OXFORD FEMS

FEMS Microbiology Ecology, 2023, **99**, 1–10

DOI: 10.1093/femsec/fiac149

Advance access publication date: 8 December 2022

Research Article

Impacts of an invasive filter-feeder on bacterial biodiversity are context dependent

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Editor: Martin W. Hahn

Abstract

Bacteria represent most of the biodiversity and play key roles in virtually every ecosystem. In doing so, bacteria act as part of complex communities shaped by interactions across all domains of life. Here, we report on direct interactions between bacteria and dreissenid mussels, a group of invasive filter-feeders threatening global aquatic systems due to high filtration rates. Previous studies showed that dreissenids can impact bacterial community structure by changing trait distributions and abundances of specific taxa. However, studies on bacterial community effects were conducted using water from Lake Michigan (an oligotrophic lake) only, and it is unknown whether similar patterns are observed in systems with differing nutrient regimes. We conducted ten short-term dreissenid grazing experiments in 2019 using water from two eutrophic lake regions—the western basin of Lake Erie and Saginaw Bay in Lake Huron. Predation by dreissenids led to decline in overall bacterial abundance and diversity in both lakes. However, feeding on bacteria was not observed during every experiment. We also found that traits related to feeding resistance are less phylogenetically conserved than previously thought. Our results highlight the role of temporal, spatial, and genomic heterogeneity in bacterial response dynamics to a globally important invasive filter feeder.

Keywords: bacterial biodiversity, filter feeders, freshwater, grazing, invasive species, predation

Introduction

Species invasion is a major problem of the Anthropocene (Vitousek et al. 1997, Dukes and Mooney 1999, Simberloff et al. 2013). In particular, it has been projected to be the biggest driver of biodiversity change in aquatic ecosystems (Sala et al. 2000). Invasive species can change the evolutionary trajectories of native species (Mooney and Cleland 2001, Strauss et al. 2006), alter species diversity (via a host of mechanisms, including allelopathy, predation, and competition) (Lavergne et al. 1999, Levine et al. 2003, Orrock et al. 2008), and modify key ecosystem processes (such as productivity, nutrient cycling) and services (such as food, recreation, and economy) (Pejchar and Mooney 2009, Higgins and Zanden 2010).

Most studies in invasion biology focus on the relationship between invasive species and macrobial biodiversity, even though the association of invasive species and microbes has now been shown to be critical in shaping invasion dynamics and its consequences (Vitousek and Walker 1989, Klironomos 2002, Callaway et al. 2004, Pringle et al. 2009, Bever et al. 2010). The ability of invasive species to form associations with new microbes (Pringle et al. 2009), feedback between invasive species and their environmental microbiome (Klironomos 2002, Callaway et al. 2004, Stinson et al. 2006), and microbe facilitated expansion of the competitive ability and niche-breadth of invasive species (Vitousek and Walker 1989) have been shown as important mechanisms determining the fate of biotic invasions and their impact on ecosystem functioning. Given the ability of invasive species to fundamentally alter ecosystems by shifting bacterial biodiversity and the outsize role of bacteria in controlling nutrient and energy fluxes in ecosystems (Cotner and Biddanda 2002, Falkowski et al. 2008), it is critical that we investigate how invasive species are impacting bacterial biodiversity.

In this study, we focus on the impact of an invasive filter feeder on freshwater systems. Invasive filter-feeders are amongst the most disruptive stressors in freshwater systems globally (Xie and Chen 2001, Sousa et al. 2014). Most notably, invasive dreissenid mussels (IDMs), commonly known as zebra and quagga mussels, are a key threat in many freshwater systems across Europe and North America, including the Great Lakes ecosystems (Zhulidov et al. 2010). IDMs are native to the Ponto Caspian basin and were first brought to North America more than 30 years ago via ballast water discharge into the Great Lakes (Hebert et al. 1989). They now continue to invade freshwater ecosystems worldwide and have spread to more than 30 states in the US (Higgins and Zanden 2010). Once introduced, IDM populations impose a strong ecological selection due to intense filter-feeding (Vanderploeg et al. 2001, 2002, Nalepa and Schloesser 2013). For example: replacement of the native mussel *Lampsilis* by the zebra mussels in Lake St. Clair increased the fraction of the water column cleared per day from 0.03 to 0.45 (Vanderploeg et al. 2002).

Previous research has shown that the filtration stress from IDMs can shift the movement of matter and flow of energy in

Received: August 22, 2022. **Revised:** November 22, 2022. **Accepted:** December 6, 2022

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ecosystems (Higgins and Zanden 2010). Thus, IDMs represent another significant layer of trophic complexity in the ecosystems they invade. It has been shown that they can cause redirection of energy and nutrients from pelagic to littoral zones (Higgins and Vander Zanden 2010; Shen et al. 2018), decline in large suspended particles (Karatayev and Padilla 1997), outbreaks of avian botulism (Yule et al. 2006), and induction of harmful cyanobacterial blooms (Vanderploeg et al. 2001, Sarnelle et al. 2005). Although several of the above studies focused on impacts on specific bacterial species (e.g. *Clostridium botulinum* and *Microcystis aeruginosa*), only a few studies have looked at the impacts of IDMs on overall bacterial abundance and biodiversity (Denef et al. 2017, Props et al. 2018). While some have reported declines in the bacterial abundance due to direct feeding (Frischer et al. 2000, Denef et al. 2017, Props et al. 2018) others have shown increases in the bacterial abundance due to indirect effects from removal of protozoan predators (nanozooplankton) via gazing (Cotner et al. 1995, Findlay et al. 1998). Similarly, the ability of IDMs to promote or impede growth of a specific species, namely, *Microcystis aeruginosa*, appears to be dependent on the system studied, potentially a function of nutrient availability in the system (Vanderploeg et al. 2001, 2002, Raikow et al. 2004, Sarnelle et al. 2005, Knoll et al. 2008). These results highlight that interactions between bacteria and invasive mussels do occur but the exact nature of these interactions remains complex and poorly understood. Expanding beyond the impact on single species to understand how invasive grazers like IDMs impact bacterial communities is critical to understanding how top-down stressors like intensified filter-feeding can (re)shape bacterial biodiversity and exert control on ecosystem-level processes.

Our previous experiments using water from one low nutrient lake (Lake Michigan) that showed that (i) IDMs alter bacterial community composition by decreasing both richness and evenness (Props et al. 2018) and (ii) there appears to be a strong signal for phylogenetic conservation of traits related to grazing resistance/susceptibility at the phylum level (Denef et al. 2017). We also showed that overall chlorophyll *a* removal correlated well with phytoplankton population reduction and the removal rate for 0.7–2 μm fraction was similar to removal of > 2μm fraction (Denef et al. 2017). However, considering the variable effects observed on a single species (*Microcystis aeruginosa)* as an apparent function of lake nutrient levels (Sarnelle et al. 2005, Knoll et al. 2008) or strains found in different environments (Vanderploeg et al. 2013), it is unclear how generalizable the findings from our previous studies are across aquatic systems of varying nutrient regimes. Hence, in this study, we report direct impacts of predation by IDMs on bacterioplankton communities of the western basin of Lake Erie (LE) and Saginaw Bay of Lake Huron (LH) using a quantitative phylogenetic marker (16S rRNA) gene sequencing method. Both of these ecosystems are high nutrient systems that have been plagued by cyanobacterial harmful algal blooms (cHABs) during the summer. They are distinct from each other in the ratio of key nutrients, N and P (Johengen et al. 2013). The western basin of LE has low N:P while Saginaw Bay of LH has high N:P and is more P-limited than LE (Johengen et al. 2013). As sampling included the time period of cHABs occurrence, our data also allowed for further assessment of the role that selective grazing by IDMs might have in promoting and suppressing various cyanobacterial species. In addition, we also evaluated the extent to which grazing impacts observed in the lab play a role in structure overall bacterial community composition *in situ*.

Materials and methods

Feeding experiments

In 2019, we conducted six experiments (6/12, 7/10, 7/25, 8/7, 8/22, 9/6) using water from inner Saginaw Bay (SB) of Lake Huron (LH) and four experiments (7/18, 7/31, 8/13, 9/18) with water collected from the western basin of Lake Erie (LE). Map showing the locations of the sites can be found in the Fig. S1. We chose WE4 and SB14 or SB15 stations as (i) they are part of the NOAA Great Lakes Environmental Research Laboratory long-term monitoring sites, and (ii) have been plagued by harmful cyanobacterial blooms of varying intensities. For LE experiments, both water and quagga mussels were collected from the WLE4 station (41° 49' 35.4" N and 83° 11' 47.4" W). For LH experiments, mussels were collected in inner Saginaw Bay at site SB14 (43° 44' 19.56" N and 83° 38' 25.55" W) or SB15 (43° 45' 40.32" N and 83° 31' 34.68" W) depending on where we could find them before the day of experiment. Water for all SB experiments, except 8/7, was collected from the SB15 station. Since the 8/7 experiment required more water and demanded multiple trips of our small boat in a limited amount of time, water for this day was collected from a site closer to the boat launch at the southern end of the bay. Quagga mussels and water (~ 450 L) were collected from the lakes one day prior to the experiment and mussels were cleaned of debris before reacclimation to the ambient lake water overnight in one or two 90 L drums and transferred to a 40-L aquarium of ambient lake water ~2 h before use in the feeding experiments to ensure that mussels were in digestive equilibrium with their food (Tang et al. 2014). At the time of transfer to the 40-L aquarium the mussels were sorted into mesh baskets to enable easy transfer to the feeding buckets described below. Empty mesh baskets were also included for control treatments.

All experiments, except for the ones conducted on 8/7 and 8/13, consisted of 3 controls and 4 mussel treatments. Since the water for the 8/7 and 8/13 experiments had high chlorophyll concentration, we decided to include a whole water and a diluted water sample type (whole water + 0.2 μm filtered lake) to bring down the chl-a to 4 μg/L, a value below the incipient limiting concentration so that that we could observe a feeding effect that would have been masked at higher concentrations. Thus, for these experiments, we ended up including 2 replicates for control and experimental treatments for each sample type (whole water and diluted). For the downstream analysis, however, control and quagga treatments from both sample types were considered together since the bacterial community composition within the treatment groups is the same and increasing sample size allowed for a more robust statistical quantification.

Feeding experiments were conducted in 20-L high-density polyethylene (HDPE) buckets that had been cleaned using bleach followed by milliQ water rinses, dried, and then filled with 16 L of lake water. Quagga buckets received 20–25 mussels previously sorted into mini baskets to allow for attachment. Average lengths and weights of mussels among experiments ranged between 20 and 21 mm and 13–15 mg dry weight/individual. Control buckets received empty mini-baskets. Once the mussels were added to the treatment buckets, we visually observed them to record the time when mussels opened their siphon as this indicates active feeding and thus, the beginning of the experiment. This occurred between 10 and 38 min. We then allowed the experiments to run anywhere between 2 to 4 h depending on how long it took the mussels to deplete the total chlorophyll by 30%–60% monitored every hour by taking a 25-mL sample for immediate spectral

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fluorometric analysis with a bbe-Moldaenke FluoroProbe II. On the days when chlorophyll depletion was absent or very low, we let the experiment run for ∼ 4 h. Removal rate for bacteria with high nucleic acid content has been estimated to be 43000 ± 3000 cells ml $^{-1}$ h $^{-1}$ (Props et al. 2018). Previous studies have also shown that IDM feeding rates are high for particles in the 5–40 μm size-class (Tang et al. 2014) although food quality is an important factor determining clearance rates (Vanderploeg et al. 2001).

Filtration and DNA extraction

At the end of each experiment, 2 L water was sampled from each bucket in sterile Nalgene bottles for bacterial community analysis. Bacteria were then collected on 47 mm 0.22 μm PES membrane Millipore Express filters fitted to Pall polycarbonate filter holders using portable Masterflex peristaltic pumps. The pumps were allowed to run for 10 min and the volume of water filtered was recorded (refer to the metadata file for volume information). After 10 min, filters were folded using sterile forceps, transferred into sterile cryovials, and flash frozen in liquid nitrogen before being stored in the −80°C freezer. At the end of the field season, DNA was extracted from the filters with the DNeasy Blood & Tissue kit using the modified Qiagen AllPrep Universal kit protocol (McCarthy et al. 2015), which used the sequence of procedures and buffers of the AllPrep DNA/RNA kit without RNA extraction.

Quantitative 16S rRNA gene sequencing and analysis

To enable conversion of 16S rRNA gene relative abundance to absolute abundance measures, we added a spike-in standard mix from ATTC (3 Strain Tagged Genomic DNA Even Mix—MSA 1014) containing engineered 16S rRNA gene tags of *Escherichia coli, Clostridium perfringens,* and *Staphylococcus aureus* to the extracted DNA prior to sequencing. The stock solution of this mix contains 1090909 genome copies per μl. Based on our prior optimization and the amount of DNA in our samples, we calculated that the percentage of reads recovered by adding 0.05 μl of the stock spike-in mix per sample would yield sufficient reads to make a proper estimation of the absolute read counts in our samples without overwhelming the sample with spike-in reads. Thus, we performed serial dilution such that 1 μL of the diluted solution contained the same number of copies as 0.05 μL of the concentrated spike-in solution and added it to each sample.

After adding the spike-in solution, we sequenced the V4 region of the 16S rRNA gene using the 515F/806R primer set (developed by Kozich et al. 2013) at the Microbiome Core at the University of Michigan Medical School, Ann Arbor, MI using the MiSeq Reagent Kit v2 (500-cycles) (Cat. number: MS-102–2003). Reads were mapped to the reference spike-ins using bwa mem with default parameters (Li and Durbin 2009). The resulting bam files were processed with bbtools pileup.sh to count the number of spike-in reads mapped to each reference. Then, bbtools filter.sh was used to remove reads that mapped to the spike-ins (Bushnell et al. 2017). Operational taxonomic units (OTUs) were constructed with mothur v1.45.3 (Schloss et al. 2009) and assigned taxonomy using TaxAss with both silva v132 and the freshtrain2018 database curated by the McMahon Lab as references (https://github.com/McMahonLab/TaxAss). Raw sequence data is available on the NCBI SRA through BioProject ID PRJNA909839.

All downstream analyses were performed using the absolute 16S rRNA gene count data estimated using the spike-in data. Since we knew the number of genome copies added and recovered for each sample in the sequencing run, absolute counts for OTUs were calculated using mark-recapture method, a commonly used approach in ecology to estimate population sizes. We converted the number of reads into absolute counts using the following formula:

$$N_{xi}\ otu = [N_i\ eng\ X\ R_{xi}\ otu]\ / R_i\ eng$$

where

N_{xi} otu = number of estimated 16S rRNA gene copies of OTUx in sample *i*

N_i eng = number of engineered 16S rRNA gene copies added to sample *i*

R_{xi} otu = number of reads recovered for OTUx in sample *i*

R_i eng = mean number of reads recovered for engineered 16S rRNA genes in sample *i*

To calculate R_i eng, we took the average of the recovered tags for all three species—*E.coli, S.aureus, C.perfringens*—as long as they were within three standard deviations and considered any value outside this range as an outlier. Finally, we transformed the N_{xi} otu values for each OTU by using the volume information recorded for each experimental treatment.

Statistical methods

We performed all statistical analyses in Rstudio (version 1.4.1103) using tidyverse, phyloseq, vegan, lme4, lmerTest, ggplot packages and custom functions written by Michelle Berry (Berry et al. 2017a). Raw mothur output files, metadata, and reproducible R markdown files are available on the github page <https://github.com/nikeshd/LE_SB_feedingExperiments_2019). Since read counts for OTUs were already adjusted using spike-in information, we did not scale them. For the total number of 16S rRNA gene counts comparison, we assumed negative binomial distribution after performing dispersion test on our data, which indicated overdispersion, and fit a generalized linear model to see if the mussels treatment was significant in predicting the response variable. For the alpha-diversity analysis, we fit a Linear Mixed-Effects Model using the lmer function from the lme4 package with date as the random variable. For beta-diversity analyses, we performed PERMANOVA tests using the adonis function from the vegan package to see if the centroids and dispersion of groups were different. Finally, to determine how feeding was similar or different for each OTU based on date, we performed an ANOVA test (likelihood ratio test) between an interactive model (which allowed interaction between treatment and date) and an additive model (which restricted varying date effects) for the top 1% OTUs. Detailed methods for statistical analyses and figure generation can be found on the github page.

Results

In 2019, we performed ten quagga mussel feeding experiments with water collected from Lake Erie (LE, four experiments) and Lake Huron (LH, six experiments) to look at the direct impacts of grazing on bacterial biodiversity. Quagga mussels were observed to be open with feeding siphons extended during all experiments, and we measured variation in feeding activity (due to variation in rates of water filtering and rates of rejection of ingested food as pseudofeces) by measuring changes in chlorophyll *a*.

Impacts on chlorophyll a levels

To assess feeding levels on the combined eukaryotic and cyanobacterial phytoplankton community in each experiment, we monitored declines in chlorophyll *a* in the quagga mussel treat-

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ment relative to the control. We observed more chlorophyll *a* removal in LE (up to 47%) than LH experiments (up to 12%) and significant declines in two out of four LE experiments and two out of six LH experiments (Table 1).

Impacts on total 16S rRNA gene copy numbers

We quantified total 16S rRNA gene copy numbers by leveraging the recovery of spike-in controls which were added to samples in known quantities prior to sequencing. As we found that the total 16S rRNA gene count data was overdispersed for both lakes (*P*-value < 0.05), we compared 16S rRNA gene copy abundance between quagga mussel treatment and controls by fitting a generalized linear mixed model (GLMM). The model assumed a negative binomial distribution of the data rather than a Poisson distribution as the Akaike information criterion (AIC) for the negative binomial models was much lower (AIC for LE = 605 vs 178102 and AIC for LH = 870 vs 88992). Results from the GLMM indicated that quagga mussels caused a decline in the total 16S rRNA gene copies via grazing (Fig. 1) and the mussel treatment was significant in predicting the total number 16S rRNA gene copies in both LE (*P*-value = 0.0007) and LH (*P*-value = 0.004).

Impacts on alpha diversity

We used linear mixed effects models (LMEM) with date as a random effect to assess the impacts of quagga mussels on observed richness and diversity (based on the Inverse Simpson index)—two different approaches to conceptualizing alpha diversity. We found that quagga mussels decreased Inverse Simpson (Fig. 2, both *P*-value < 0.05) but not observed richness (Fig. S3, both *P* values > 0.1) estimates of bacterial communities in both lakes. Estimated variance of the random effect of date (calculated by dividing the variance explained by date by variance explained by residuals + date) for Inverse Simpson was low for Lake Erie (~6%) but very high (~88%) for Lake Huron. Additionally, the variance parameters indicated with 95% confidence that the difference between Inverse Simpson values of quagga and control treatments was 4.3–11.4 for LH and 8.2–15.7 for LE.

Impacts on bacterial community composition

PERMANOVA (permutational multivariate analysis of variance) analyses based on the Bray–Curtis dissimilarity metric showed that quagga mussels significantly altered bacterial community composition for only 3 out of 10 experiments, all of which were performed using water collected from Lake Erie (Table 2, Fig. 3). The one LE experiment (7/31/19) with no significant shift in composition was the one with the lowest effect on chlorophyll *a* level (Table 1) and was marked by a more distinct bacterial community composition relative to other LE experiments (Fig. 3). Bacterial community composition of control and quagga mussel treatments were not significantly different for any of the LH experiments. LH bacterial community composition was also distinct from LE water samples (Fig. S4). For the LE dates where we did see a significant shift in bacterial community composition, quagga mussel treatment explained 50%–70% of the variation.

Impacts of feeding on bacterial OTUs

To assess whether feeding rate was a function of OTU abundance, we performed linear regressions with $log2\frac{mean\ quagga\ mussel\ treatment\ abundance}{mean\ control\ treatment\ abundance}$ as the response variable and $log10(control\ treatment\ abundance)$ as the independent variable for LE experiments. We ran the regressions two times—once for the most abundant OTUs (ones that ranked in the top 200 for each experiment) (Fig. 4) and another time for all OTUs including the rare ones (Fig. S5). For the most abundant OTUs (top 200), we did not observe any significant trend (*P*-values > 0.1) for any experiment. When we included all OTUs, we saw a significant negative relationship between abundance and removal by quagga mussel feeding (*P*-values < 0.05) for 3 out of 4 experimental dates (all except 7/31/19) (Fig. S5).

We also assessed OTU level feeding resistance/susceptibility to quagga mussels for the top OTUs in LE experiments conducted on 7/18/19, 8/13/19, and 9/18/19. We then categorized these OTUs based on whether their response to grazing by quagga mussels was contingent on date (Fig. S6A) or consistent across experiments without any interaction with date (Fig. S6B). We found that OTUs within a given phylum can vary in terms of their resistance/susceptibility to grazing. Furthermore, OTUs whose response to grazing depended on interaction with date were distributed across several phyla (Fig. S6B).

Relation between cyanobacteria abundance and feeding rates

The removal in chlorophyll *a* by quagga mussels was negatively correlated with the total number of cyanobacterial 16S rRNA gene copies detected and to the number of *Microcystis* 16S rRNA gene copies detected (Fig. 5). Due to the observed negative relationship between total cyanobacterial abundance and quagga mussel feeding, we assessed the extent and variability of mussel feeding on cyanobacteria OTUs whose mean control abundance was more than 750 counts, which amounts to 0.05% of the average total sample counts. We did not find any significant difference between the mean control and quagga mussel treatment abundance values for any of these OTUs based on t-tests. However, based on qualitative observation, we saw that *Pseudanabaena* and *Aphanizomenon* OTUs tend to be susceptible to feeding, *Microcystis* and *Snowella* OTUs tended to be resistant to feeding, and *Cyanobium* OTUs demonstrate the most variation depending on the lake and date (Fig. 6).

Discussion

Although invasive filter-feeders like zebra and quagga mussels are widespread and represent an added layer of trophic complexity in freshwater ecosystems, their impacts on the overall bacterial biodiversity has received very little attention. Bacteria represent a functionally and metabolically highly diverse group of organisms (Falkowski et al. 2008) and their role in linking trophic structure to the flow of energy has been recognized in ecology for a long time now (Lindeman 1942). As such, if we want to better understand how the rapid spread of invasive filter-feeders is impacting freshwater ecosystems, we argue that it is important to investigate the impacts of intensified filter-feeding on the freshwater microbiome. Our group previously showed that predation by quagga mussels directly impacts bacterial abundance and community composition (Denef et al. 2017, Props et al. 2018). However, it remained unclear if those findings were generalizable as the study was limited to one oligotrophic system, namely Lake Michigan (LM). In this study, we include two additional lake ecosystems (LE and LH), both of which are eutrophic but differ in nutrient profiles. We found that the quagga mussels altered overall diversity but the effects of predation at the individual experiment level varied over time and depending on the lake system, suggesting a complex context-dependence of the impact of IDMs on aquatic systems.

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Table 1. The percentage of chlorophyll *a* (chl *a*) removed was calculated by dividing the difference between the mean final chl *a* reading of the control and quagga treatments by the mean final chl *a* reading of the control treatments. P and t-stat values from t-tests are reported. The asterisk indicates significant difference in the final mean chl *a* readings between control and quagga treatments.

Chlorophyll a summary

Lake	Date	Control final chl *a*	Quagga final chl *a*	t-stat	P-value	Removal %
Erie	7/18/19	7.2	3.9	30.1	**0.001***	46.1
Erie	7/31/19	47.1	44.1	1.2	0.286	6.2
Erie	8/13/19	4.0	3.6	0.8	0.575	9
Erie	9/18/19	2.8	1.5	13.4	**< 0.001***	47.7
Huron	6/12/19	8.5	7.5	4.7	**0.005***	10
Huron	7/10/19	8.8	8.7	0.3	0.771	1.4
Huron	7/25/19	21.0	20.8	0.6	0.549	0.8
Huron	8/7/19	11.6	10.2	9.4	**0.040***	12.3
Huron	8/22/19	14.6	15.0	-0.7	0.531	-2.5
Huron	9/6/19	24.7	23.2	3.3	0.064	6.1

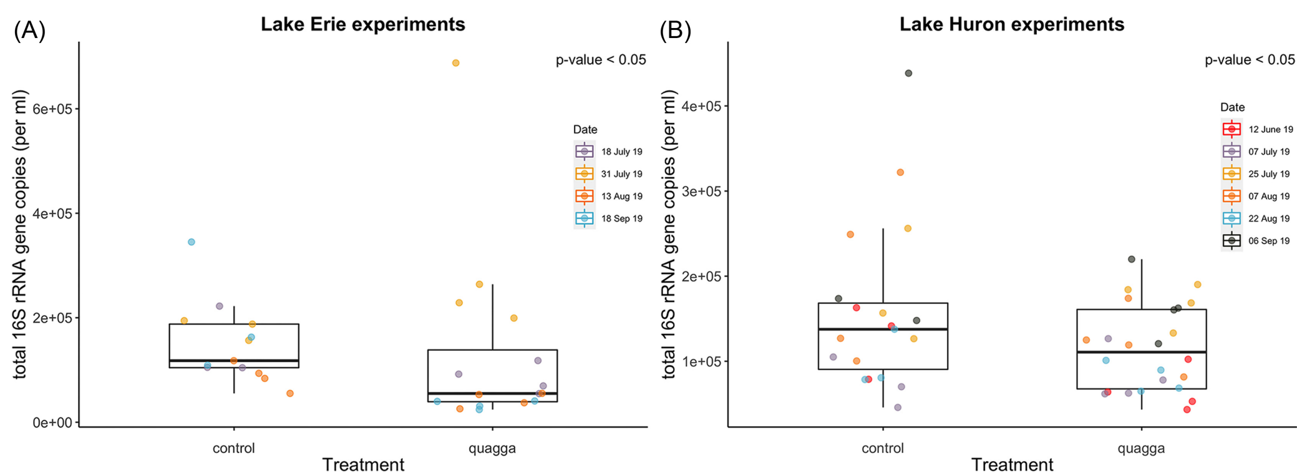

Figure 1. Direct effects of feeding by quagga mussels on bacterial abundance. Each circle represents the total 16S rRNA gene copies detected per mL water filtered at the end of each experiment from a control or a quagga mussel treatment replicate. Water was collected from **(A)** Lake Erie or **(B)** Lake Huron in 2019. Colors differentiate experiments by date.

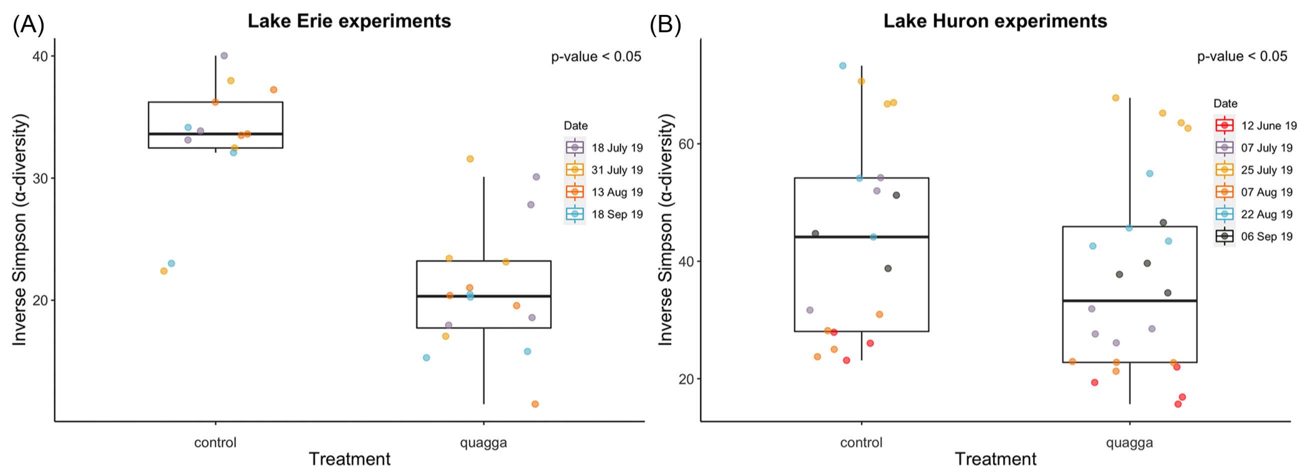

Figure 2. Direct effects of feeding by quagga mussels on the alpha diversity of bacterial communities of **(A)** Lake Erie and **(B)** Lake Huron. Inverse Simpson, used here, is an index that measures alpha diversity of a given community by incorporating both richness and evenness, with higher values indicating higher diversity. Each circle here represents a control or a quagga mussel treatment replicate from the feeding experiments conducted on different dates (differentiated by color).

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Table 2: R^2 and P values from PERMANOVA (permutational multivariate analysis of variance) analysis based on the Bray–Curtis dissimilarity between control and quagga mussel treatment communities for each experiment conducted using water collected from Lake Erie and Lake Huron. The asterisk indicates significant difference in the centroids and dispersion of control and quagga mussel treatment groups (shown in Fig. 3) for that experiment.

Permutational multivariate analysis of variance (PERMANOVA) analysis			
Lake	Date	R^2	P-value
Erie	7/18/19	0.49	**0.024***
Erie	7/31/19	0.30	0.119
Erie	8/13/19	0.54	**0.024***
Erie	9/18/19	0.69	**0.033***
Huron	6/12/19	0.46	0.074
Huron	7/10/19	0.19	0.322
Huron	7/25/19	0.13	0.583
Huron	8/7/19	0.19	0.274
Huron	8/22/19	0.22	0.342
Huron	9/6/19	0.23	0.244

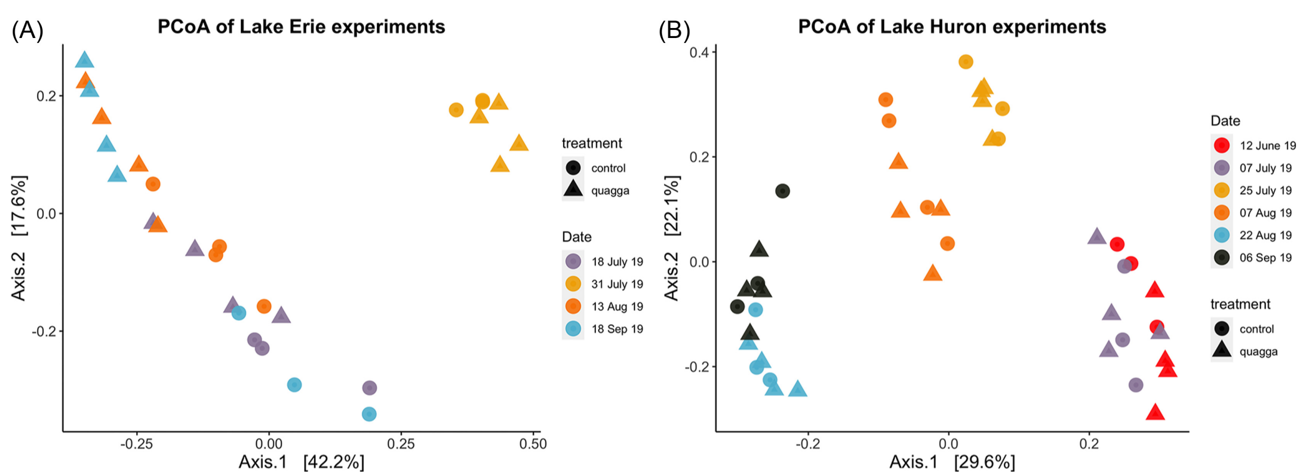

Figure 3. Direct effects of feeding by quagga mussels on the community composition of bacterioplankton from **(A)** Lake Erie and **(B)** Lake Huron. Circles and triangles represent control and quagga treatments, respectively. Colors represent different dates on which feeding experiments were performed. A PCoA with control samples from experiments from both lakes represented in a single analysis is provided in Fig. S4.

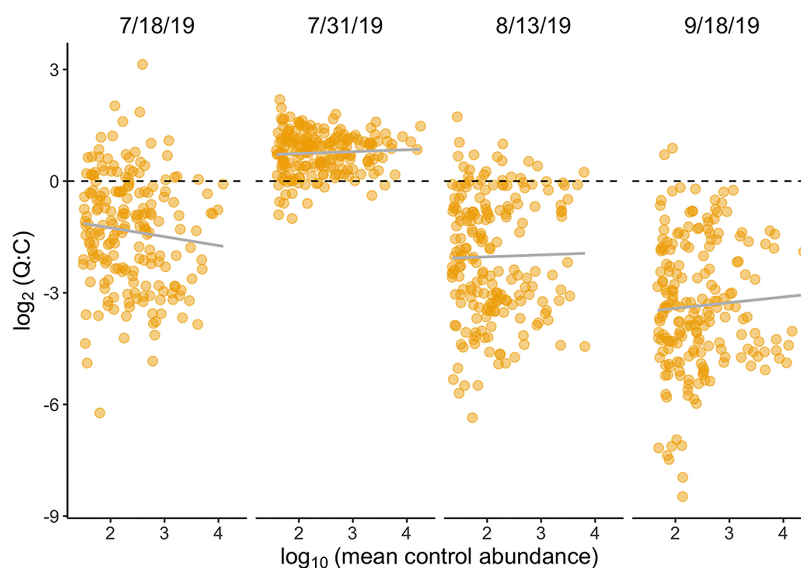

Figure 4. Assessment of a relationship between OTU abundance and removal by quagga mussels. Linear regression of log mean abundance in the control treatments as the independent variable (x-axis) and log of the ratio of mean quagga mussel treatment abundance: mean control treatment abundance as the dependent variable (y-axis) for Lake Erie feeding experiments. Each dot represents an OTU. OTUs that ranked as top 200 based on mean control abundance were selected for each experimental date (full data set in Fig. S5). P-values were > 0.1 for all regressions, suggesting that abundant taxa are not being preferentially consumed (or disproportionately escaped predation) by quagga mussels.

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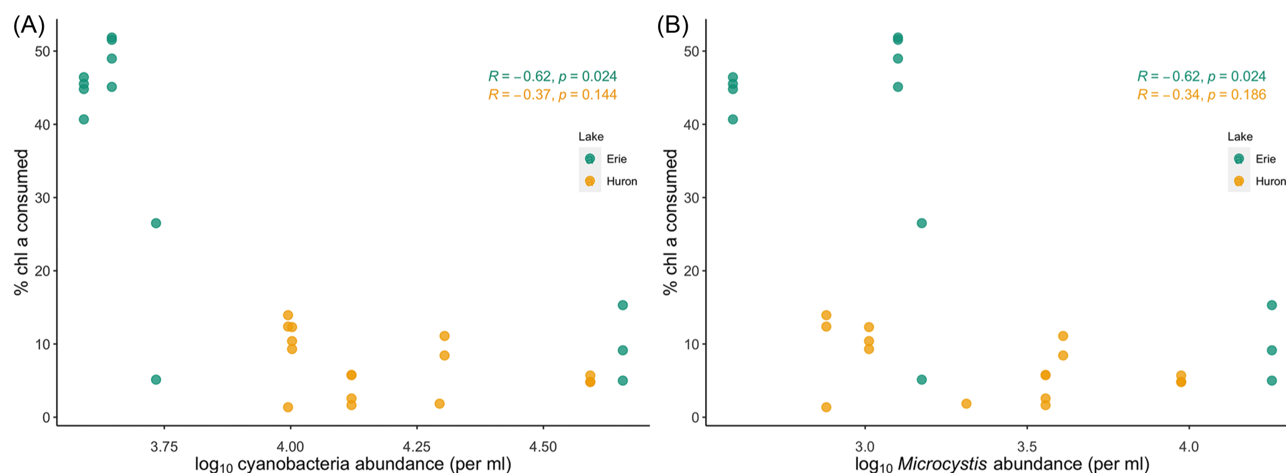

Figure 5. Linear regression of log mean abundance of **(A)** cyanobacteria and **(B)** *Microcystis* in the control treatment as the independent variable (X-axis) and % chlorophyll removed in the quagga treatments as the dependent variable (Y-axis).

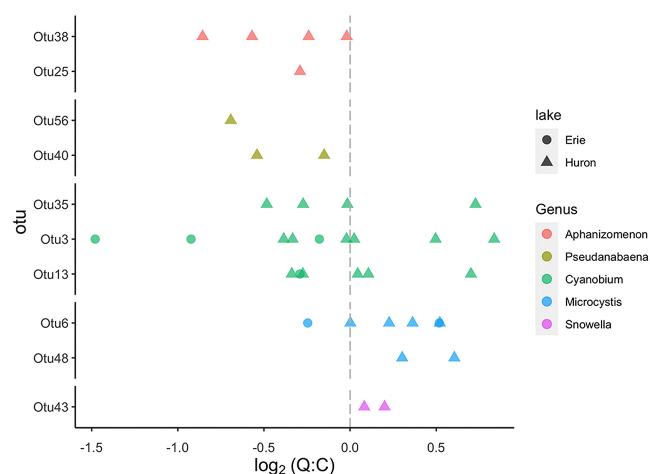

Figure 6. OTU level feeding response of cyanobacteria OTUs with more than 750 gene copies (> 0.05% of the average total number of 16S rRNA gene copies detected per sample). Each dot represents a $\log_2$ fold change of that corresponding OTU during one of the Lake Erie (circle) or Lake Huron (triangle) experiments. OTUs are color coded by genus level classification.

Grazing by IDMs decreases overall bacterial abundance and diversity

Our hypothesis that the exposure of bacterioplankton to intensified filter-feeding would lead to a decline in the total bacterial abundance was supported by our observations in both lakes (Fig. 1). This finding extends observations in an oligotrophic lake system (Denef et al. 2017, Props et al. 2018), and short term experiments using water from the Hudson River, NY (Frischer et al. 2000), though is in contrast to the long term *in situ* effects observed in the Hudson River (Findlay et al. 1998). The long term Hudson River study linked the observed doubling of bacterial numbers to indirect effects due to the removal of planktonic predators of bacteria by zebra mussels. Our feeding experiments ranged between 2 to 4 h. Hence, all the changes we observed were due to direct impacts from mussel predation, as we previously assessed by tracking changes in abundance across all plankton functional groups (Denef et al. 2017).

Consistent with previous results, we observed a reduction in diversity (Fig. 2), although in this study it seemed only driven by a reduced evenness rather than by a reduction in evenness and richness observed before (Props et al. 2018). These effects on diversity, which also resulted in shifts in community composition (Fig. 3; Table 2), were the result of selective removal of some taxa, whereas others remained unchanged. Which specific taxonomic groups were affected was only partially comparable to what we observed before and some inconsistencies arose. Previously, we had observed strong phylogenetic conservation of traits related to grazing resistance/susceptibility apparent at the phylum level (Denef et al. 2017), related to niche partitioning between particle-association and a free-living life style (Schmidt et al. 2016), as particle-associated and larger bacteria are more likely to be consumed by dreissenid mussels than free-living bacteria. Evasion of grazing by *Betaproteobacteria* (OTU 2) and *Actinobacteria* (OTU 1, OTU 7, OTU 8, and OTU 9), both of which are overrepresented in free-living habitats (Schmidt et al. 2016, Denef *et al.* 2017), and removal of *Armatimonadetes* and *Verrucomicrobia* was in line with observations in Lake Michigan. Response of OTUs belonging to *Planctomycetes*, *Cyanobacteria*, *Alphaproteobacteria* and *Bacteroidetes* phylum were at odds with previous observations. To some extent this can be explained by the nature of particles in the studied systems. In eutrophic systems, the particle fraction is often dominated by colonial cyanobacteria, while in oligotrophic systems, colonial cyanobacterial are not dominant members of the phytoplankton community and in general pico- and nanoplankton become important offshore components of the phototrophic and heterotrophic communities (Carrick et al. 2015). In addition, for contrasting Lakes Michigan (LM) with LE and SB, IDMs in the case of LM were likely responsible for shifting the community toward dominance by small phytoplankton, particularly picoplankton, whereas their filtering activities in LE and SB shifted the community toward dominance by microplankton in the form of colonial cyanobacteria (Vanderploeg et al. 2002, 2012, Vanderploeg et al. 2009, Carrick et al. 2015). Study of *Microcystis* in Lake Taihu has shown *Plantomycetes* to be associated with mucilaginous cyanobacterial blooms (Cai et al. 2013). Similarly, *Bacteriodetes* have also been shown to increase in abundance when there is high external dissolved organic carbon (DOC) or alga-derived DOC as would be found in eutrphophic systems (Newton et al. 2011, Cai et al. 2013). Association of these phyla with cyanobacterial blooms may explain why despite making up a large portion of the particle-associated fraction (Newton et al. 2011), they exhibited a varied response to mussel feeding in experiments conducted with wa-

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ter collected from eutrophic ecosystems. Our results indicate a shallower depth of trait conservation than what we previously reported, and context-dependence of grazing effects likely driven by the nature of particulate matter.

Environmental and/or genetic heterogeneity drives OTU level response to IDM grazing

We also noted that while some taxa responded consistently to grazing across experiments in LE and LH, many taxa responded differently to grazing depending on the date of the experiment (Fig. S6). One explanation is that OTUs based on 97% sequence identity of the 16S rRNA gene do not provide enough genetic resolution to delineate bacterial lineages that are ecologically distinct and that species- or strain-level successional patterns are likely occurring at the temporal and spatial scales that we sampled across (Woodhouse et al. 2016, Berry et al. 2017b). Another explanation for this variation in feeding response at the OTU level is that traits related to feeding resistance/susceptibility are expressed based on the interplay between the OTU type and other a/biotic factors, in other words due to phenotypic plasticity in grazing resistance traits in function of environmental conditions (Lima and Dill 1990, Agrawal 2001, Werner and Peacor 2003). As an example, literature on the interactions between grazers and *Microcystis*, known for high levels of genotypic and phenotypic variation, has shown that grazing can be selective in nature depending on the toxin level (Vanderploeg et al. 2001, White et al. 2011, Chislock et al. 2013), colony size/morphology (Dionisio Pires et al. 2005, Tang et al. 2014, White and Sarnelle 2014), and genotype (Sarnelle et al. 2005, White et al. 2011, Chislock et al. 2013, Ger and Panosso 2014, Ger et al. 2016). Thus, both mechanisms are likely at play to create the feeding resistance/susceptibility trait variation that we observe in our experiments. Furthermore, it should be noted that access to a larger size range, high population densities, and varying levels of sensitivity to toxic *Microcystis* strains makes IDM grazing different to grazing by other common aquatic zooplankton (Vanderploeg et al. 2001).

High levels of cyanobacteria and *Microcystis* correlates with overall reduction in feeding

In contrast to our previous findings in an oligotrophic system (Denef et al. 2017, Props et al. 2018), several individual experiments saw limited to no effect on bacterial abundance, diversity, and community composition (Table 2). This was in line with limited feeding activity based on measured changes in chlorophyll *a* levels (Table 1). Zebra and quagga mussels are known to adjust feeding activity based on food quality and quantity (Vanderploeg et al. 2001, Vanderploeg et al. 2009, Johengen et al. 2013), specifically the presence of *Microcystis,* a cyanobacterial genus that is a dominant member of many toxic algal blooms (Fishman et al. 2010, De Stasio et al. 2014, Berry et al. 2017a). Selective rejection by dreissenid mussels of *Microcystis* has been experimentally shown to contribute to the worsening of *Microcystis*-dominated cyanobacterial blooms following the invasion by dreissenid mussels in Saginaw Bay of LH and the western basin of LE (Vanderploeg et al. 2001). Yet, there have been conflicting reports on the ability of dreissenid mussels to consume *Microcystis* in the literature, with some reports indicating avoidance by dreissenid mussels (Vanderploeg et al. 2001), while others showed declines of *Microcystis* following the IDM invasion (Bastviken et al. 1998, White et al. 2011, Waajen et al. 2016). Our data indicated *Microcystis* evaded significant removal by quagga mussels across all experiments, and high levels of *Microcystis* correlated with low feeding rates on the overall phyto- and bacterioplankton community (Fig. 5B).

However, we also observed that feeding by quagga mussels was strongly reduced for LH but not for LE experiments even when the total *Microcystis* counts for samples from the two lakes were about the same. For these samples, the total cyanobacterial counts were much lower for LE samples compared to LH samples. Indeed, total cyanobacterial abundance showed a clear pattern in reduced feeding by quagga mussels with increased cyanobacterial levels (Fig. 5A). Taken together, these observations suggest that although higher abundance of *Microcystis* correlates with reduction in mussel feeding, other members of the cyanobacterial community are also likely important in explaining the observed shifts in the feeding behavior of quagga mussels. We observed varied responses across cyanobacterial OTUs that indicated taxa other than *Microcystis* may contribute to the feeding response of dreissenid mussels, in particular certain abundant *Cyanobium* OTUs.

Grazing by IDMs is not the primary force shaping bacterial community composition *in situ*

OTUs belonging to acI (OTU 1, OTU 7, OTU 9), betI (OTU 2), bacV (OTU 21), Nostocaceae (OTU 25), and Microcystaceae (OTU 6) family were dominant members of the bacterial community. We evaluated the hypothesis whether taxa with high abundance in our samples originating from lakes that have high densities of quagga mussels are either (1) less susceptible to predation due to adaptive grazing resistance traits that result in a higher abundance in the lake or (2) are more susceptible to predation due to higher encounter frequency. We saw a lack of significant positive or negative correlation based on the regressions of control abundance and $\log_2$ fold change for the top 200 OTUs in our LE experiments (Fig. 4). This suggests that grazing resistance traits are distributed across high and low ranked OTUs, and that the direct effects of IDM grazing we observe in the lab are not the dominant factors shaping bacterial community composition *in situ*. We saw a significant negative relationship when we included all OTUs but this relationship was driven mainly due to the apparent increase of rare OTUs in the quagga mussel treatments relative to the controls, most likely due to stochastic factors of sampling. Specifically, the removal of bacteria by quagga mussel feeding makes it more likely for rare OTUs to be sampled more often as a high number of cells from the abundant OTUs has been removed from the sample.

Previous analyses of quagga mussel predation at the OTU level was based on relative abundance (Denef et al. 2017) and hence, interpretation of the results were limited to comparison with predation pressure experienced by the average bacterium. Since we used quantitative spike-in methods in this study, we can now say that decrease in abundance or lack thereof suggests whether the OTUs are truly being eaten by dreissenid mussels or not. We noted that the number of 16S rRNA gene copies recovered appeared to be lower than expected based on the number of cells observed in these systems (Olapade 2018). As our spike-in controls were added after extraction this indicated relatively low extraction efficiencies. Spike-ins prior to extraction would allow for a control on extraction efficiencies, especially variation between samples (Satinsky et al. 2013). In this context, we interpret the increase in 16S rRNA gene copies in the quagga mussel treatment relative to the control across most OTUs observed in the July 31 experiment in Lake Erie as an experimental artifact, most likely extraction biases leading to higher DNA recovery in the quagga mussels treatments relative to the control. This is because we did not see evidence of active growth of the phytoplankton (Table 1).

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Conclusion and outlook

Our study highlights that the impacts of predation by invasive filter-feeders like quagga mussels on bacterial biodiversity is not the same across ecosystem types. Nutrient status of the system, temporal dynamics of bacterial populations, strain-level heterogeneity, and other a/biotic factors all play a role and need to be considered if we want to better understand how one of the most deleterious species is impacting the primary producers and decomposers of the aquatic food web. Trait-based approaches that will help identify functional traits underpinning grazing resistance/susceptibility will be important in linking community composition shifts induced by intensified filter-feeding to modified ecosystem processes such as carbon cycling and toxin production.

Acknowledgments

This work was supported by funding from the NOAA Great Lakes Omics program distributed through the UM Cooperative Institute for Great Lakes Research (NA17OAR4320152 to V.J.D.), through the NOAA Cooperative Agreement with the Cooperative Institute for Great Lakes Research (CIGLR) at the University of Michigan (NA17OAR4320152), and the National Science Foundation (Division of Environmental Biology-1737680) to VJD. This is Great Lakes Environmental Research Laboratory Contribution Number 2015 and CIGLR contribution number 1204.

Supplementary data

Supplementary data are available at *FEMSEC* online.

Conflict of interest statement. None declared.

References

Agrawal AA. Phenotypic plasticity in the interactions and evolution of species. *Science* 2001;**294**:321–6.

Bastviken DTE, Caraco NF, Cole JJ. Experimental measurements of zebra mussel (Dreissena polymorpha) impacts on phytoplankton community composition. *Freshwater Biology* 1998;**39**:375–86.

Berry MA, Davis TW, Cory RM *et al.* Cyanobacterial harmful algal blooms are a biological disturbance to Western Lake Erie bacterial communities. *Environ Microbiol* 2017a;**19**:1149–62.

Berry MA, White JD, Davis TW *et al.* Are oligotypes meaningful ecological and phylogenetic units? A case study of microcystis in Freshwater Lakes. *Front Microbiol* 2017b;**08**.

Bever JD, Dickie IA, Facelli E *et al.* Rooting theories of plant community ecology in microbial interactions. *Trends Ecol Evol* 2010;**25**:468–78.

Bushnell B, Rood J, Singer E. BBMerge – Accurate paired shotgun read merging via overlap. *PLoS One* 2017;**12**:e0185056.

Cai H-Y, Yan Z, Wang A-J *et al.* Analysis of the attached microbial community on mucilaginous cyanobacterial aggregates in the eutrophic Lake Taihu reveals the importance of planctomycetes. *Microb Ecol* 2013;**66**:73–83.

Callaway RM, Thelen GC, Rodriguez A *et al.* Soil biota and exotic plant invasion. *Nature* 2004;**427**:731–3.

Carrick HJ, Butts E, Daniels D *et al.* Variation in the abundance of pico, nano, and microplankton in Lake Michigan: historic and basin-wide comparisons. *J Great Lakes Res* 2015;**41**:66–74.

Chislock MF, Sarnelle O, Jernigan LM *et al.* Do high concentrations of microcystin prevent Daphnia control of phytoplankton? *Water Res* 2013;**47**:1961–70.

Cotner JB, Biddanda BA. Small players, large role: microbial influence on biogeochemical processes in pelagic aquatic ecosystems. *Ecosystems* 2002;**5**:105–21.

Cotner JB, Gardner WS, Johnson JR *et al.* Effects of zebra mussels (Dreissena polymorpha) on bacterioplankton: evidence for both size-Selective consumption and growth stimulation. *J Great Lakes Res* 1995;**21**:517–28.

De Stasio BT, Schrimpf MB, Cornwell BH. Phytoplankton communities in Green Bay, Lake Michigan after invasion by dreissenid mussels: increased dominance by cyanobacteria. *Diversity* 2014;**6**:681–704.

Denef VJ, Carrick HJ, Cavaletto J *et al.* Lake bacterial assemblage composition is sensitive to biological disturbance caused by an invasive filter feeder. *mSphere* 2017;**2**:e00189–17.

Dionisio Pires LM, Bontes BM, Van Donk E *et al.* Grazing on colonial and filamentous, toxic and non-toxic cyanobacteria by the zebra mussel Dreissena polymorpha. *J Plankton Res* 2005;**27**:331–9.

Dukes JS, Mooney HA. Does global change increase the success of biological invaders? *Trends Ecol Evol* 1999;**14**:135–9.

Falkowski PG, Fenchel T, Delong EF. The microbial engines that drive earth's biogeochemical cycles. *Science* 2008;**320**:1034–9.

Findlay S, Pace ML, Fischer DT. Response of heterotrophic planktonic bacteria to the zebra mussel invasion of the tidal Freshwater Hudson River. *Microb Ecol* 1998;**36**:131–40.

Fishman DB, Adlerstein SA, Vanderploeg HA *et al.* Phytoplankton community composition of Saginaw Bay, Lake Huron, during the zebra mussel (Dreissena polymorpha) invasion: a multivariate analysis. *J Great Lakes Res* 2010;**36**:9–19.

Frischer ME, Nierzwicki-Bauer SA, Parsons RH *et al.* Interactions between zebra mussels (Dreissena polymorpha) and microbial communities. *Can J Fish AquatSci* 2000;**57**:591–9.

Ger KA, Faassen EJ, Pennino MG *et al.* Effect of the toxin (microcystin) content of Microcystis on copepod grazing. *Harmful Algae* 2016;**52**:34–45.

Ger KA, Panosso R. The effects of a microcystin-producing and lacking strain of Microcystis on the survival of a widespread tropical copepod (Notodiaptomus iheringi). *Hydrobiologia* 2014;**738**:61–73.

Hebert PDN, Muncaster BW, Mackie GL. Ecological and genetic studies on Dreissena polymorpha (Pallas): a new mollusc in the Great Lakes. *Can J Fish AquatSci* 1989;**46**:1587–91.

Higgins SN, Zanden MJV. What a difference a species makes: a meta–analysis of dreissenid mussel impacts on freshwater ecosystems. *Ecological Monographs* 2010;**80**:179–96.

Johengen TH, Vanderploeg HA, Liebig JR Effects of algal composition, seston stoichiometry, and feeding rate on zebra mussel (Dreissena polymorpha) nutrient excretion in two laurentian Great Lakes. *Quagga and Zebra Mussels* 2013, 0 ed. CRC Press, 469–84.

Karatayev AY, Padilla DK. The effects of *Dreissena polymorpha* (pallas) on aquatic communities in Eastern Europe. *J Shellfish Res* 1997;**16**:187–203.

Klironomos JN. Feedback with soil biota contributes to plant rarity and invasiveness in communities. *Nature* 2002;**417**:67–70.

Knoll LB, Sarnelle O, Hamilton SK *et al.* Invasive zebra mussels (*Dreissena polymorpha*) increase cyanobacterial toxin concentrations in low-nutrient lakes. *Can J Fish AquatSci* 2008;**65**:448–55.

Kozich JJ, Westcott SL, Baxter NT *et al.* Development of a dual-Index sequencing strategy and curation pipeline for analyzing amplicon sequence data on the MiSeq Illumina Sequencing Platform. *Appl Environ Microbiol* 2013;**79**:5112–20.

Lavergne C, Rameau J-C, Figier J. The invasive Woody weed ligustrum robustum subsp. walkeri threatens native forests on La Réunion. *Biological Invasions* 1999;**1**:377.

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Levine JM, Vilà M, Antonio CMD *et al.* Mechanisms underlying the impacts of exotic plant invasions. *Proc R Soc Lond B Biol Sci* 2003;**270**:775–81.

Li H, Durbin R. Fast and accurate short read alignment with Burrows–Wheeler transform. *Bioinformatics* 2009;**25**:1754–60.

Lima SL, Dill LM. Behavioral decisions made under the risk of predation: a review and prospectus. *Can J Zool* 1990;**68**:619–40.

Lindeman RL. The trophic-Dynamic aspect of ecology. *Ecology* 1942;**23**:399–417.

McCarthy A, Chiang E, Schmidt ML *et al.* RNA preservation agents and nucleic acid extraction method bias perceived bacterial community composition. *PLoS One* 2015;**10**:e0121659.

Mooney HA, Cleland EE. *The evolutionary impact of invasive species*. PNAS 2001;98(10):5446-5451.

Nalepa TF, Schloesser DW. *Quagga and Zebra Mussels: Biology, Impacts, and Control*, 2nd Edn. Boca Raton, FL, USA: CRC Press, 2013.

Newton RJ, Jones SE, Eiler A *et al.* A guide to the natural history of Freshwater Lake bacteria. *Microbiol Mol Biol Rev* 2011;**75**:14–49.

Olapade OA. Community composition and diversity of coastal bacterioplankton assemblages in Lakes Michigan, Erie, and Huron. *Microb Ecol* 2018;**75**:598–608.

Orrock JL, Witter MS, Reichman OJ. Apparent competition with an exotic plant reduces native plant establishment. *Ecology* 2008;**89**:1168–74.

Pejchar L, Mooney HA. Invasive species, ecosystem services and human well-being. *Trends Ecol Evol* 2009;**24**:497–504.

Pringle A, Bever JD, Gardes M *et al.* Mycorrhizal symbioses and plant invasions. *Annu Rev Ecol Evol Syst* 2009;**40**:699–715.

Props R, Schmidt ML, Heyse J *et al.* Flow cytometric monitoring of bacterioplankton phenotypic diversity predicts high population-specific feeding rates by invasive dreissenid mussels. *Environ Microbiol* 2018;**20**:521–34.

Raikow DF, Sarnelle O, Wilson AE *et al.* Dominance of the noxious cyanobacterium microcystis aeruginosa in low-nutrient lakes is associated with exotic zebra mussels. *Limnol Oceanogr* 2004;**49**:482–7.

Sala OE, Stuart Chapin F, III *et al.* Global biodiversity scenarios for the year 2100. *Science* 2000;**287**:1770–4.

Sarnelle O, Wilson AE, Hamilton SK *et al.* Complex interactions between the zebra mussel, dreissena polymorpha, and the harmful phytoplankter, microcystis aeruginosa. *Limnol Oceanogr* 2005;**50**:896–904.

Satinsky BM, Gifford SM, Crump BC *et al.* Chapter twelve - Use of internal standards for quantitative metatranscriptome and metagenome analysis. In: DeLong EF (ed), *Methods Enzymol* 2013, Vol **531**. Cambridge, MA, USA: Academic Press, 237–50.

Schloss PD, Westcott SL, Ryabin T *et al.* Introducing mothur: open-Source, platform-Independent, community-Supported software for describing and comparing microbial communities. *Appl Environ Microbiol* 2009;**75**:7537–41.

Schmidt ML, White JD, Denef VJ. Phylogenetic conservation of freshwater lake habitat preference varies between abundant bacterioplankton phyla. *Environ Microbiol* 2016;**18**:1212–26.

Shen C, Liao Q, Bootsma HA *et al.* Regulation of plankton and nutrient dynamics by profundal quagga mussels in Lake Michigan: a one-dimensional model. *Hydrobiologia* 2018;**815**:47–63.

Simberloff D, Martin J-L, Genovesi P *et al.* Impacts of biological invasions: what's what and the way forward. *Trends Ecol Evol* 2013;**28**:58–66.

Sousa R, Novais A, Costa R *et al.* Invasive bivalves in fresh waters: impacts from individuals to ecosystems and possible control strategies. *Hydrobiologia* 2014;**735**:233–51.

Stinson KA, Campbell SA, Powell JR *et al.* Invasive plant suppresses the growth of native tree seedlings by disrupting belowground mutualisms. *PLoS Biol* 2006;**4**:e140.

Strauss SY, Lau JA, Carroll SP. Evolutionary responses of natives to introduced species: what do introductions tell us about natural communities? *Ecology Letters* 2006;**9**:357–74.

Tang H, Vanderploeg HA, Johengen TH *et al.* Quagga mussel (Dreissena rostriformis bugensis) selective feeding of phytoplankton in Saginaw Bay. *J Great Lakes Res* 2014;**40**:83–94.

Vanderploeg HA, Johengen TH, Liebig JR Feedback between zebra mussel selective feeding and algal composition affects mussel condition: did the regime changer pay a price for its success? *Freshwater Biology* 2009;**54**:47–63.

Vanderploeg HA, Liebig JR, Carmichael WW *et al.* Zebra mussel (Dreissena polymorpha) selective filtration promoted toxic microcystis blooms in Saginaw Bay (Lake Huron) and Lake Erie. *Can J Fish AquatSci* 2001;**58**:1208–21.

Vanderploeg HA, Nalepa TF, Jude DJ *et al.* Dispersal and emerging ecological impacts of Ponto-Caspian species in the Laurentian Great Lakes. *Can J Fish AquatSci* 2002;**59**:1209–28.

Vanderploeg HA, Pothoven SA, Fahnenstiel GL *et al.* Seasonal zooplankton dynamics in Lake Michigan: disentangling impacts of resource limitation, ecosystem engineering, and predation during a critical ecosystem transition. *J Great Lakes Res* 2012;**38**:336–52.

Vanderploeg HA, Wilson AE, Johengen TH *et al.* Role of selective grazing by dreissenid mussels in promoting toxic microcystis blooms and other changes in phytoplankton composition in the Great Lakes. *Quagga and Zebra Mussels: Biology, Impacts, and Control* 2nd ed. Boca Raton, FL, USA: CRC Press, 2013, 509–23.

Vitousek PM, D'Antonio CM, Loope LL *et al.* Introduced species: a significant component of Human-Caused global change. *New Zealand J Ecol* 1997;**21**:1–16.

Vitousek PM, Walker LR. Biological invasion by Myrica Faya in Hawai'i: plant demography, nitrogen fixation, ecosystem effects. *Ecological Monographs* 1989;**59**:247–65.

Waajen GWAM, Van Bruggen NCB, Pires LMD *et al.* Biomanipulation with quagga mussels (Dreissena rostriformis bugensis) to control harmful algal blooms in eutrophic urban ponds. *Ecol Eng* 2016;**90**:141–50.

Werner EE, Peacor SD. A review of trait-Mediated indirect interactions in ecological communities. 2003.

White JD, Kaul RB, Knoll LB *et al.* Large variation in vulnerability to grazing within a population of the colonial phytoplankter, Microcystis aeruginosa. *Limnol Oceanogr* 2011;**56**:1714–24.

White JD, Sarnelle O. Size-structured vulnerability of the colonial cyanobacterium, microcystis aeruginosa, to grazing by zebra mussels (Dreissena polymorpha). *Freshwater Biology* 2014;**59**:514–25.

Woodhouse JN, Kinsela AS, Collins RN *et al.* Microbial communities reflect temporal changes in cyanobacterial composition in a shallow ephemeral freshwater lake. *ISME J* 2016;**10**:1337–51.

Xie P, Chen Y. Invasive carp in China's Plateau Lakes. *Science* 2001;**294**:999–1000.

Yule AM, Barker IK, Austin JW *et al.* Toxicity of Clostridium botulinum type E neurotoxin to Great Lakes fish: implications for avian botulism. *J Wildl Dis* 2006;**42**:479–93.

Zhulidov AV, Kozhara AV, Scherbina GH *et al.* Invasion history, distribution, and relative abundances of Dreissena bugensis in the old world: a synthesis of data. *Biological Invasions* 2010;**12**:1923–40.

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