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Dreissena in the Great Lakes: Benthic Community Impacts and Facilitation

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Dreissena in the Great Lakes: Benthic Community Impacts and Facilitation

by

Sonya Bayba

An Abstract of a Thesis

in

Great Lakes Environmental Science

Submitted in Partial Fulfillment

of the Requirements for the Degree of

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ABSTRACT OF THESIS

Non-native invasive *Dreissena* mussels have altered the flow of energy in numerous freshwater systems by diverting nutrients from pelagic to littoral benthic food-webs, thus reducing primary production available to deep offshore benthos. Though the effect of the nearshore-dwelling *Dreissena polymorpha* (zebra mussel) on benthos has been studied thoroughly, little is known about the deep, offshore impacts of *Dreissena rostriformis bugensis* (quagga mussel). In the last two decades, quagga mussels have displaced zebra mussels in shallow Great Lakes regions and colonized previously uninhabited offshore lake regions. It is likely that the spread of quagga mussels into deep profundal areas has resulted in new interactions with offshore benthic communities. If there are positive interactions present, I expect positive correlations between quagga mussel and total non-dreissenid benthos and for taxonomic structures to be affected by *Dreissena*. Here, I investigate whether the positive impacts of quagga mussels on benthic communities previously observed in the nearshore benthos also occur in offshore benthos due to the recent quagga mussel colonization. I also investigate changes in nearshore and offshore benthic community composition in the presence and absence of quagga mussels. Benthic survey data collected under the Cooperative Science and Monitoring Initiative from Lake Michigan in 2015 and Lake Huron in 2017 were used in this study. Increased *Dreissena* abundance correlated with total non-dreissenid benthos regardless of depth and taxonomic structures of benthic communities change with depth and appear to be affected by dreissenid presence.

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Sonya Bayba

A Thesis
in
Great Lakes Environmental Science

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Introduction

Interactions between non-native and native species can affect community composition and diversity (Bruno et al., 2005; Rodriguez, 2006). Communities can respond to non-native species in a variety of ways and response to non-native presence can be species specific; some native species can be negatively impacted whilst other are positively impacted (Panetta and Gooden, 2017). Both positive and negative species interactions are linked to community structure (Rietkerk and van de Koppel, 2008; Bruno et al., 2005). However, research in invasion biology generally has been framed by negative interactions between non-native invaders and native ecosystems (Warren et al., 2017; Colautti and MacIsaac, 2004).

Positive interactions are influential but can take many forms, making them difficult to detect (Altieri, 2010). If the effects of non-native species increase habitat complexity then native species richness and species abundance is likely to increase as well (Crooks, 2002). Small-scale positive interactions that commonly occur across multiple trophic levels and functional groups influence large scale patterns (Altieri, 2010; Rietkerk and van de Koppel, 2008). Positive interactions, such as intraspecific short-range facilitation, have been observed among marine mussels as conspecifics are a favorable surface for attachment especially in habitats consisting of soft sediment (Rietkerk and van de Koppel, 2008). In some cases, positive interactions occur between non-native and native species if the non-native acts as an ecosystem engineer. Ecosystem engineers increase habitat complexity or heterogeneity to the direct or indirect benefit of other organisms and can therefore affect access or availability of a habitat's resources (Jones et al., 1994; 1997).

Native organisms have been observed benefiting from the presence of mussels fulfilling the role of ecosystem engineer (Bertness, 1984) as they play four main ecosystem level roles: trophic, nutrient cycling, structural, and monitors and indicators (Dame, 1996). Suspension feeding by bivalves impacts plankton as well as suspended sediments. Bivalves affect nutrient cycling by consuming particulate and dissolved organic matter and excreting inorganic nutrients. Structurally, they impact both the physical and biological environment. Physically, bivalves create structure with their shells and can move or stabilize sediments. Biologically they affect community structure in the water column and on the benthos by which they can influence stability, diversity and interspecies links.

Dreissena polymorpha (zebra mussel) and *D. rostriformis bugensis* (quagga mussel) transform benthic landscapes by aggregating in large densities that create novel habitats for several benthic species. Both dreissenid species are native to the Ponto-Caspian basin of Eastern Europe and have colonized lakes and rivers throughout Europe and North America (Karatayev et al., 1997). Zebra mussels mostly occur in shallow waters as they are limited to warmer littoral areas where there is an abundance of food and hard substrates for attachment (Beekey et al., 2004; Ricciardi et al., 1997; Stewart and Haynes, 1994; Stewart, Miner and Lowe, 1998a; 1998b; reviewed in Karatayev et al. 1997; 2002). In small inland lakes, zebra mussels impact the invaded area by many ways, from disrupting municipal water intakes and recreational activities, to severe alteration of ecosystem processes. Zebra mussels increase the rate of sedimentation and amount of particulate organic matter in sediments through filter feeding activities and biodeposition of feces and pseudofeces (Dobson and Mackie, 2011; Stewart, Miner and Lowe, 1998a; 1998b). As such, zebra mussels deplete energy from the pelagic-profundal pathway and transfer it to the benthic-littoral pathway (Higgins and Vander Zanden 2010). The zebra mussel

induced biodeposition is utilized by benthic macroinvertebrates (especially detritivores), resulting in a net increase in diversity, abundance and biomass (Izvekova and Lvova-Kachanova, 1972; Stewart and Haynes, 1994; Stewart, Miner and Lowe, 1998a; 1998b). Zebra mussels often create a large population of effective suspension feeders resulting in radical changes in native benthic community composition (Lvova-Kachanova and Izvekova, 1978; Karatayev et al., 1997; 2002; Burlakova et al., 2005, 2012; Ward and Ricciardi, 2007).

In contrast to zebra mussels, quagga mussels can colonize the deep profundal zone of large lakes. The quagga mussel's ability to survive on soft substrates, allocate metabolic energy toward growth and reproduction when food is limiting, and reproduce at lower temperatures allow them to live at depths inaccessible to zebra mussels (Roe and MacIsaac, 1997; Claxton and Mackie, 1998; Nalepa et al., 2010, Karatayev et al., 2015). Zebra and quagga mussels often co-exist. However, because of their faster and stronger byssus thread attachment, zebra mussels precede quagga mussels in nearly all invasion scenarios (Mackie, 1991; Peyer et al., 2009). After the initial zebra mussel invasion, quagga mussels will out-compete them over time. Because quagga mussels are a congener of zebra mussels and are slightly slower to invade, isolating direct and indirect impacts associated only with quagga mussel invasions is very difficult (Karatayev et al., 2015).

One of the direct impacts invasive dreissenids have on an invaded-range is illustrated by their interactions with native benthic macroinvertebrates. In aquatic ecosystems, benthic macroinvertebrates provide ecological services such as sediment mixing, organic material decomposition, nutrient cycling resulting in enhanced plant and microbial growth (Covich et al., 1999). Benthic macroinvertebrates also serve as a food source for many fish species thus providing energy flow to higher trophic levels (Vander Zanden and Vadeboncoeur, 2002).

Because of their roles within aquatic environments, benthic macroinvertebrates are often incorporated in monitoring efforts as bioindicators of ecosystem and water quality conditions in many water bodies including the Great Lakes (Barbiero et al., 2018a).

Great Lakes benthic macroinvertebrate taxa richness and density generally decrease with increasing depth, a general trend linked with a decrease in spring chlorophyll availability with increased depth (Burlakova et al., 2018b). In all five Great Lakes, a stark change in benthic community composition occurs at approximately 70m depth, resulting in a distinct nearshore benthic community (<70 meters, shallow) and an offshore benthic community (>70m, deep). The 70m depth separation of benthos mirrors a drop off in spring chlorophyll concentrations which also occurs at approximately 70 meters depth suggesting that spring chlorophyll availability may be a limiting factor for Great Lakes benthos (Burlakova et al., 2018b). Offshore habitat typically is homogeneous (silt, lacking hard substrates, and less complex), and the communities are dominated by Malacostraca (mainly amphipod *Diporeia*) and Oligochaeta. Conversely, nearshore habitats are heterogenous (mixture of substrates, sand, rocks, presence of shoreline etc.), and the communities have greater species richness.

The zebra mussel was first spotted within the Laurentian Great Lakes in Lake Erie in 1986 (Carlton 2008). Shortly thereafter (1989), quagga mussels were also reported in Lake Erie and both species eventually spread throughout lakes Ontario, Michigan, and Huron (Mills et al., 1993; Marsden et al., 1993; Nalepa et al., 2001). Early in the invasion, the Great Lakes were dominated by zebra mussels occupying shallow depths, however after approximately 7-13 years they were nearly completely displaced by quagga mussels in most of the Great Lakes (Jarvis et al., 2000; Patterson et al., 2005; Watkins et al., 2007; Nalepa et al., 2010; Karatayev et al., 2011, 2013) affecting many aspects of the ecosystem. Typically, native sphaeriids, unionids, and filter

feeding chironomids decline in a zebra mussel invasion scenario. Many collectors and scrapers (e.g., isopods, amphipods, gastropods, mayflies, trichopterans, oligochaetes, and chironomids) abundances typically increase in the presence of *Dreissena* due to direct and indirect positive interactions (Karatayev et al., 1997; Burlakova et al., 2012; 2005). Patterns such as Lake Huron's lake wide increase in Oligochaeta post dreissenid invasion and increases in littoral non-dreissenid and non-*Diporeia* benthos (Burlakova et al., 2018b) align with the dreissenid impacts outlined in Higgins and Vander Zanden (2010), a meta-analysis that combined most of research conducted on small lakes with primarily zebra mussel invasions. Because deep water habitat within Lakes Huron and Michigan has been colonized by thriving quagga mussel communities, it is possible that facilitative interactions, typically observed nearshore, may be occurring between *Dreissena* and various benthic taxa in offshore communities.

I have two main objectives: [1] explore correlations between *Dreissena* and total non-dreissenid benthos of Lakes Michigan and Huron along a depth gradient consistent with facilitative interactions and [2] characterize effects of dreissenid presence and absence on benthic community composition in Lake Huron and Lake Michigan. Given that zebra mussels impart positive impacts on nearshore benthic communities, I predict that the spread of their congeners, quagga mussels, into deep offshore areas results in new facilitative interactions with offshore benthic communities. Therefore, I expect a positive correlation between quagga mussel (density and biomass) and total non-dreissenid benthos (density and biomass). Additionally, I expect the following taxa, chosen through literature review, to be affected by dreissenid presence through trophic interactions: Oligochaeta, Gastropoda, *Diporeia*, Chironomida, and Sphaeriidae. I predict that Oligochaeta, Chironomida and Gastropoda densities will be higher in the presence of

Dreissena. I also predict that *Diporeia* and Sphaeriidae densities will be lower in the presence of *Dreissena*.

Methods

Benthic Sampling

Benthic macroinvertebrates were collected from each of 124 stations located throughout Lake Michigan in July 2015 and 119 stations located throughout Lake Huron in 2017. Three replicate samples were collected in Lake Michigan using a Ponar grab with a sampling area of 0.048 m^2 (Nalepa et al., 2017) and in Lake Huron using US EPA Research Vessel *Lake Guardian* Ponar grab (sampling area 0.052 m^2). A total of 370 samples were collected from Lake Michigan (Fig. 1). In the CSMI Lake Michigan 2015 data set contained 30 samples had no *Dreissena* present. 357 samples were collected from Lake Huron (Fig. 2). Of the 357 samples, 145 did not contain *Dreissena*. Samples that contained no benthic organisms due to environmental conditions of (i.e. bedrock or bad weather resulting in a failed Ponar) were excluded from analysis.

Samples were elutriated in the field through a 500 μm mesh sieve and preserved with neutral buffered formaldehyde with Rose Bengal stain to a formalin concentration of 5–10%. All organisms were picked out of samples using dissecting microscopes under low magnification. Whenever possible, invertebrates were identified to species. Quagga mussels were counted and weighed. Oligochaetes and Chironomids were mounted on slides and identified to the lowest practical taxonomic level using a compound microscope; other organisms were identified under a dissecting microscope. Chironomids were usually identified to genus. Immature oligochaetes were identified to the lowest taxonomic level possible, usually family. All organisms were counted and weighed. Oligochaete fragments, though counted, were not included in the densities

but were considered in biomass. Average density (ind. m^{-2}) and biomass (g m^{-2}, total wet weight, molluscs with shells) of total non-dreissenid benthos were calculated for each sample. Sample processing and taxonomic identification was conducted by the Great Lakes Center at Buffalo State College (Nalepa et al., 2017; Karatayev et al., 2020). I use the old division of Oligochaeta by families Enchytraeidae, Lumbriculidae, Naididae and Tubificidae, comparable with previously published data, despite the fact that only three orders are currently recognized (Enchytraeida, Lumbriculida and Tubificida) and former families of Naididae and Tubificidae are now combined in one family Naididae (Erseus et al., 2008). For convenience, I use a combined name ("*Dreissena*" or dreissenids) unless I refer to a species (*D. polymorpha, D. r. bugensis*), and *Diporeia* when referring to *Diporeia* sp.

Data analysis

Facilitation

I used a generalized linear mixed model (GLMM) assuming a Poisson error distribution to evaluate non-*Dreissena* benthic macroinvertebrate density as a function of lake depth and *Dreissena* density using the lme4 package (Bates et al., 2015) in the R software package, version 3.6.0 (2019 The R Foundation for Statistical Computing). I included a depth x *Dreissena* interaction effect in case the effects of *Dreissena* change with depth. Given that three subsamples were taken at each sample site, I included sample as a random effect to account for autocorrelation in the clustering sampling. I also used a GLMM model with a Poisson error distribution to evaluate non-*Dreissena* benthic macroinvertebrate biomass as a function of lake depth and *Dreissena* biomass. The models were not collinear (VIF & lt; 2.0), car package (Fox

and Weisberg, 2011), and I included an observation-level random effect in the GLMMs to account for overdispersion ($\varphi > 2.0$) (e.g., Elston et al., 2001). Continuous interaction plots were used to visualize non-additive effects and interpret the model slope out comes. Data from Lakes Michigan and Huron were analyzed separately.

Community Characterization

I characterized the benthic communities in samples taken < 70m depth (nearshore community) and samples collected at depths > 70m (offshore community). Then, within these pre-established groups, I examined benthic community differences associated with dreissenid presence and absence. The PRIMER7 (Version 7.0.13, Primer-e-Ltd. 2015) package was used to analyze non-dreissenid benthos in the presence and absence of *Dreissena* by depth zone within each lake. Benthos density data were transformed (square root) to reduce the dominant contribution of extremely abundant species and then a sample-to-sample similarity of macroinvertebrate community composition (density) was assessed using the Bray-Curtis similarity index (BC) (Bray and Curtis, 1957; Clarke, 1993). To visualize the differences among the various communities, nonmetric multidimensional scaling (NMDS) was used on the results of the BC matrices (Kenkel and Orloci, 1986; Clarke, 1993). To test the significance of differences among communities with *Dreissena* and without *Dreissena*, a non-parametric analogue of ANOVA-analysis of Similarities (ANOSIM) was used on BC similarity matrices to identify differences among the two groups using permutation/randomization (Clarke, 1993). I used SIMPER (‘‘Similarity Percentage’’) analysis to summarize the contribution of each taxon to the average BC dissimilarity between groups with *Dreissena* and groups without *Dreissena*.

Two-sample *t*-tests were performed to compare taxa densities in the presence and absence of *Dreissena* within the nearshore and offshore zones. The following taxa and groups were selected through literature review because they are impacted by dreissenid presence: Oligochaeta (including families Lumbriculidae, Enchytraeidae, Tubificidae and Naididae) Gastropoda, *Diporeia*, Chironomida, and Sphaeriidae. F tests were performed to assess homoscedasticity and where the assumption was not met, Welch's two sample *t*-test was performed. All tests were considered significant at $p < 0.05$. When multiple tests were conducted on the same data a sequential Bonferroni correction was applied to related sets of repeated tests to adjust the critical alpha considered for statistical significance (Rice, 1989).

Results

Facilitation

Lake Michigan

A depth x *Dreissena* density interaction term indicated that a decline in total non-dreissenid benthos with increasing depth was reduced by increased *Dreissena* density (Fig. 3a; *coeff.* < -0.0001, *SE* < 0.001, *z-value* = -4.178, *p-value* = 0.001). Similarly, a depth x *Dreissena* biomass interaction term indicated that a decline in total non-dreissenid benthos with increasing depth was lessened by increased *Dreissena* biomass (Fig. 3b; *coeff.* < -0.001, *SE* < 0.001, *z-value* = -4.178, *p-value* < 0.001).

Lake Huron

A depth x *Dreissena* density interaction term indicated that a decline in total non-dreissenid benthos with increasing depth was lessened by increased *Dreissena* density (Fig. 3c; *coeff.* < 0.001, *SE* < 0.001, *z-value* = 2.856, *p-value* = 0.004). Similarly, a depth x *Dreissena* biomass interaction term indicated that a decline in total non-dreissenid benthos with increasing depth was diminished by increased *Dreissena* biomass (Fig. 3d; *coeff.* < 0.001, *SE* < 0.001, *z-value* = 2.409, *p-value* = 0.016). Interaction effects were detected in both Lake Huron and Lake Michigan density and biomass data sets.

Community Characterization

Nearshore Offshore Comparison

Non-dreissenid benthos density was lower offshore than nearshore in Lake Huron (*df* = 298.580, *t-value* = 6.728, *p-value* < 0.001, α = 0.017, Welch's two sample *t*-test) and Lake Michigan (*df*= 297.580, *t-value* = 9.000, *p-value* < 0.001, α = 0.017, Welch's two sample *t*-test) (Fig. 4). Lake Michigan had a mean species richness of 9.9 ± 0.4 (± standard error of the mean) species per sample in the nearshore and three times lower richness (3.6 ± 0.2 species per sample, *df* = 349.450, *t-value* = 15.529, *p-value* < 0.001, α = 0.05, Welch's two sample *t*-test) in the offshore. Accordingly, Lake Michigan nearshore total non-dreissenid benthos density was higher as well (4382.8 ± 325.8 m^{-2}) compared to the total non-dreissenid benthos density offshore (1335.9 ± 92.1 m^{-2}). Lake Huron had an average species richness of 9.3 ± 0.3 species per sample in the nearshore whilst the offshore zone had an average species richness of 3.1 ± 0.2 (*df* = 352.360, *t-value* = 15.906, *p-value* < 0.001, *α* = 0.05, Welch's two sample *t*-test). Lake Huron mean nearshore density of total non-dreissenid benthos was 4204.1 ± 308.2 m^{-2} and its mean offshore density was 1461.3 ± 266.8 m^{-2}. In Lake Huron, there was a difference in community

composition between offshore and nearshore communities (*R* = 0.093, *p-value* = 0.003, one-way ANOSIM). The average dissimilarity percentage was 73.3% (SIMPER), and the main contributors to nearshore and offshore community dissimilarity were oligochaetes. Specifically, immature oligochaetes, tubificids, and lumbriculid *Stylodrilus heringianus*, sphaeriids and amphipod *Diporeia* sp. were the main contributors to dissimilarity between nearshore and offshore benthic communities (Fig. 4). Tubificids and sphaeriids occurred in higher densities nearshore, while lumbriculids and *Diporeia* sp. were more abundant offshore. Similarly, differences in community composition were detected between nearshore and offshore communities in Lake Michigan (Fig. 8, *R* = 0.214, *p-value* = 0.001, one-way ANOSIM). Here, nearshore and offshore communities had an average dissimilarity of 74.4% (SIMPER). The main taxa that contributed to depth zone dissimilarity within Lake Michigan were more abundant immature oligochaetes and tubificid *Potamothrix vejdovskyi* in the nearshore, and *S. heringianus* and *Diporeia* offshore (Fig. 4).

Lake Michigan nearshore zone

A total of 259 nearshore samples were collected from Lake Michigan in 2015. Of these samples, 14 did not contain *Dreissena*. Differences in community composition associated with dreissenid presence were detected (*R* = 0.445, *p-value* = 0.001, one-way ANOSIM test based on BC similarity coefficients). Samples with *Dreissena* appeared to be more tightly grouped whereas samples that contained no *Dreissena* were mostly spread on the peripheries of the cluster (Fig. 7). Samples with and without *Dreissena* had an average dissimilarity 81.9% with immature lumbriculids contributing the most to the total dissimilarity (11.3%), followed by immature tubificids without hairs (7.9%) and tubificid *P. vejdovskyi* (7.6%) (SIMPER). All the taxa that

listed as major contributors to dissimilarity between communities with and without *Dreissena* were oligochaetes.

With *Dreissena* present, there were higher densities of Oligochaeta (*df* = 90.50, *t-value* = 8.338, *p-value* < 0.001, α = 0.017, Welch's two sample *t*-test) and Chironomidae (*df* = 241.730, *t-value* = 3.788, *p-value* < 0.001, α = 0.025, Welch's two sample *t*-test), whereas densities of Sphaeriidae were unaffected (*df* = 13.098, *t-value* = -1.240, *p-value* = 0.237, α = 0.025, Welch's two sample *t*-test, Table 1). Gastropoda were only present in the < 70m depth range when *Dreissena* were also present, and no *Diporeia* sp. were found in these nearshore samples. The density of species belong to Oligochaeta families Lumbriculidae (*df* = 51.756, *t-value* = 8.267, *p-value* < 0.001, α = 0.017, Welch's two sample *t*-test), Enchytraeidae (*df* = *t-value* = 5.144, *p-value* < 0.001, α = 0.017, Welch's two sample *t*-test), Tubificidae (*df* = 116.710, *t-value* = 6.636, *p-value* < 0.001, α = 0.017, Welch's two sample *t*-test), and Naididae (*df* = 247.78, *t-value* = 2.386, *p-value* = 0.018, α = 0.017, Welch's two sample *t*-test) all were higher in the presence of *Dreissena* (Table 1).

Lake Michigan offshore zone

111 samples were collected at depths exceeding 70m in 2015. Of the 111 samples collected, only 16 lacked dreissenids. At the offshore stations, macroinvertebrate communities differed in terms of composition in the presence of *Dreissena* (Fig. 7, *R* = 0.285, *p-value* = 0.002, one-way ANOSIM). Average dissimilarity between samples with *Dreissena* and without *Dreissena* was 62.5% (SIMPER). Higher abundance of *Diporeia* (29.8%), and lower densities of lumbriculids in

samples without *Dreissena* contributed most to group dissimilarity (immature lumbriculids: 19.1% contribution, *S. heringianus*: 9.8% contribution).

Oligochaeta (*df* = 64.84, *t-value* = 5.057, *p-value* < 0.001, α = 0.017, Welch's two sample *t*-test), and Chironomidae (*df* = 77.865, *t-value* = 2.686, *p-value* = 0.009, α = 0.025, Welch's two sample *t*-test) densities were higher in samples with *Dreissena*, while *Diporeia* sp. (*df* = 17.115, *t-value* = -3.248, *p-value* = 0.005, α = 0.025, Welch's two sample *t*-test) and Sphaeriidae (*df* = 18.9, *t-value* = -2.672, *p-value* = 0.015, α = 0.025, two sample *t*-test) densities were lower when *Dreissena* were present (Table 1). Gastropods were not found at depths >70m. Lumbriculidae (*df* = 15, *t-value* = 4.753, *p-value* < 0.001, α = 0.017, Welch's two sample *t*-test), and Enchytraeidae (*df* = 94, *t-value* = 3.125, *p-value* = 0.003, α = 0.017, Welch's two sample *t*-test) densities were higher when *Dreissena* were present in samples. Tubificidae (*df* = 104.690, *t-value* = 1.742, *p-value* = 0.085, α = 0.017, Welch's two sample *t*-test) and Naididae (*df* = 94, *t-value* = 1.751, *p-value* = 0.083, α = 0.017, Welch's two sample *t*-test) densities appeared to be unaffected by dreissenid presence (Table 1).

Lake Huron nearshore zone

A total of 270 samples were collected at depths less than 70 meters from Lake Huron during the CSMI 2017 survey. Of these samples, 105 did not contain *Dreissena*. Differences in non-dreissenid benthic community composition were detected when comparing communities with and without *Dreissena*, but the difference was not large (Fig. 10, *R* = 0.169, *p-value* = 0.001, one-way ANOSIM). Groups were dissimilar (average dissimilarity 74.3%, SIMPER) due to higher presence of oligochaetes in samples with *Dreissena* (immature oligochaetes contributed 13.2%, immature lumbriculids were 8.4%, and immature tubificids without hair were 7.8%).

The density of total Oligochaeta was higher in samples that contained *Dreissena* (*df* = 267.33, *t-value* = 4.347, *p-value* < 0.001, α = 0.017, Welch's two sample *t*-test,). Densities of Gastropoda appeared unaffected (*df* = 175.27, *t-value* = 1.580, *p-value* = 0.116, α = 0.025, Welch's two sample *t*-test). *Diporeia* sp. densitiy was lower when *Dreissena* were present in samples (*df* = 113.240, *t-value* = -3.380, *p-value* = 0.001, α = 0.025, Welch's two sample *t*-test). Chironomidae (*df* = 1081.660, *t-value* = -0.445, *p-value* = 0.657, α = 0.025, Welch's two sample *t*-test) and Sphaeriidae (*df* = 174.510, *t-value* = -1.564, *p-value* = 0.120, α = 0.025 Welch's two sample *t*-test) densities were unaffected by *Dreissena* presence. Lumbriculidae (*df* = 268.000, *t-value* = 2.781, *p-value* = 0.006, α = 0.017, two sample *t*-test), Enchytraeidae (*df* = 218.680, *t-value* = 2.497, *p-value* = 0.013, α = 0.017, Welch's two sample *t*-test), Tubificidae (*df* = 266.200, *t* = 2.655, *p* = 0.008, α = 0.017, Welch's two sample *t*-test) and Naididae (*df* = 169.350, *t* = 3.276, p-value = 0.001, α = 0.017, two sample *t*-test) densities all were higher when *Dreissena* were present in nearshore communities (Table 2).

Lake Huron offshore zone

A total of 87 samples were collected at depths exceeding 70 meters from Lake Huron during the CSMI 2017 survey. Of these samples, 40 did not contain *Dreissena*. The NMDS ordination revealed grouping of samples according to dreissenid presence and absence. Where *Dreissena* were present samples appeared to be more tightly grouped, while samples that contained no *Dreissena* appeared on the peripheries of the cluster (Fig. 10). There was dissimilarity in non-dreissenid benthic community composition in samples with and without *Dreissena* (*R* = 0.335, *p-value* = 0.001, one-way ANOSIM). Communities were dissimilar (average dissimilarity 65.9%, SIMPER) due to high numbers of oligochaetes when *Dreissena* were present and low numbers of

Diporeia sp. and Sphaeriidae where *Dreissena* were absent. Percent contribution to sample group dissimilarity is listed for the following taxa: 25.9% for immature oligochaetes, 21.8% for immature lumbriculids, 12.4% for *S. heringianus*, *Diporeia* at 9.6%, and 5.6% for *Pisidium* sp.

Oligochaeta density was higher when *Dreissena* were present (*df* = 47.291, *t-value* = 4.083, *p-value* = 0.001, α = 0.017, Welch's two sample *t*-test, Table 2). Chironomidae density was not affected (*df* = 82.56, *t-value* = 0.334, *p-value* = 0.739, α = 0.025, Welch's two sample *t*-test). Sphaeriidae density was lower when *Dreissena* were present (*df* = 54.019, *t-value* = -3.987, *p-value* < 0.001, α = 0.025, Welch's two sample *t*-test), *Diporeia* sp. density appeared unaffected by *Dreissena* presence (*df* = 85.000, *t-value* = -1.770, *p-value* = 0.080, α = 0.025, Welch's two sample *t*-test). Gastropods were not found at depths exceeding 70m. Lumbriculidae density was higher when *Dreissena* were present (*df* = 50.255, *t-value* = 3.934, *p-value* < 0.001, α = 0.025, Welch's two sample *t*-test, Fig. 10). Densities of Enchytraeidae (*df* = 56.530, *t-value* = 2.842, *p-value* = 0.006, α = 0.025, Welch's two sample *t*-test) were higher in the presence of *Dreissena*, while densities of Tubificidae were not (*df* = 85.000, *t-value* = 0.377, *p-value* = 0.707, α = 0.025, two sample t-test). Naididae were not found in samples collected at depths exceeding 70m (Table 2).

Discussion

In both lakes Michigan and Huron, there was a decline in total non-dreissenid benthos with increasing depth. However, the decline in total non-dreissenid benthos with increasing depth was lessened by increased *Dreissena*. Differences in community composition were detected between nearshore and offshore communities. Further analysis revealed that *Dreissena* presence or

absence was associated with differences in community composition within nearshore and offshore zones. Dreissenid presence was strongly associated with higher densities in Oligochaeta in both depth zones.

Facilitation

The invasion of dreissenid species is associated with an increase in littoral benthos and decrease in profundal benthos (Higgins and Vander Zanden, 2010). However, my results suggest that an increase in total non-dreissenid benthos may be occurring throughout Lake Michigan and Lake Huron regardless of depth, as the interaction effects indicates that the presence of *Dreissena* lessens the negative impacts of depth on total non-dreissenid benthos density and biomass. Such patterns suggest that short-range facilitative effects of *Dreissena* are not limited to shallow depths and can be found where quagga mussels alone have colonized deep water habitats.

Positive correlative patterns could be the result of a combination of effects such as biodeposition and increased benthic habitat complexity through the formation of druses (i.e. *Dreissena* aggregations on surfaces). A diversity of benthic macroinvertebrates can take advantage of the nutrients, foraging spots and refuge areas made available via the formation of dreissenid aggregations (Karatayev et al., 2002; 2007).

Prior to this study, an overall decrease in non-dreissenid benthos was detected post dreissenid invasion throughout the Great Lakes, driven mainly by decreases in *Diporeia* (Burlakova et al., 2018b). However, nearshore communities also experienced increases in non-dreissenid and non-*Diporeia* benthos density, and offshore communities had non-dreissenid and non-*Diporeia* zoobenthos density remain relatively unimpacted. (Burlakova et al., 2018b). Though I found patterns suggesting increases in density associated with *Dreissena*, methodology

and analytical procedures were not similar. Previously, studies may have been unable to detect offshore increases in total non-dreissenid benthos due to the presence of a density dependant detection threshold. Since quagga mussels have recently colonized areas that were once unoccupied, they may have been at densities that were too low to have detectable impacts. Perhaps a lag in detection of these interactions occurred due to quagga mussels having recently reached a sufficient density to have a measurable facilitative impact on non-dreissenid benthos (Panetta and Goodman, 2017).

The previously detected decrease in total non-dreissenid benthos was driven by the disappearance of *Diporeia* and native mussel species resulting in major shifts in dominant benthic taxa within lakes Huron and Michigan (Nalepa et al., 1998; Watkins et al., 2007, Barbiero et al., 2011; Burlakova et al., 2018b). My analysis included densities of *Diporeia* sp. with total non-dreissenid benthos throughout the project. When comparing study results, it should be noted that though *Dreissena* were held separately from total benthos for analysis, *Diporeia* were not. The formerly dominant group *Diporeia* sp. was over-taken by *Dreissena* and Oligochaeta (Burlakova et al., 2018b). Post dreissenid invasion, Lakes Michigan and Huron experienced a decrease in overall lake-wide benthic densities driven by declines in *Diporeia* and Sphaeriidae (Burlakova et al., 2018b). Causes and mechanisms for the decrease in *Diporeia* in the Great Lakes Basin are still unknown. Most research suggests dreissenid mussels are linked to the decline ("food limitation hypothesis", Nalepa, 1998; Watkins et al., 2007), however, *Diporeia* do not show signs of starvation and some populations declined in Lake Michigan in areas where *Dreissena* were not present (Nalepa et al., 2006). Though *Diporeia* continue to decline in Lake Michigan (Nalepa et al., 2017) there are instances in freshwater systems where dreissenids and *Diporeia* coexist (Watkins et al., 2012).

Community Characterization

Total non-dreissenid benthos density and species richness were higher in the nearshore zones of both lakes, aligning with the findings of previous studies (Burlakova et al., 2018b). Most changes in taxa average density aligned with documented changes depicting dreissenid invasion impacts on benthic macroinvertebrate communities (Burlakova et al., 2012; 2018b, Ward and Ricciardi, 2007).

When *Dreissena* were present, higher Oligochaeta density was found in both lakes nearshore and offshore. The increase was driven by higher occurrences of immature oligochaetes, suggesting augmented reproduction. Oligochaetes drove an increase of total non-dreissenid and non-*Diporeia* benthos when *Dreissena* were present; Tubificidae, Naididae (species typically found in the nearshore), Lumbriculidae and Enchytraeidae (found in the offshore) particularly benefitted (Burlakova et al., 2018b). My data support these findings as similar patterns were found in both lakes for total Oligochaetes, Tubificidae, Naididae, Lumbriculidae and Enchytraeidae taxa indicating the possible presence of positive interactions among these benthic species and invasive *Dreissena*.

Gastropods were only found in the nearshore and had a higher density in the presence of *Dreissena*. Collectors and scrapers (such as Oligochaetes and Gastropods respectively), benefit from the presence of *Dreissena* (Burlakova et al., 2005). Biodeposition (i.e. feces, pseudofeces and increased rate of sedimentation), increased availability of bottom algae, periphyton and bacteria growing on dreissenid shells all combine to provide food, habitat complexity and refuge largely benefitting oligochaetes, gastropods, certain chironomid species and various other taxa

(Karatayev et al., 1997; Burlakova et al., 2012; 2005). Moreover, in Lake Michigan in the nearshore zone gastropods were found only in the presence of *Dreissena*.

In Lake Michigan, chironomid density was higher in the presence of *Dreissena* but in Lake Michigan no effect was detected. Mixed results are to be expected as chironomid species are functionally diverse and respond differently to dreissenid presence. Filter-feeding species, including chironomids and Sphaeriidae are typically negatively impacted by dreissenid presence due to composition for food resources (Burlakova et al., 2005) while other chironomid species benefit from dreissenid induced biodeposition (Izvekova and Ivova-Katchanova, 1972.). No *Diporeia* were found in the nearshore zone of Lake Michigan. *Diporeia* and Sphaeriidae of Lake Huron had lower densities in the presence of *Dreissena* regardless of the depth zone. Before the dreissenid invasion, *Diporeia* accounted for over half of total benthos abundance in Lakes Michigan and Huron but, by ~2014 had declined to a fraction of its previous abundance. *Diporeia* numbers continue to decline in Lake Michigan (Nalepa et al., 2017) and Lake Huron (Karatayev et al., 2020).

Indirect and direct positive interactions (e.g. habitat modification and providing food source) play key roles in community structuring in physically stressful ecosystems (Rodriguez, 2006, Bruno et al., 2003; 2001). The stress gradient hypothesis suggests that the impact of positive interactions on community dynamics/composition increases as environmental stressors increase in intensity (Angelini et al., 2011; Fugère et al., 2012; Suarez, 2017; Bruno, 2003). The strength and nature of interactions can change along stress gradients. For example, at the small scale, increased abundance of a species has a positive effect on other individuals in the area when under conditions of low abiotic stress but where abiotic stress is moderate-high the positive interactions become increasingly influential on the surrounding community composition. In Lake

Huron, the effects of dreissenid presence were more pronounced in the offshore than the nearshore, indicating that the magnification of this facilitative interaction may be taking place as greater depths where the environment is physically stressful due to a number of variables (food availability, harsh temperatures etc.). However, in Lake Michigan the effect of *Dreissena* on the offshore benthic communities was lower than the nearshore communities. Other influencing factors such as the very small number of samples that did not contain *Dreissena*, and differences between Huron and Michigan's overall lake productivity may have contributed to the dissimilar outcomes. In recent years Lake Huron has become an extremely oligotrophic system (Barbiero et al., 2018b). In Lake Huron it is possible that the impacts of dreissenid induced biodeposition are higher because nutrients may be more of a stressor (or a limiting factor) for profundal zoobenthos than it is in Lake Michigan.

Invasive species can have direct and indirect positive interactions along with their negative impacts. Positive interactions can be influential, but they are often overlooked in invasion biology. The results of this study indicate that dreissenid mussels appear to facilitate both nearshore and offshore benthic communities, mitigating the impact of depth on total benthos density and biomass. Though individual species and taxa respond differently to the invader, Oligochaeta are major contributors to the overall dissimilarity between benthic communities with and without *Dreissena*.

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Taxa	Nearshore		Offshore	
	With *Dreissena*	Without *Dreissena*	With *Dreissena*	Without *Dreissena*
Oligochaeta	3636.9 ± 297.4	566.4±217.2	1111.3±100.9	440.0±86.2
Lumbriculidae	767.5 ± 55.7	124.2±54.3	916.0±72.3	386.9±84.6
Enchytraeidae	80.2 ± 9.6	17.8±7.5	33.8±5.6	10.4±5.0
Tubificidae	2376.7±250.3	403.7±160.4	154.3±64.7	37.5±17.4
Naididae	411.5±163.3	20.7±12.7	1.3±0.7	0
Diporeia	0	0	157.13±54.0	848.86±206.0
Gastropoda	5.72±1.7	0	0	0
Chironomidae	606.39±297.4	146.41±39.8	29.86±6.2	9.06±4.6
Sphaeriidae	26.43±6.8	164.15±110.9	6.54±1.8	20.70±5.0

Table 1. Mean densities (ind. m^{-2} ± SE) of taxa when *Dreissena* are present and absent within nearshore (<70m depth) and offshore (>70m depths) zones collected from Lake Michigan 2015.

Taxa	Nearshore		Offshore	
	With *Dreissena*	Without *Dreissena*	With *Dreissena*	Without *Dreissena*
Oligochaeta	4386.8 ± 408.7	2159.5 ± 308.9	2206.1 ± 459.9	315.5 ± 54.5
Lumbriculidae	544.4 ± 45.6	335.4 ± 61.2	949.5 ± 186.0	200.8 ± 40.1
Enchytraeidae	56.4 ± 14.5	16.9 ± 6.3	17.9 ± 4.8	3.4 ± 1.7
Tubificidae	2119.6 ± 302.0	1059.3 ± 261.3	26.0 ± 7.6	21.5 ± 9.5
Naididae	187.5 ± 49.6	23.8 ± 6.3	0	0
Diporeia	4.1 ± 3.4	59.6 ± 16.1	43.9 ± 18.7	95.6 ± 22.8
Gastropoda	31.6 ± 14.7	7.9 ± 2.7	0	0
Chironomidae	357.4 ± 45.3	395.8 ± 73.4	28.5 ± 7.4	25.3 ± 5.7
Sphaeriidae	100.9 ± 31.3	197.8 ± 53.5	10.2 ± 2.7	36.3 ± 6.0

Table 2. Mean densities (ind. m^{-2} ± SE) of taxa when *Dreissena* are present and absent within nearshore (<70m depth) and offshore (>70m depths) zones collected from Lake Huron in 2017.

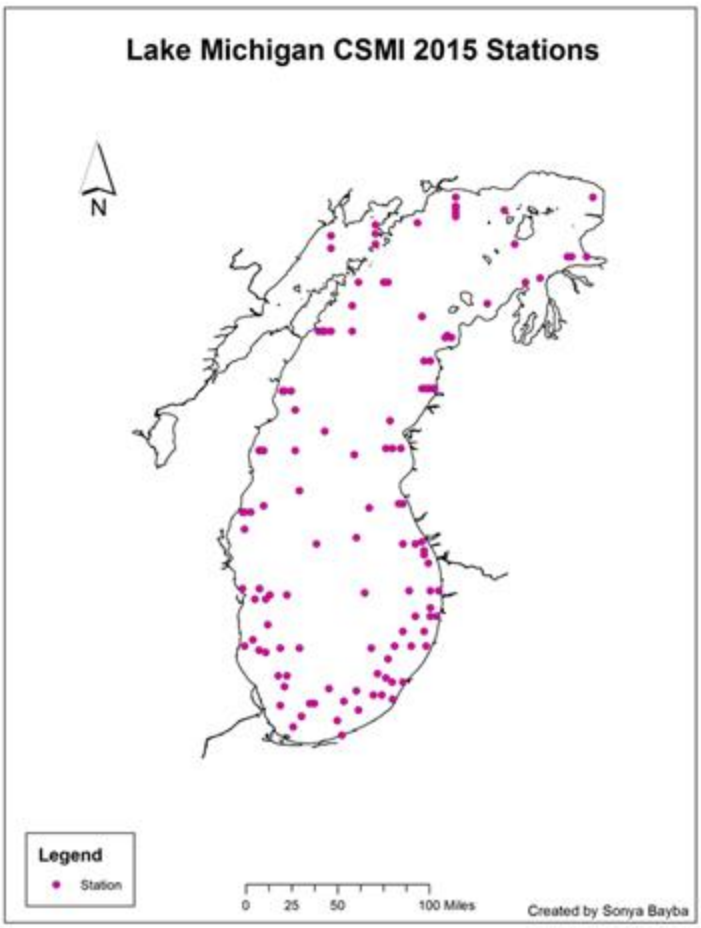

Figure 2. Location of stations where benthic samples were taken during the Lake Michigan Cooperative Science and Monitoring Initiative survey in 2015. Sample location data provided by Great Lakes Center and Lake Michigan shoreline data provided by Michigan's Department of Natural Resources (DNR) and accessed through the GIS Open Data State of Michigan site (Michigan Department of Natural Resources, 2019).

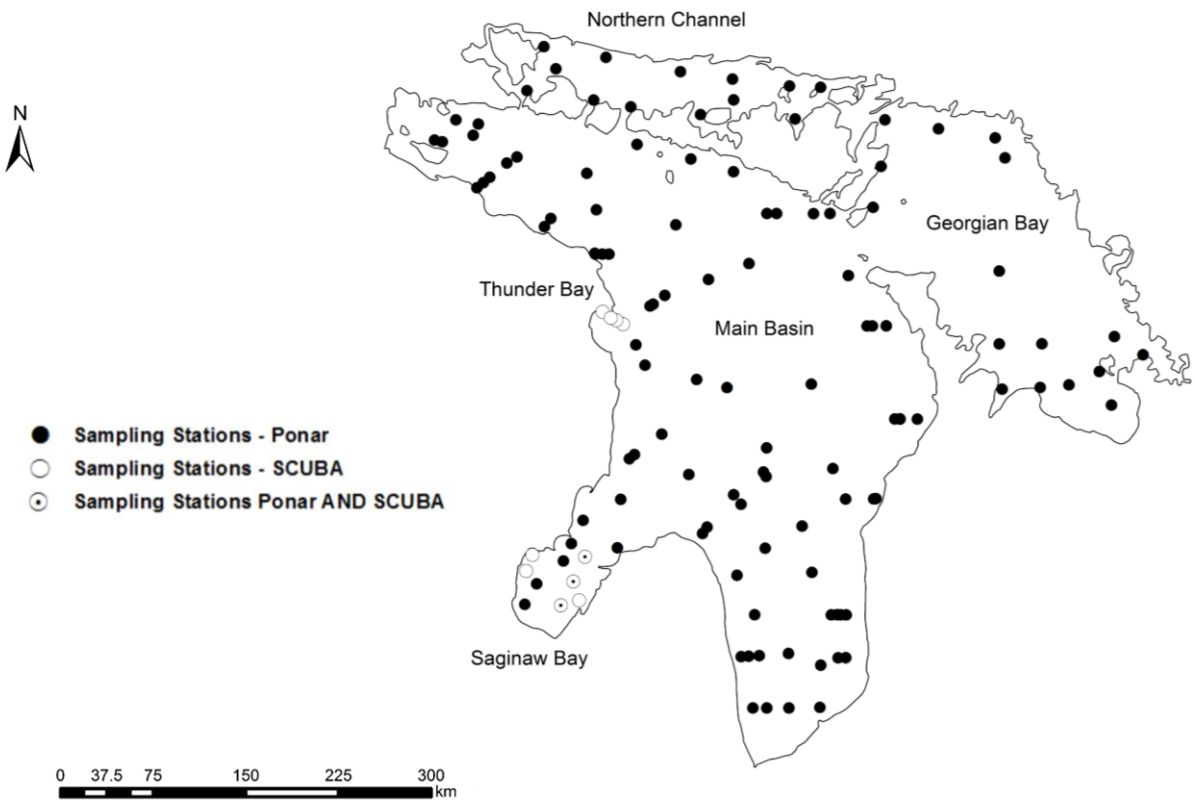

Figure 2. Location of stations where benthic samples were taken during the Lake Huron Cooperative Science and Monitoring Initiative survey in 2017. Sample location data provided by Great Lakes Center and map was created by Knut Mehler (Karatayev et al., 2020).

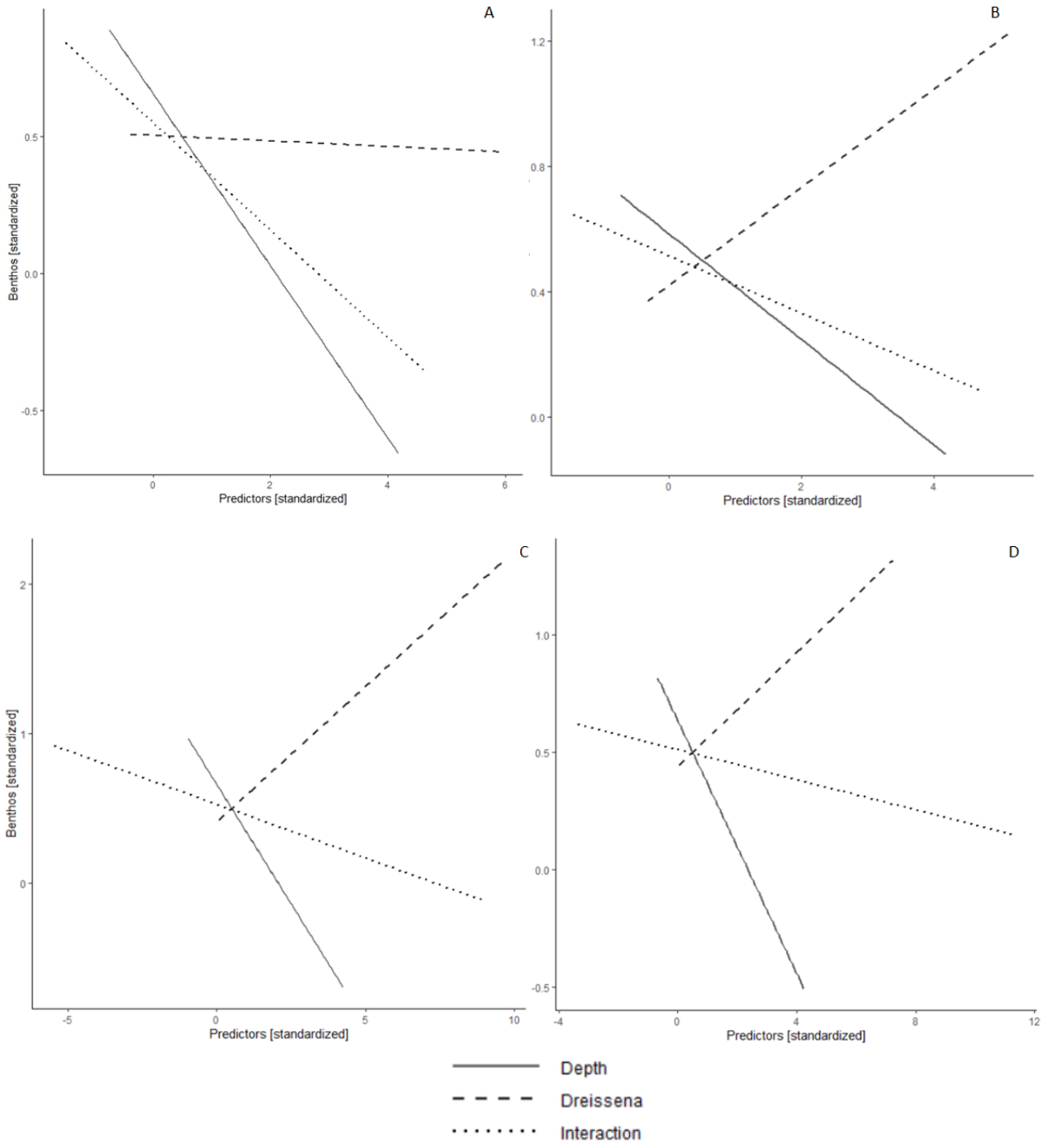

Figure 3. Density (A) and biomass (B) data for Lake Michigan 2015 and density (C) and biomass (D) data for Lake Huron 2017. Depth x *Dreissena* interaction term indicated that a decline in total non-dreissenid benthos with increasing depth was lessened by increased *Dreissena* in both lakes. The terms were standardized for graphing.

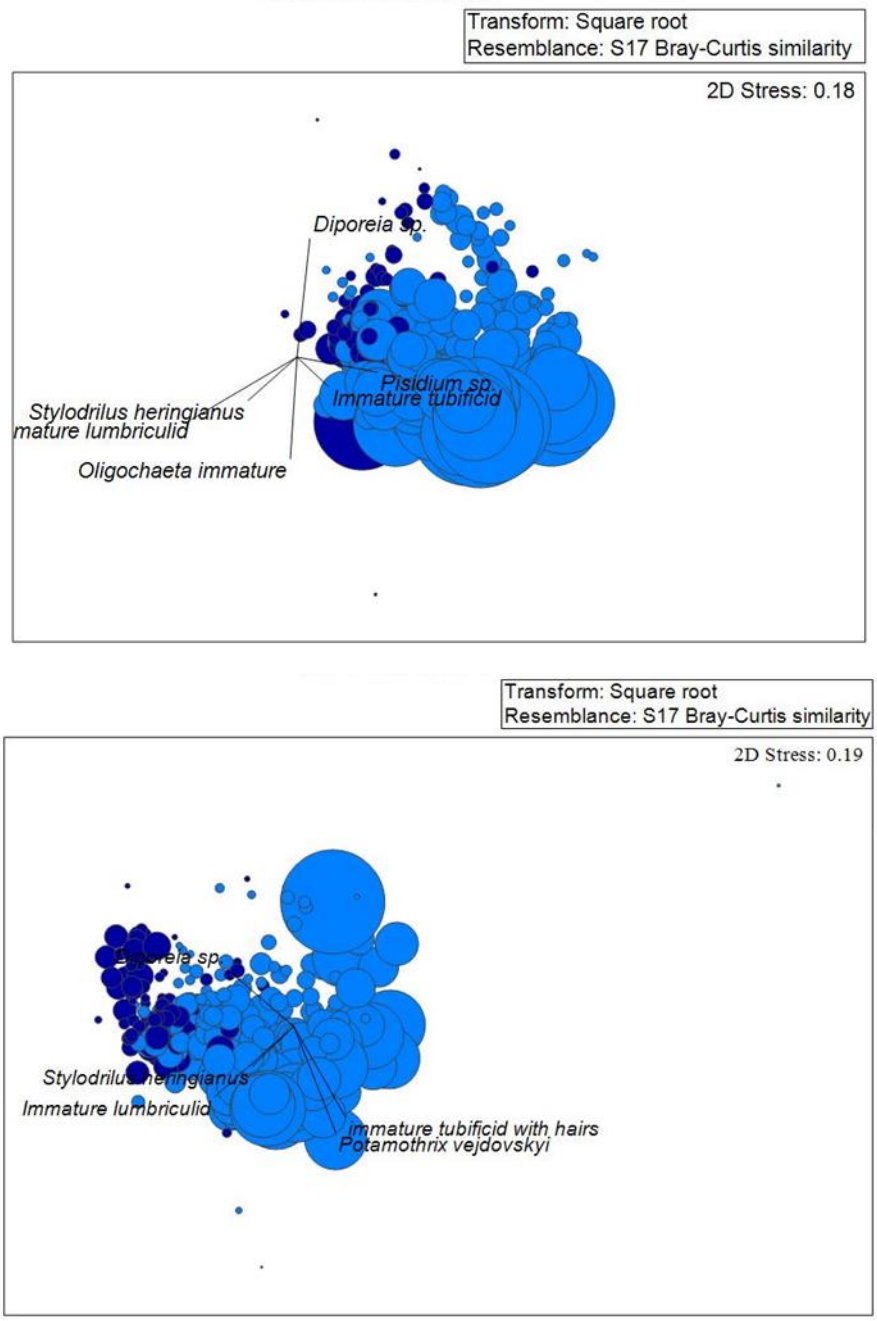

Figure 4. Lakes Huron (top) and Michigan (bottom) NMDS bubble plots of total non-dreissenid benthos density. Samples are separated into nearshore (collected at <70m depth, light blue) and offshore (collected at > 70m depth, dark blue) groups. Vectors indicate the taxa that contributed most to the dissimilarity between nearshore and offshore benthic communities identified by SIMPER analysis.

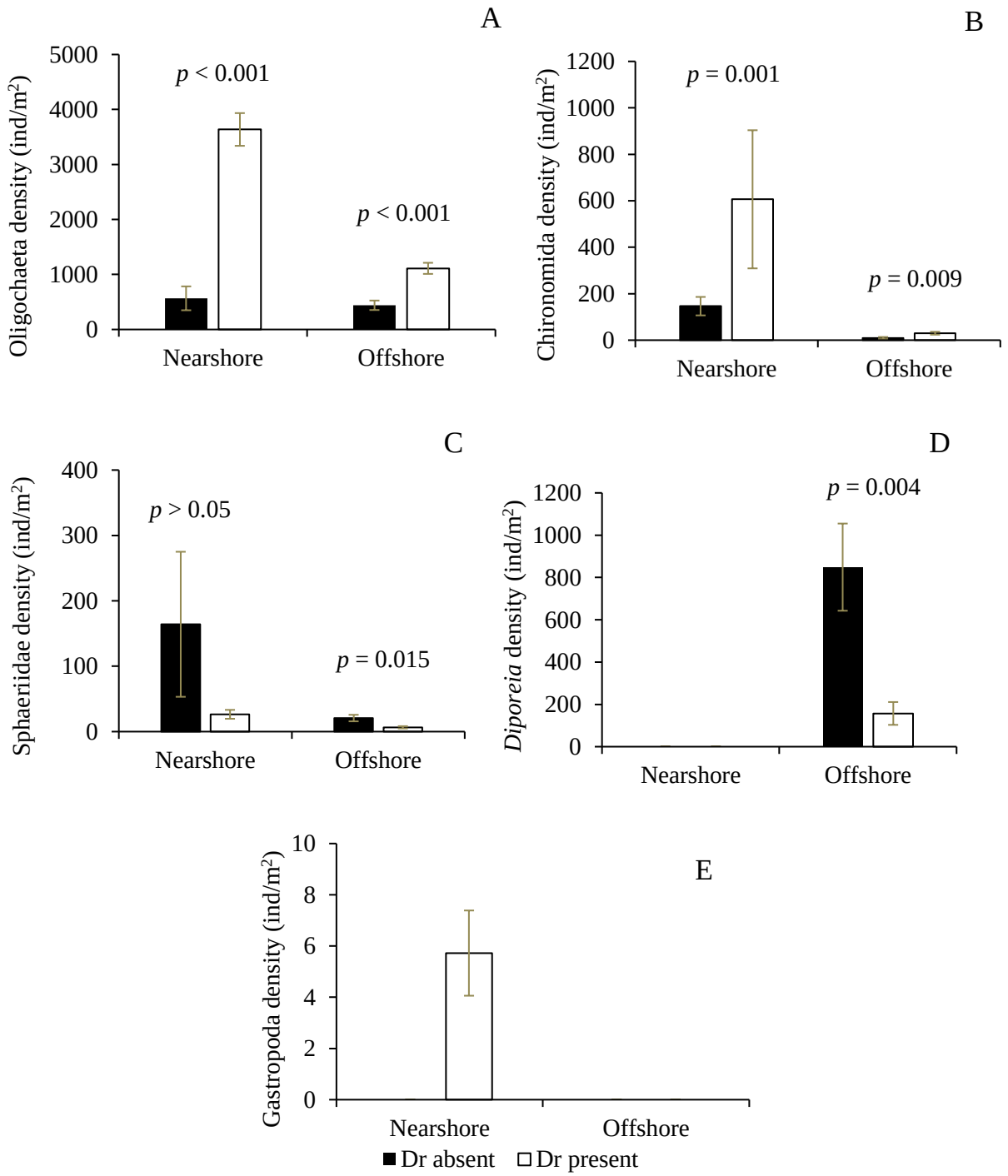

Figure 5. Mean density (± SE) of Oligochaeta (A), Chironomida (B), Sphaeriidae (C), *Diporeia* (D) and Gastropoda (E) in samples collected from Lake Michigan in 2015 containing *Dreissena* (white) and samples without *Dreissena* (black). The samples are separated by nearshore (depth <70m) and offshore (depth >70m) communities. The significance of two-sample *t*-tests are indicated for each pair of taxa at each depth zone. *Diporeia* sp. were absent from nearshore samples (D) and Gastropoda (E) were not present at depths >70m and in nearshore samples without *Dreissena*. Y axis scales are adjusted per taxa and are not uniform.

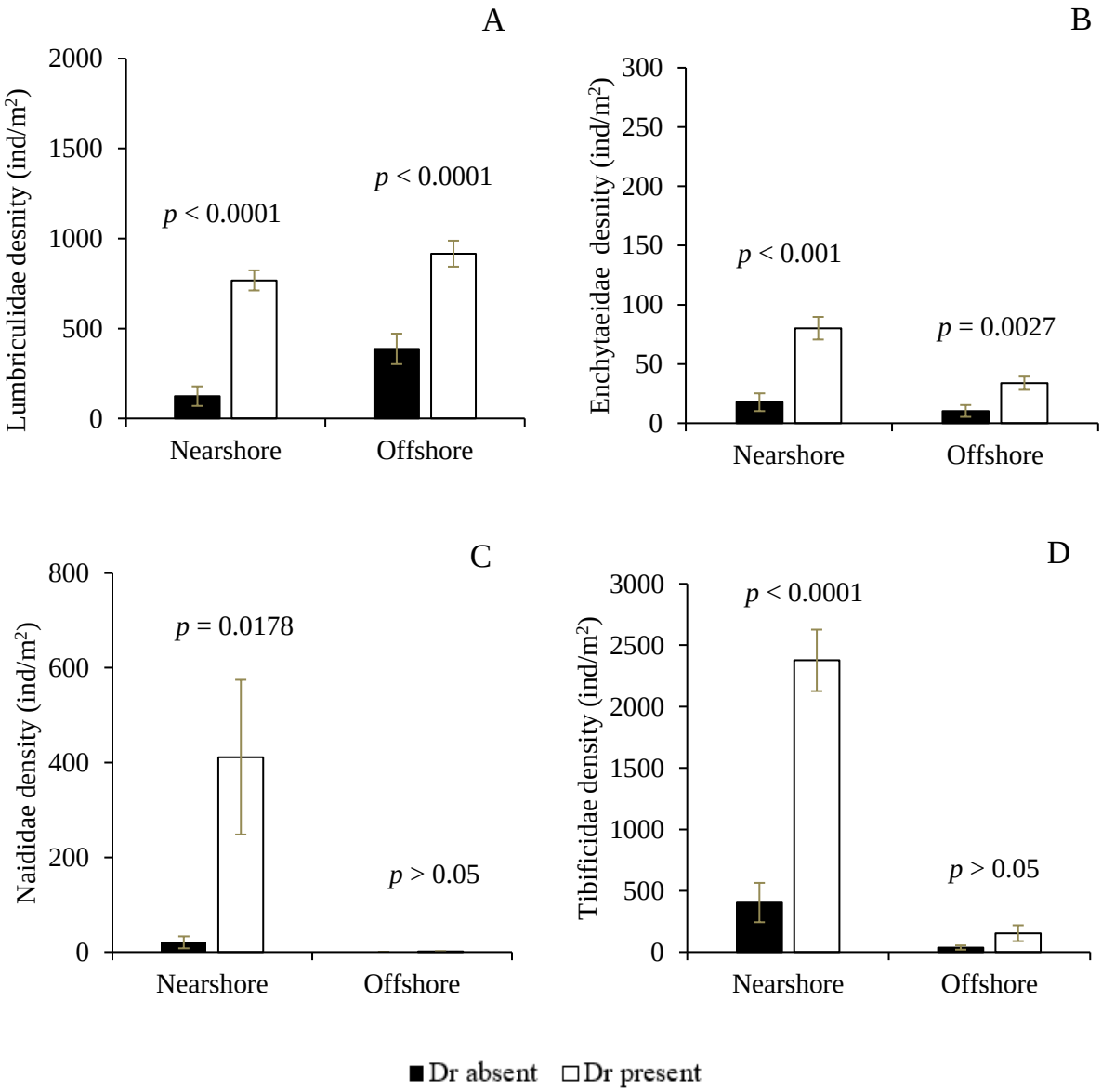

Figure 6. Mean density (± SE) of Oligochaeta families Lumbriculidae (A), Enchytraeidae (B), Naididae (C) and Tubificidae (D) in samples collected from Lake Michigan in 2015 containing *Dreissena* (white) and without *Dreissena* (black). The samples are grouped by depth with nearshore samples collected at depths < 70m and offshore samples collected at depth > 70m. The significance of two-sample *t*-tests are indicated for each pair of taxa at each depth zone. Standard error is shown, and y scales were adjusteed per taxa density and are not uniform for all graphs.

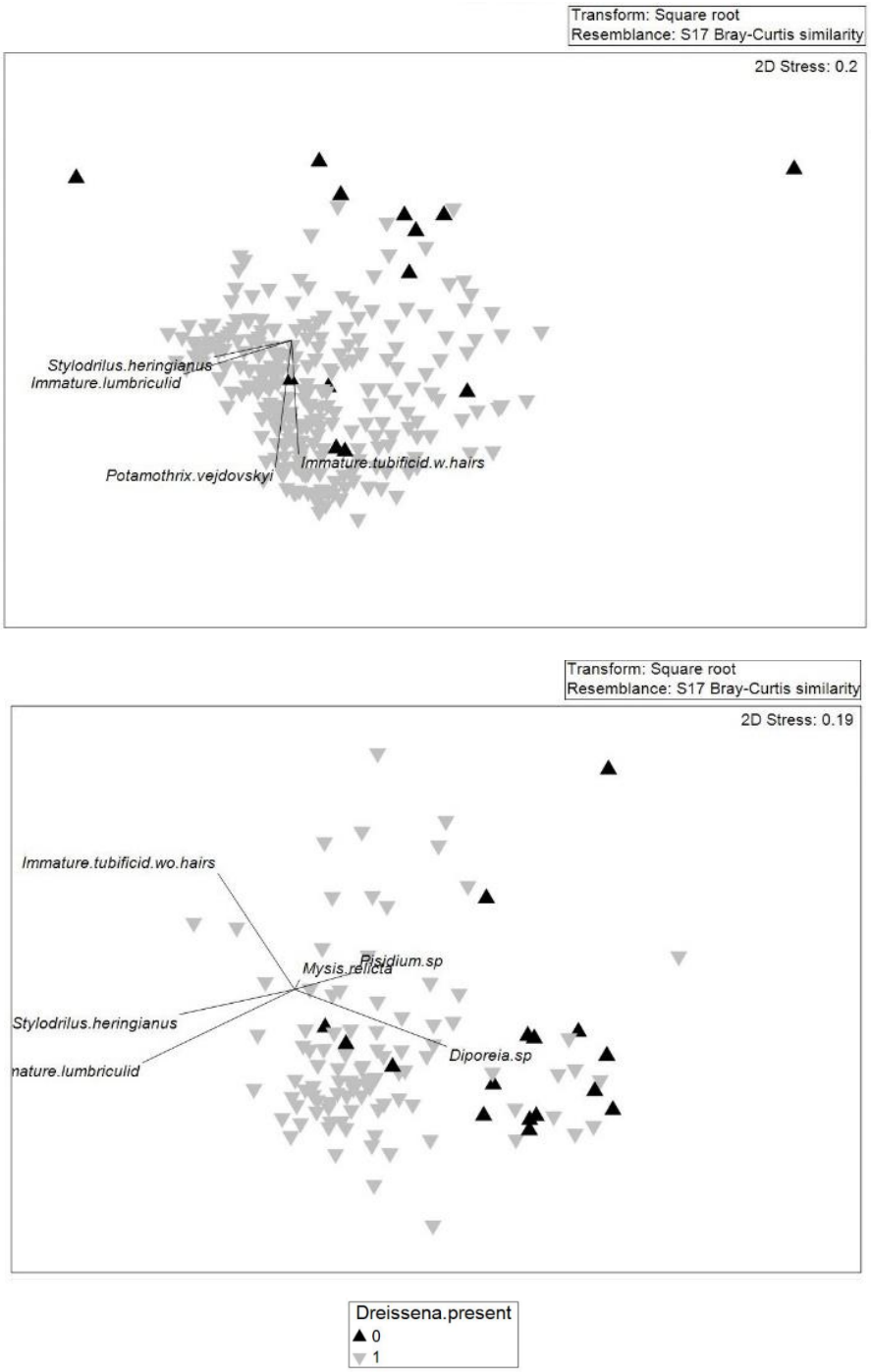

Figure 7. NMDS plot of square root transformed benthic community densities (excluding *Dreissena*), based on Bray-Curtis similarities, in samples collected from Lake Michigan in 2015. The first ordination plot presents all samples collected at depths <70m (top) and the second - samples collected at depth > 70m (bottom). Vectors indicate the species/groups that contributed most to the dissimilarity between samples with *Dreissena* (gray triangles) and samples without *Dreissena* (black triangles) identified by SIMPER analysis.

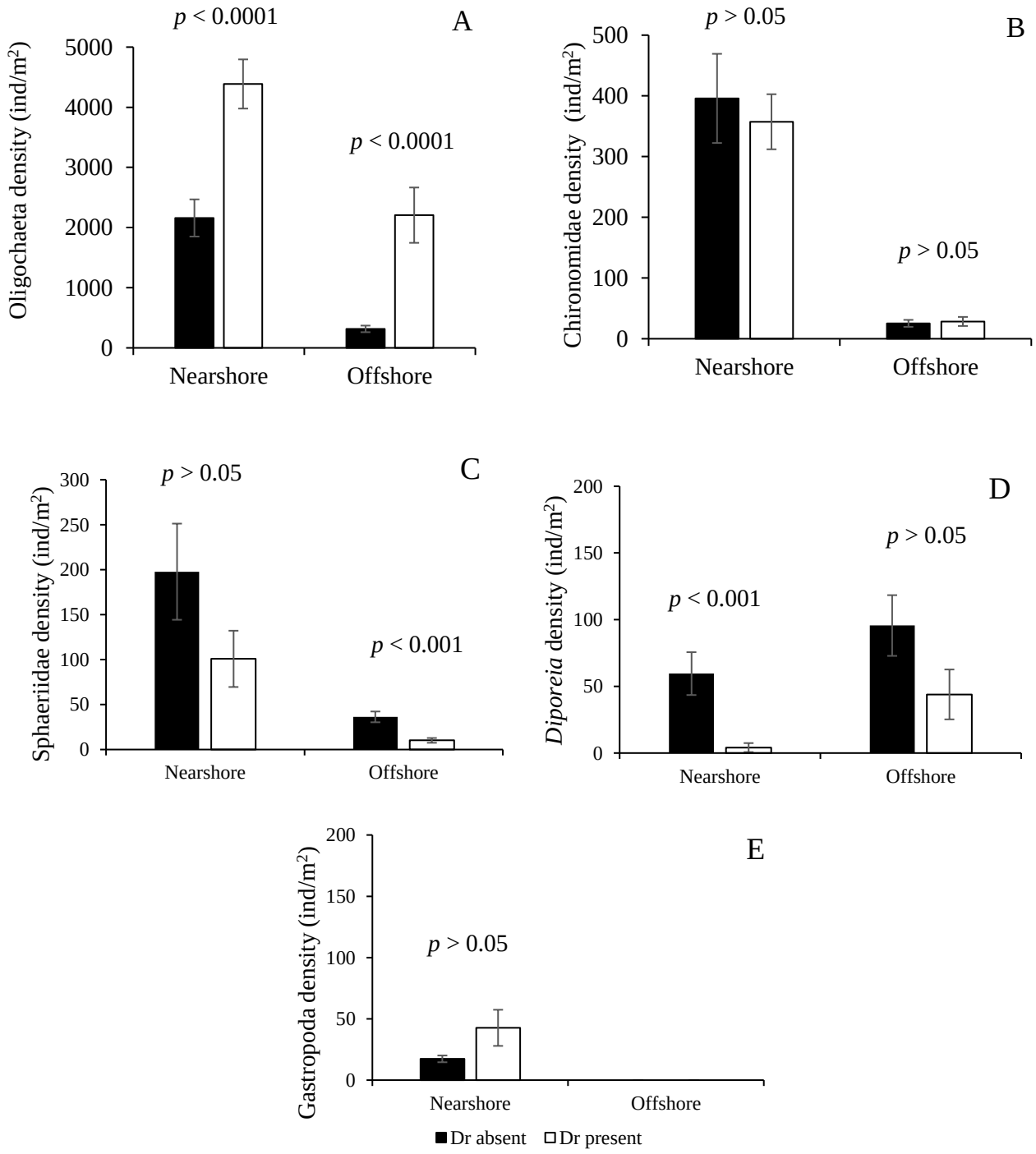

Figure 8. Mean density (± SE) the following major taxa: Oligochaeta (A), Chironomidae (B), Sphaeriidae (C), *Diporeia* sp. (D) and Gastropoda (E) for Lake Huron 2017. The samples are categorized by *Dreissena* absence (black) and presence (white) and depth at which they were sampled. Nearshore samples were collected at depths < 70m and offshore samples were collected at depths > 70m. Y axis scales are adjusted per taxa and standard error is displayed. The significance of two-sample *t*-tests are indicated for each pair of taxa at each depth zone.

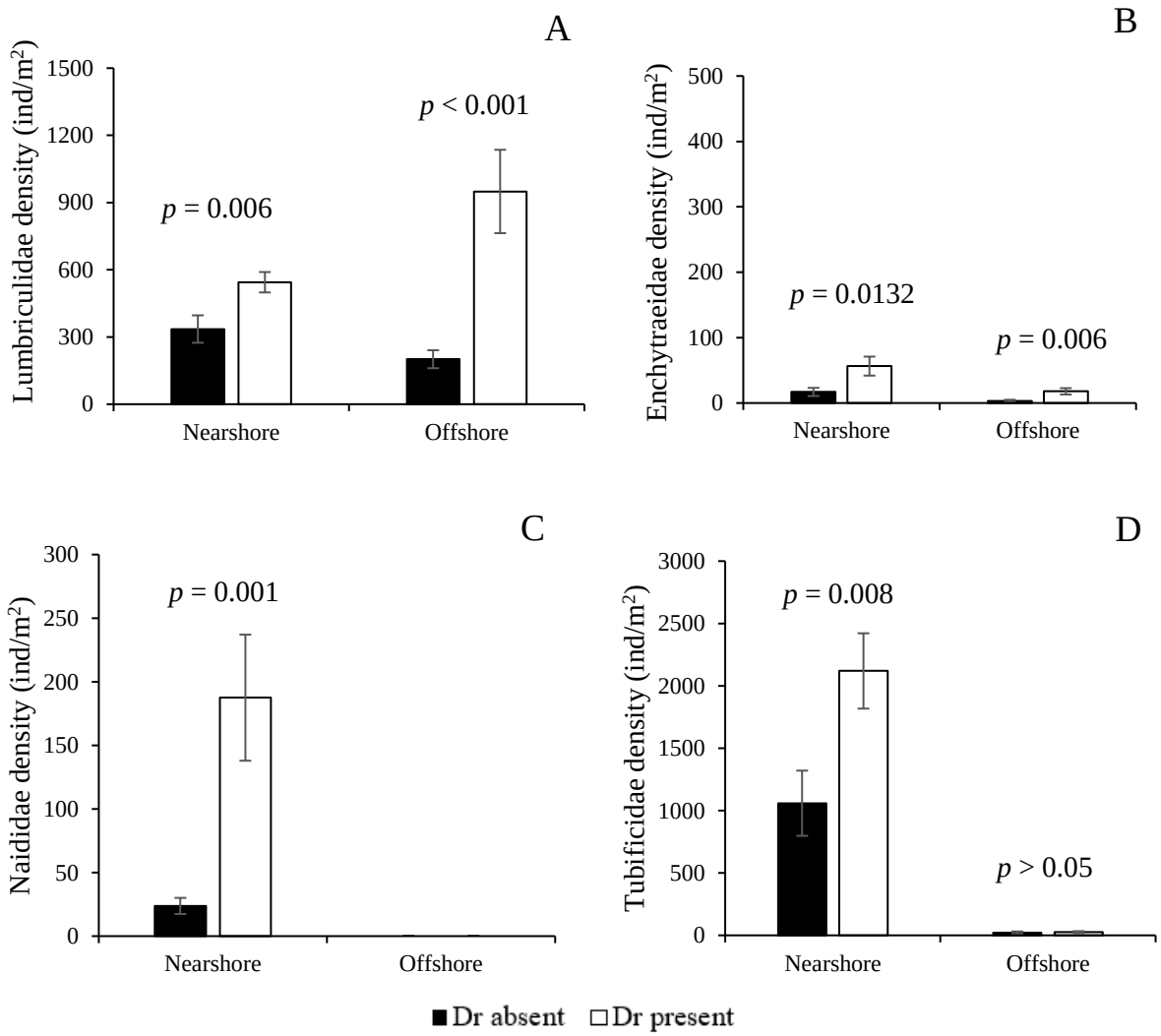

Figure 9. Mean density (± SE) of Oligochaeta families Lumbriculidae (A), Enchytraeidae (B), Naididae (C) and Tubificidae (D) in samples collected from Lake Huron in 2017 containing *Dreissena* (white) and without *Dreissena* (black). The samples are grouped by depth with nearshore consisting of samples collected at depths < 70m and offshore consisting of samples collected at depth > 70m. Standard error is shown, and y scales were adjusteed per taxa density and are not uniform for all graphs. The significance of two-sample *t*-tests are indicated for each pair of taxa at each depth zone.

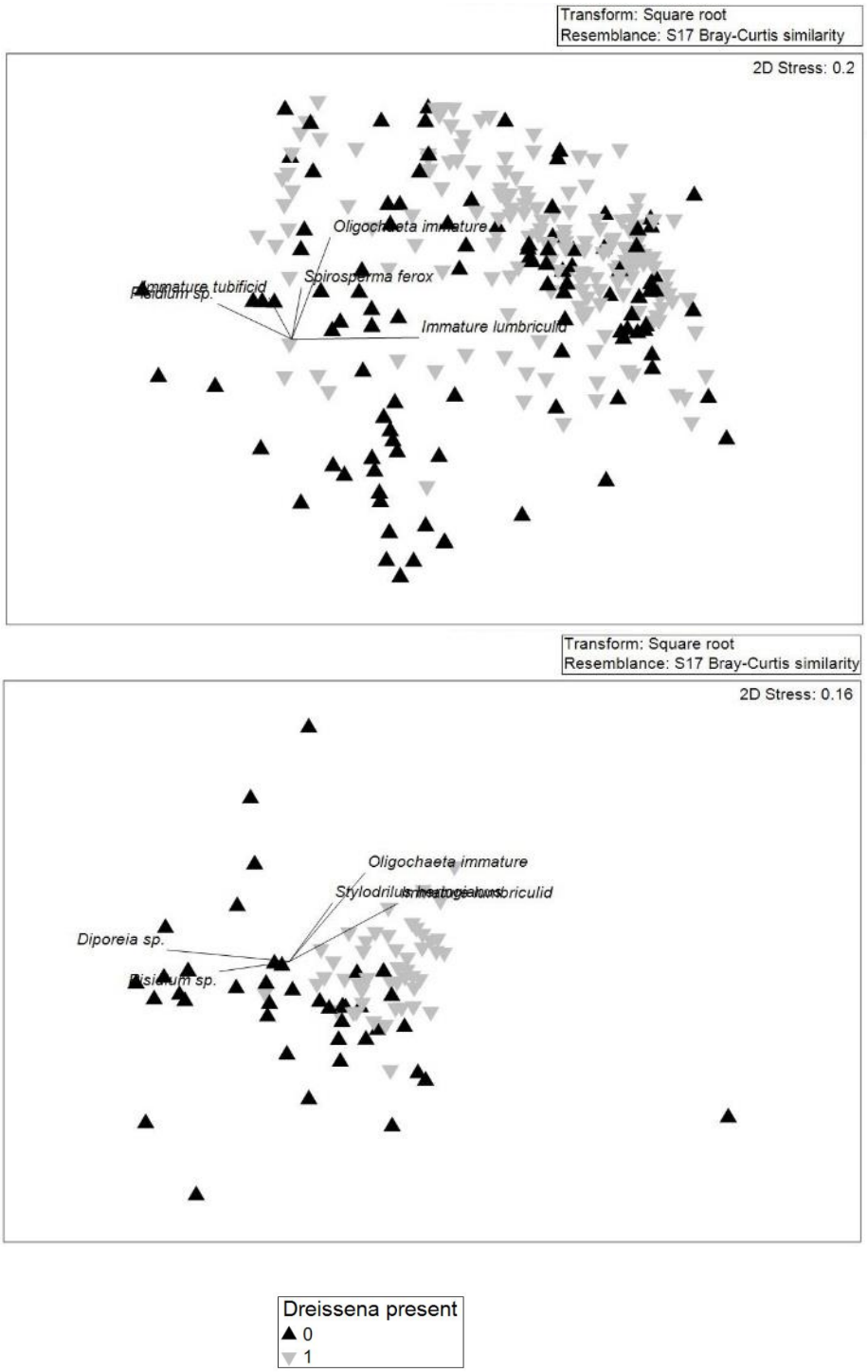

Figure 10. NMDS plot of square root transformed non-dreissenid benthic community densities, based on sample to sample Bray-Curtis similarities, in samples collected from Lake Huron in 2017. The first ordination plot consists of samples collected at depths <70m (top) and the second ordnation samples collected at depth > 70m (bottom). Vectors indicate the species/groups that contributed most to the dissimilarity between samples with *Dreissena* (gray triangles) and samples without *Dreissena* (black triangles).