata*) from 2016 to 2018 (Supplemental Fig. S5). Zebra mussels may benefit detritivores through biodeposition of pelagic resources and the creation of complex druse structures that collect detritus (Karatayev et al. 1997, 2002, Stewart et al. 1998, Burlakova et al. 2012) and benefit grazers/scrapers through the stimulation of periphyton growth (Lowe and Pillsbury 1995, Ricciardi et al. 1997). The complex structure of clumped zebra mussel shells may also provide refugia from predation or disturbance for small invertebrates (Ricciardi et al. 1997, Stewart et al. 1999). The post-invasion reinforcement of the pre-invasion detritivore dominance is supported by our models, which showed no strong shifts in community composition from 2016 to 2018 (Fig. 4a) and no significant, directional changes in diversity, richness, or evenness indices (Table 1). However, it is critical to note these analyses intentionally exclude zebra mussel biomass, which dominated the zoobenthos community at most depths (1, 3, and 5 m) by 2018 and comprised >99% of total biomass at 1 m, representing a drastic shift in community composition consistent with zebra mussel-inclusive changes in other invaded lakes (Burlakova et al. 2005).

One curious change in the zoobenthos was the reappearance of *Chaoborus* spp., a zooplanktivorous Dipteran. Historically, *Chaoborus* were abundant in Lake Mendota but declined rapidly ~1950, remaining rare or undetectable in periodic benthic sampling (Lathrop 1992, Karatayev et al. 2013) and routine zooplankton sampling until 2018 (Magnuson et al. 2021b). *Chaoborus* biomass increased from 2016 to 2018, which is unexpected given the documented history of declines in zooplankton and zooplanktivores generally (Karatayev et al. 1997, Hecky et al. 2004, Higgins and Vander Zanden 2010) and *Chaoborus* specifically (Strayer and Smith 2001, Dzialowski et al. 2018) following zebra mussel invasions in other systems. No clear mechanistic link was found between increases in *Chaoborus* and zebra mussel invasion, and continued monitoring and analysis of pelagic data is needed to address this issue. Importantly, zoobenthos biomass increased at deeper sites without zebra mussel colonization, even when *Chaoborus* were excluded from our analysis.

Phytobenthos increase, especially cyanobacterial and filamentous taxa

The phytobenthos has received relatively little attention in the zebra mussel invasion literature compared to the zoobenthos or pelagic biological communities (Higgins and Vander Zanden 2010). However, the general understanding of zebra mussel-driven benthification posits that increased light penetration and nutrient enrichment of the benthos stimulates the growth of benthic green algae, diatoms, and macrophytes (Karatayev et al. 1997, Higgins and Vander Zanden 2010). The observed response of phytobenthos density in Lake Mendota from 2016 to 2018 was similar to that of zoobenthos biomass, exhibiting on average a 4-fold increase in density (Fig. 3b) across our depth gradient (1–10 m),

even at depths where intense zebra mussel colonization did not occur.

Pillsbury et al. (2002) also reported 4-fold increases of benthic algae following zebra mussel invasion of Saginaw Bay in Lake Huron, driven largely by filamentous green algae. Benthic green algae decreased in our data from 2016 to 2018, becoming undetectable by 2018. However, our data may not fully reflect the realities of benthic green algae in Lake Mendota. Nearshore mats of filamentous green algae such as *Cladophora* are a common impact of zebra mussel invasion (Stević et al. 2013, Armenio et al. 2016), particularly in the Laurentian Great Lakes (Higgins et al. 2008, Barton et al. 2013). Anecdotally, large mats of detached filamentous green algae were visually commonplace along the Lake Mendota shoreline throughout our study. Overgrowth of filamentous green algae on rocks and zebra mussel druses became so conspicuous in July 2017 that we returned to one site (transect A, 1 m depth) and cut out the mat with scissors, estimating an average biomass of 2900 g m^{-2} wet weight (or 224 g m^{-2} dry weight). Our phytobenthos methods likely significantly underestimated the density of filamentous green algae, possibly because of mismatched timing between sample collection and algal mat growth as well as the difficulty of capturing large filaments in our phytobenthos subsampling and enumeration methods. Notably, *Cocconeis pediculus*, a diatom and common epiphyte of *Cladophora* (Stevenson and Stoermer 1982, Higgins et al. 2008; Supplemental Fig. S6), increased 2800%. Although we did not quantify the relationship between *Cocconeis* and *Cladophora* abundance, this 26-fold increase in a *Cladophora* epiphyte may be a proxy indicator of filamentous green algal growth on hard substrates, suggesting the 4-fold increase in overall phytobenthos density we observed may be an underestimation of the true response, especially among filamentous green algae taxa on hard substrates.

Increases in the phytobenthos were most pronounced among filamentous taxa, including a fine, threadlike cyanobacterial species of the *Jaaginema-Schizothrix* genus complex. Zebra mussels are known to promote planktonic and lake-surface cyanobacterial blooms, most often in low-nutrient lakes (Raikow et al. 2004, Knoll et al. 2008). Our finding that zebra mussel invasion promoted benthic cyanobacteria in a eutrophic lake provides an unexpected insight into the relationship between zebra mussels and cyanobacteria. We also noted increases in the diatom genus *Staurosira* spp., which together with *Jaaginema* spp. increased following zebra mussel invasion in a freshwater system in Ukraine (Barinova et al. 2017). Overall phytobenthos diversity and richness fell by half, driven by the loss of all green algal taxa and many diatom taxa, although most taxa that disappeared were rare even in 2016. The community shifted moderately from 2016 to 2018, dominated in 2018 by only a handful of cyanobacteria (*Jaaginema-Schizothrix* complex) and diatoms (*Staurosira* spp., *C. pediculus*, and *Navicula* spp.), most of which were common prior to the invasion. Notably, many of the taxa that increased share the ability to form long chains.

Macrophytes increase at depth despite static water clarity

Our long-term macrophyte analysis (2000–2018) showed greater variability in biomass at deeper depths (3–4 m) than shallower depths (1–2.5 m), seeming to oscillate with a period of ~6 years (Fig. 5a). The trough of the most recent long-term cycle of deep macrophytes aligns with the 2015 detection of zebra mussels in Lake Mendota, followed by an increase in biomass through 2018. Short-term analysis confirmed this trend, with shallow macrophytes remaining steady while deep macrophytes significantly increased from 2015 to 2018.

Macrophytes are sensitive to a variety of biotic and abiotic conditions (Zhu et al. 2006), so it is difficult to determine whether the zebra mussel invasion drove this change or if it is a continuation of established long-term patterns. However, increased deep macrophyte growth is consistent with classic zebra mussel benthification (Karatayev et al. 2002, Zhu et al. 2006, Higgins and Vander Zanden 2010) in which phytoplankton consumption by zebra mussels clears the water column and increases light penetration, a fundamental avenue by which zebra mussels directly alter their physical environment (i.e., light availability; Zhu et al. 2006). Because macrophytes are often light limited in eutrophic lakes (Wetzel 2001, Zhu et al. 2006), deep macrophytes are most affected by water-column shading and therefore may respond more sensitively to changes in water clarity than shallow macrophytes.

Our analysis of long-term trends in water clarity showed no evidence for seasonal or annual increases in Secchi depth following invasion (Fig. 6), however, defying modeled predictions for zebra mussel invasion of Lake Mendota (Reed-Andersen et al. 2000). High maximum and mean water clarity in the last 2 years of observation (2019–2020) may indicate that the expected rapid increase in clarity may be occurring, albeit delayed (Fig. 6b), but large variation in those recent data obscures the interpretation of any post-invasion trend.

Static water clarity during 2016–2018 challenges the conventional assumption that increased light penetration would be the major driver of increases in

phytobenthos and macrophyte abundance. Instead, we speculate that increases of phytobenthos and macrophytes in Lake Mendota were strongly driven by nutrient enrichment of benthic habitat through zebra mussel excretion and pseudofeces deposition. Benthification in the absence of increased light penetration is not without precedent, although most examples come from the Laurentian Great Lakes. In the Western Basin of Lake Erie, zebra mussels (and subsequently the congeneric quagga mussel) drove benthification without improving water clarity, perhaps because of intense nonpoint source sediment and nutrient loading, which offset the increase in filter feeding (Barbiero and Tuchman 2004, Karatayev et al. 2018). Static water clarity was also observed during the invasion of Green Bay in Lake Michigan. Concurrent reduction of algae-grazing zooplankton taxa likely offset the filter feeding by zebra mussels, resulting in no large changes in water clarity in Green Bay (de Stasio et al. 2008).

Why zebra mussels did not significantly improve water clarity in Lake Mendota as predicted (Reed-Andersen et al. 2000) is unclear. Notably, we did not directly sample water clarity in the nearshore areas where phytobenthos and macrophyte abundances increased; instead, we made the assumption that offshore Secchi depth measurements are a reasonable indicator of lake-wide conditions in an inland system with a well-mixed epilimnion such as Lake Mendota. Although nearshore and offshore water clarity may not be tightly coupled in much larger invaded systems (e.g., the Laurentian Great Lakes; Bailey et al. 1999, Makarewicz et al. 1999, Pennuto et al. 2012), offshore water clarity measurements may be a reliable indicator of nearshore zebra mussel impacts for inland lakes more comparable in size and shape to Lake Mendota (Idrisi et al. 2001, Eimers et al. 2005, Karatayev et al. 2021).

Possible explanations for static water clarity include relatively slow epilimnion and whole-lake filtration rate estimates (45 and 75 days) by this zebra mussel population compared to turnover times of many algal taxa (hours to weeks). Parameters such as nutrient loading, hydrodynamics (Noordhuis et al. 2016), and lake morphometry (Karatayev et al. 2021) can also influence what kinds of ecosystem states arise following zebra mussel invasions. An increase in cumulative precipitation and intense rainfall events combined with a watershed dominated by agricultural land use has led to rising levels of nonpoint source nutrient loading to Lake Mendota over the last several years (unpublished NTL-LTER data). Furthermore, in 2009 Lake Mendota was invaded by an extremely abundant population of a predatory zooplankter, spiny water flea (*B. longimanus*), triggering a trophic cascade that decreased water clarity by ~1 m (Walsh et al. 2016) by reducing algae-grazing zooplankton populations. Similar to Western Lake Erie and Green Bay, these biotic and abiotic drivers could be suppressing any water clarity improvements that zebra mussel filtration might otherwise produce.

Invasive species are typically associated with negative impacts on ecosystem services. For example, Lake Mendota, a hub of recreational activity for the urban population of Madison, Wisconsin, recently suffered losses of ~US$140 million worth of recreational and aesthetic ecosystem services when a previous invasion of *B. longimanus* reduced lake water clarity (Walsh et al. 2016). Zebra mussels, however, can positively impact business revenues and property values by improving water clarity along lakefront communities (Limburg et al. 2010). The lack of rapid clarity improvements observed for Lake Mendota may limit any economic upside of this invasion. Instead, we have documented increases in potentially toxic benthic cyanobacterial abundance (Fig. 3b) and observed anecdotal increases in the frequency of unsightly and health-hazardous filamentous algal mats and cyanobacterial blooms washing ashore. Regardless of water clarity, we speculate that zebra mussels may be negatively impacting other water quality indicators to this point in the invasion, but continued monitoring is needed.

Conclusions

The benthos of Lake Mendota saw rapid zebra mussel colonization of rocky habitat reaching densities of >30 000 m^{-2} within 2 years of detection, followed by increases of (non-zebra mussel) zoobenthos (300%), phytobenthos (300%), and deep macrophytes (900%), patterns consistent with our general understanding of zebra mussel invasion and benthification in lakes. We observed no obvious rapid improvements in our long-term indicator of water clarity (i.e., light penetration), which is one of 2 major drivers of benthification in other systems. Although not directly tested here, we speculate that benthic nutrient enrichment through zebra mussel excretion and deposition of pelagic resources may have more strongly driven the observed increase in benthic organism abundance. Novel, complex microhabitats created by zebra mussel shells may have also benefitted benthic taxa. We documented 2 other curious findings: strong increases in benthic cyanobacteria, which is an atypical response to invasion for a nutrient-rich lake such as Lake Mendota, and the reappearance of a historically abundant and pelagic-feeding macroinvertebrate, *Chaoborus* spp. Our results serve as an important reminder that biological invasions are highly context-dependent phenomena, even for

species with a long and relatively well-documented invasion history.

Stimulation of the benthic–littoral pathway is only half of the benthification story. An analysis of the pelagic–profundal pathway of the Lake Mendota food web is required to more fully understand the scope and drivers of ecological change over our study period, including the lack of rapid water clarity improvement. Major pelagic variables such as phytoplankton abundance and nutrient concentrations show little indication of strong trends from 2016 to 2018. However, these pelagic variables may be strongly influenced by climatic drivers such as rainfall, which has been increasing in frequency and intensity (INFOS Yahara 2020) and has likely caused increased nutrient loading from the agriculture-dominated watershed of Lake Mendota (Carpenter et al. 2018; unpublished NTL-LTER data), potentially delaying the expected positive effects of zebra mussels on water clarity. Citizen scientist efforts reported a 4-fold increase in the frequency of "strong" cyanobacterial blooms in Lake Mendota from 2015 to 2019 (Clean Lakes Alliance 2020), which is consistent with zebra mussel invasion but typically occurs in low-nutrient lakes (Raikow et al. 2004, Knoll et al. 2008). These data mirror our findings of cyanobacterial proliferation in the phytobenthos. Preliminary analysis of stable isotope data indicates that many Lake Mendota fishes are showing increased reliance on littoral resources following invasion (unpublished NTL-LTER data), an intuitive finding considering the 4-fold increase in zoobenthos biomass. A more thorough integration of the long-term, routine monitoring data available for Lake Mendota would be a natural next step but is beyond the scope of this study.

Our study provides a short-term perspective on what could be a long-term and dynamic future of zebra mussels in Lake Mendota. For example, a prominent concept in invasion biology is the boom–bust dynamic, during which periods of exponential population growth to extreme peak densities are followed by population crashes, leading to temporal variation in invader abundance and impact (Lockwood et al. 2013, Strayer et al. 2017). However, the actual frequency of boom–bust dynamics among invasive species in general and zebra mussels in particular is difficult to study because of the limited availability of long-term data (Strayer et al. 2017, Strayer et al. 2019). Continued long-term monitoring of Lake Mendota is ongoing through the NTL-LTER program, which should track the temporal variability of the zebra mussel population and its impacts. Those data may also better describe ecological linkages between zebra mussels and the pelagic zone, such as phytoplankton abundance, as well as how littoral fishes may be capitalizing on new benthic resources. Those data may also more convincingly assign zebra mussel causation to the benthic changes we observed, which, with only 3 years of data, may be reasonably criticized as natural variation or temporal trends caused by other factors. Further integration of benthic communities into the long-term ecological monitoring of lakes is critical to understanding the relative importance of the pelagic–profundal and benthic–littoral pathways to overall ecosystem function in Lake Mendota and elsewhere, especially as zebra mussels couple these 2 food-web subsystems in an ever-growing number of invaded lakes.

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Author contributions

MJS, MJVZ, LEB, AYK, and RLL designed research. MJS, TPS, PAW, and RLL performed research. MJS wrote the manuscript. MJVZ, LEB, AYK, RLL, TPS, and PAW revised the manuscript.

Disclosure statement

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