THE INVASION OF DREISSSENID MUSSELS INTO LAKE SIMCOE AND THEIR EFFECT ON BENTHIC INVERTEBRATES

by

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ABSTRACT

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Keywords: Dreissenid mussel, Zebra Mussel, Quagga Mussel, Lake Simcoe, Benthic Invertebrate, Invasion.

The establishment of dreissenid mussels (zebra mussel, *Dreissena polymorpha* and the quagga mussel *Dreissena rostriformis bugensis*) in Lake Simcoe in 1997 and 2008, respectively, in Lake Simcoe has drastically altered the benthic invertebrate community in the lake. Non-dreissenid benthic invertebrate abundance greatly declined in the year 2009 during the quagga mussel invasion, whereas dreissenid abundance increased greatly in the same time period. Pre-invasion abundance of gastropods, amphipoda, oligliochaetes, plecypoda and chironomids followed similar density patterns after zebra mussel establishment. A decline in several taxa to undetectable densities was found post-quagga mussel invasion, except for chironomids. These changes in benthic communities have likely impacted fish populations because fish had to shift to hard shelled food sources possibly causing decreased fish health and decreased individual growth, a direct result of the zebra mussel as they invade shallower depths. The gastropod and chironomid populations were able to slightly increase their populations in 2017, facilitated by an increase in quagga mussels. Water quality of Lake Simcoe has also likely been negatively impacted by dreissenid mussel establishment, given changes in benthic community, oxygen presence, and nutrients available.

CONTENTS

Table of Contents

FIGURES

ACKNOWLEDGEMENTS

I would like to thank my supervisor Dr. Michael Rennie for all his help in putting this thesis together and making it what it is today. The staff of the Lake Simcoe Fisheries Assessment Unit and the Aquatic Development and Research Section of the Ontario Ministry of Natural Resources and Forestry previously collected and counted data, and a subset of 2017 samples were sorted and counted by Victoria Langen (MSc Biology, Lakehead University, 2019).

LITERATURE REVIEW

Invasive species

Ecosystems everywhere have drastically changed over the last hundred years through non-native species invasions. Most invasions happen as a direct result of human action; agriculture, travel, and trading (Williamson 1996, Mooney and Cleland 2001). These actions have made it possible for many organisms to cross borders and continents, therefore increasing their invasive potential of organisms (Mooney and Cleland 2001). Though only 1% of introduced species actually become established in a non-native area (and most introduced species experience a lag of several years of years before their populations explode) (Williamson 1996), the impacts of that 1% establishment can alone cause extensive changes to non-native ecosystems. Many countries, such as New Zealand, have over 20% of the total flora made up of invasive plant species, and many islands have more invasive species than native, and where the effects of invasions are often more pronounced compared to mainland environments (Vitousek 1997). Over the last 500 years, invasive species are estimated to have come to dominate 3% of the earth's surface through takeover (Harper and White 1974, Anand 2020).

The establishment of invasive species are often facilitated by common traits, such as rapid evolution, that allows them to outcompete the native species. Invasive species often exploit open niches (e.g., the zebra mussel occupied a rocky aquatic habitat in North America where nothing was there prior) or displace the niches of similar native species through negative interactions (Spanier 1991). Rapid evolution is the rapid change in allele frequency over a few short generations and can arise from novel genotypes. One example of an invasive species exploiting open niches is an invasive fish species to the Red Sea, *Sargocentron rubrum,* that was able to hunt during the night unlike any other local species, allowing them to occupy an unoccupied niche and resulted in a huge population increase shortly after invasion (Golani 2013). There is growing research about the mechanisms invaders use to exclude entire populations. For example, the native gecko (*Lepidodactylus lugubris)* was completely replaced by the invasive gecko (*Hemidactylus frenatus)* through higher resource use efficiency and a superior competition for food resources of the invasive over the native gecko (Petren and Case 1996). The outcome of these invasions can also result in the loss of native species through competitive exclusion. Invasive species can also often adapt quickly to new environments, and often display rapid rates of morphological evolution relative to local populations. For example, the invasive fruit fly (*Drosophila subobscura)* was able to adapt their wing size in just 20 years after invasion, making them more aerodynamic and able to travel further distances (Huey et al. 2000, Cheng and Sun 2016).

Invasive Dreissenid Mussels in Aquatic Ecosystems

In aquatic environments, perhaps the currently most feared invasive species in parts of North America is the zebra mussel (*Dreissena polymorpha*) and its close cousin the quagga mussel (*Dreissena bugensis*). Collectively known as dreissenid mussels, they are small 'D' shaped mussels roughly the size of a human fingernail, with light and dark brown stripes. Unlike other native North American mollusks, they have small hair-like filaments, called byssal threads, that help them attach themselves to hard surfaces such as boats (Peyer et al. 2009). Zebra mussels (*Dreissena polymorpha*) were first detected in the North American Great Lakes in 1988, in Lake Erie. By 1989, they had reached densities exceeding 75,000/ m^2 in a water withdrawal facility along the shore of Lake Erie (Schloesser et al. 1996). Quagga mussels (*Dreissena bugensis*) were first detected a year later (1989) in the same lake, but did not establish a large population until several years later (Peyer et al. 2008). Both dreissenid species are thought to have entered the Great Lakes through ballast water of transatlantic ships, facilitated by an increase in trade among countries (Minchin et al 2002). Empty ships sailing to North America to receive goods picked up water as ballast from Europe, containing larvae and possibly juvenile dreissenids, and released this water (and organisms they harbored) in ports of Lake Erie and St. Clair as they gained their loads for transport elsewhere. When inside water ballast, adult mussels have a survivorship of 73% over 10 days in optimal conditions, while juveniles can survive transport for 11-15 days (Therriault et al. 2012).

Effects of Dreissenids on Ecosystems

Dreissenid mussels are referred to as ecosystem engineers, due to the dramatic impacts they have had in literally re-shaping the ecosystems in which they establish (Sousa et al 2009). They have caused large changes to the chemical and physical attributes that many resident species require for their habitat (Nicholls 1999). Dreissenid mussels are filter feeders, meaning they strain water for the food they require. Each mussel can filter more than one liter of water per day. Their filter feeding behavior has transformed lakes to become clearer by having decreased particulate matter, as well as nutrients concentrations and turbidity levels (Higgins and Vander

Zanden 2012), thereby altering food web structure. Moreover, suspended soils decreased by 30-40% across varying habitat types (Higgins and Vander Zanden2010).

Dreissenids affect nutrient cycling by consuming particulate and dissolved oxygen and excreting inorganic nutrients (Karatayev 2002). In places where their numbers are large, they trap nutrients in the benthic zone, therefore disrupting the natural flow of nutrients into deeper or offshore regions of the lake. This results in increased water clarity and sunlight penetrating down to deeper depths, creating water quality problems such as benthic algal fouling and off-tasting drinking water. Also, nuisance plants at greater depths start to receive more sunlight, meaning they flourish (Geisler et al. 2016). The filtration and excretions of dreissenids can decrease the amount of particulate-bound nutrients and increase soluble nutrients; phosphorus, a limiting factor in most aquatic environments, was one of the main nutrients reduced in aquatic systems due to dreissenid establishment (Higgins and Vander Zanden 2010). Though increases in soluble nutrient excretions and an increase in water clarity resulted in 16% greater photosynthetic rates in phytoplankton, the extreme loss of algal density due to filtration results in an overall reduction in total algal productivity (Higgins and Vander Zanden 2010). This loss of overall primary production has led to major negative effects on the density and abundance of native species at higher trophic levels (Higgind and Vander Zanden 2010; Rennie and Evans 2012).

Quagga mussels in particular appear to have had major impacts on the cold-water fish community of the Great Lakes. Population abundances of lake whitefish (*Coregonus clupeaformis*) declined due to changes in their forage bases. A majority of fish species gained their nutrients through both benthic and pelagic pathways; the loss of the pelagic pathway, taken by quagga mussels, has increased the importance of the benthic pathway and overall decreased reproduction, body condition and recruitment. The effect of quagga mussels on fish communities overall depends on their ability colonize deep water environments, and the magnitude of negative interactions with native benthivore species in reducing food availability for fishes (Pothoven and Madenjian 2008).

Benthic invertebrate communities have experienced major changes following dreissenid establishment. In Lake Simcoe, a shift in the dominant species was observed from typical near-shore benthic communities dominated by chironomids, oligochaetes, and ostracods to communities in 2008 dominated by dreissenids, amphipods, isopods, and gastropods (Rennie and Evans 2012). In contrast to the oft-cited negative impacts of dreissenids, some native flora and fauna may benefit from the changes brought on by dreissenids. In lakes, species that tend to benefit in the benthic region include gastropods, leeches and amphipods, increasing by 0.5 to 1.25 times, whereas total dreissenid density was typically an order of magnitude higher than all other species (Higgins 2010). In a study done to test the change of offshore food webs with the invasions of dreissenid mussels, it was determined that the trophic position of fish and zooplankton communities changed with dreissenid invasion. This is due to the shift towards nearshore energy acquisition, but there was also a change in carbon acquired through pelagic methods that corrected the shift (Rennie et al. 2013)

When dreissenid mussels filter water they can also absorb many harmful contaminants, which can become concentrated in their tissues. Organisms that feed on the mussels may, as a result, also start to accumulate these contaminants in their tissues, a process known as bio magnification. For example, the Greater Scaup (*Aythya marila*) when feeding on dreissenid mussels have been found to have high concentrations of contaminants, affecting their reproductive success and survival (Ware et al. 2012).

Promotion of Toxic Biochemicals by Dreissenids

A link has been found between toxic blue-green algal blooms (mycrosystis) and dreissenid mussel abundance. Mussels do not filter harmful algae, while at the same time ingest other harmless algae that help control microcystic levels (Raikow 2004). Dreissenids also produce nutrients that help fertilize microcystin-producing algae. Botulism Type E is a highly toxic chemical to aquatic organisms and it has been found in the tissues of some dreissenid mussels when outbreaks occur. Mechanisms in mussel beds support their spread, which provides a micro-niche for bacteria in accumulated shells and their waste products providing nutrients (Rodman et al. 2006). Species that feed on the mussels infected with Type-E botulism often die quickly. These outbreaks may even go further up the food chain to avifauna such as ducks and loons (MacDonald 2004).

Industry and Society

Various industries have experienced major impacts on daily operations due to dreissenid mussel invasions; water use industries in 1995 spent around $150,000,000 on removal, testing, cleaning, and maintenance, compared to less than $1,250,000 in 1989 (O'Neill 1997). In a study completed in 1997 testing zebra mussel impacts on 766 infrastructure companies over 35 states, it was found that 339 facilities reported a mean expenditure of $20,557 per facility. The industry most affected was nuclear power plants, spending on average $786,670 per facility; these costs were associated with use of oxidizing chemicals, molluscicides, and chemical injection systems. Other industries with high costs were drinking water treatment facilities, fossil fuel generating facilities, and industrial facilities (O'Neill 1997). The costs from the water treatment facilities were from retrofitting, planning, chemicals, and prevention.

Society also experiences effects from the invasion of dreissenid mussel's; their sharp edges pose a hazard to local swimming areas and deter people from visiting. Historical sites are also being affected as the mussels are encrusting shipwrecks entirely. This decreases the worth of the site as people can no longer view the attraction (NWRI 2004).

The government has also been attempting to stop the spread of dreissenids and help industries and society with the effects, but the massive geographic area and dense populations of dreissenid mussels make prevention and reduction difficult. In the state of Utah in 2009, the Aquatic Invasive Species Program received $1,400,000 to help with prevention efforts. The majority of that money went to hiring experts to monitor the prevention program as well to educate the public, study the species and purchase small watercrafts to monitor the area. After these expenses, which put the program in place, there was little money left over to hire prevention officers, the very people needed to enforce the laws (Adams 2020). This is the case with many government sectors where funding for invasive species prevention strategies is often well below the necessary costs to make such programs effective.

Zebra Mussels and Quagga Mussels; Similarities and Differences

The success of zebra and quagga mussels in North America have come from their similar traits, life histories, body size, genetic variability and adaptability (Stepien 2002). A substantial portion of water bodies across North America have been invaded by zebra mussels; even some small somewhat isolated lakes have been overtaken, meaning the geographical extent of impact has been far greater than the quagga mussel (Karatayev et al. 2014). Although, in almost all lakes that quagga have been introduced to, they numerically dominate in numbers over the zebra mussel and take over the lake (Rudstam and Gandino 2020). Their many differences in habitat, attachment strength, and feeding/ filtration rates have given the mussels advantages in the environment.

Zebra and quagga mussels tend to have different depth and temperature tolerances; zebra mussels tend to colonize only the littoral zone of lakes up to 7 meters depth and tend to prefer temperatures 2-4 degrees warmer than the quagga mussel (Roe and MacIssac 1996). In contrast, quagga mussels have colder temperature preferences and lower energetic requirements, colonizing the profundal (deep) zones of lakes, where the water is colder and fewer nutrients are present, as well as littoral regions (Baldwin et al 2020). With this adaptation, they can increase geographic diversity and population density, having greater system-wide effects compared to zebra mussels. Quagga mussels tend to have weaker and more fragile shells than zebra mussels, likely a result of a tradeoff between mussel strength and starvation resistance due to deeper water having very little water movement and turbulence. (Roe and MacLsaac 1996).

Zebra mussels tend to prefer hard surfaces for colonization, whereas quagga mussels can colonize both soft and hard substrates, meaning they can attach themselves to sandy lake bottoms. Veligers are larval stages of mussels; quagga mussels produce a large number of these so that they can gain settling space before any zebra mussels can colonize, meaning quagga mussels can quickly dominate all areas including substrata of lake bottoms (Rudstam and Gandino 2020). Quagga mussels have weaker byssal threads than zebra mussels, which prevents them from dominating high-velocity systems. By contrast, zebra mussels produce much stronger byssal threads, and are produced at a faster rate (approx. double that of quagga mussels) and, as such, have lower dislodgement rates than quagga mussels, and a greater mechanical force is required to detach them (Peyer et al 2008). Furthermore, studies have shown that zebra mussels byssal thread production can be highly plastic, adapting to local conditions faster than quagga mussels (Peyer et al 2008).

Quagga mussels tend to have a lower metabolic rate than zebra mussels and, as a result, are more resistant to starvation, which can become a very useful adaption under high densities. Additionally, quagga mussels appear to have higher growth rates than zebra mussels under low food densities; in a lab experiment when zebra mussels and quagga mussels were starved for days, zebra mussels had higher mortality (56%)

compared to quagga mussels (6%; Baldwin et al 2020). Quagga mussels also appear to grow faster than zebra mussels when predator karimones are present (Rudstam and Gandino 2020). However, quagga mussels tend to be more vulnerable to predation because of their thinner shells, and lower attachment strength (Rudstam and Gandino 2020).

Lake Simcoe

Lake Simcoe is a large freshwater lake located in Southern Ontario. With a surface area of $772km^{2,}$ Lake Simcoe is the 5^{th} largest inland lake in Ontario. It had two main bays, Kempenfelt Bay and Cook’s Bay, with a maximum depth of 41 meters. The lake is home to 55 fish species, including Lake Trout and Lake Whitefish. Lake Simcoe’s fisheries hold great social and ecological importance to the surrounding community; an estimated 172,000 people visited in 1990 (Evans et al 1995). Many invasive species have invaded the lake including northern pike (1920), common carp (1869), and rainbow smelt (1961), strongly altering the structure of the fish community (Evans et al 1995). Zebra mussels were first discovered in Lake Simcoe in 1995, and quagga mussels were found a few years later in 2004. The lake has experienced a variety of changes in the last 300 years, including climate change, nutrient loading from watersheds and municipal wastewater, and invasive species. Although the specific stressor causing changes cannot be concluded without a doubt, the timeline of dreissenid mussel invasion is consistent with many major changes seen in Lake Simcoe, including reduced nutrient levels and a decline in the density and abundance of the benthic invertebrate community, increased water clarity, increases in submerged aquatic vegetation, and nutrient remineralization (North et al. 2013).

There is good reason to believe these changes in Lake Simcoe may have been caused by dreissenids. In Lake Simcoe, dreissenid mussels have been estimated to be able to filter the entire lake more than 10 times during the open water season (Ozersky 2015; North et al 2013). Dreissenids are estimated to have altered the importance of nearshore benthic derived carbon in Lake Simcoe, due to the filtration of dreissenids in shallow regions of the lake once established (Rennie et al. 2013). Lake Simcoe has experienced major declines in both zooplankton and phytoplankton since the 1990's (North et al. 2013). This is suspected to result from an impact of dreissenids, who greatly decreased the density of the phytoplankton despite higher photosynthesis rates. Zooplankton that feed on the phytoplankton experienced a bottom up reduction as their food source was reduced. Benthic invertebrate densities at the 10 and 15 meter depths greatly increased in Lake Simcoe between 1982 and 2009, mainly due to the addition of dreissenid density (Rennie 2012). At the 5-meter- deep site there was a decrease in density as dreissenids don't tend to colonize the 5-meter depth in Lake Simcoe.

A study examining Lake Simcoe specifically allows differentiation of the distinctive impacts of each dreissenid species because the invasion periods of each were spread out over a period of 13 years. Lake Simcoe provides a clearer model of the specific impacts of each mussel species compared to the Great Lakes, that were taken over by both species but at similar times, making it impossible to evaluate species-specific impacts to the ecosystem. Currently in Lake Simcoe, dreissenids occupy most available depths in the main basin, and we can use data from previous years to obtain a clear idea of the changes seen in the aquatic community over the invasion periods (Rennie and Evans 2012).

INTRODUCTION

Reports of new invasive species appear in the news almost daily. Due to the breakdown of geographic barriers, we are seeing a huge colonization of flora and fauna from various continents that are novel to the ecosystems they invade, with dramatic and unintended impacts. Invasive or alien species are causing a toll on local species diversity and ecosystem processes (Mooney and Hobbs 2000). Mainly, the invasive species can alter the evolutionary pathway of local (endemic) species through niche displacement, competitive exclusion, hybridization, introgression, predation and extinction (Mooney and Cleland 2001). The result is a swamping of local species, sometimes to the brink of extinction.

Benthic Invertebrates are critically important in both terrestrial and aquatic ecosystems, having major roles in many physical, chemical and biological processes (Covich 1999). They are a critical bridge between primary production and fishes (Prather 2012). They also support movement of resources between ecosystems and accelerate nutrient transfer by converting resources to a usable dissolved nutrient through feeding activities such as excretion (Covich et al. 1999). Benthic invertebrates promote decomposition as they are dominant consumers of dead organic matter for energy (Covich 1999). Finally, they can be used as bio indicators of ecosystem health, based on their varying degrees of sensitivity to pollution and environmental changes (Brage 2002). For example, the insect *Ephemoptera* (mayflies) are typically pollution sensitive taxa, and are used as models when an ecosystem has high pollution levels.

In 1982, several dreissenid mussels from Europe (zebra mussel, *Dreissena polymorpha*; quagga mussel *Dreissena rostriformis bugensis*) became invasive species to North America, their primary invasion believed to be through water ballast of ships (Ricciardi et al. 1997; Therriault 2012). Many organizations and governments attempted to slow the rate of introduction but were unsuccessful as the rate of water transport continues to increase and limited resources prevents every boat from being searched. Their secondary dispersal method is believed to be a result of recreational boating; by attaching themselves to watercraft and trailers or existing in life binges/wells. A program in 2011 designed to slow the spread, inspected commercial hauling of boats and identified 25 infected boats bound for BC (Therriault et al. 2012). Programs like these are moderately successful but commercial hauling is only half of the fouled boats traveling, meaning the other half unknowingly spread the mussels.

Zebra mussels were the first invasive dreissenid species to North American lakes. Zebra mussels are filter feeders found in freshwater ecosystems, forming belts around the shore and found up to a depth of 45 m in some lakes, with densities highest at regions 2-4 m from the shore (Stanczykowska and Lewandowski 1992). Large zebra mussel populations have the ability to completely alter the ecology of aquatic systems. In the majority of infested lakes, zebra mussels represent over 85% of the benthic population (Riccardi et al. 1997). Their filter feeding activity removes phytoplankton from the water column and moves it to the benthic areas of the lake (Hecky et al. 2004). Their filtration capacity is high enough to decrease suspended particle matter and increase water clarity in lakes, which can lead to an increase in the depth which aquatic macrophytes can occupy at deeper thermoclines (Therriault 2012). Zebra mussels can also cause lake eutrophication and lower the oxygen present in the deep waters, resulting in the decline in distribution and abundance of many benthic communities to decline in distribution and abundance (Jimenez 2011). The invasion of zebra mussels has also resulted in a decrease in available food and increased competition with other invertebrates. As a result, many benthic organisms have decreased, such as the *Sphaeriids* that share the same ideal depths as zebra mussels.

The quagga mussel can be found in lakes where zebra mussels are not initially present, but typically zebra mussel invasions are often typically followed by quagga mussels (*Dreissena rostriformis bugensis).* The quagga mussel is characteristically very similar to the zebra mussel, possessing the same biology that result in their domination of aquatic ecosystems, although there are a few key differences. Quagga mussels are often found in deeper and colder water bodies (Dermott and Munawar 1993). This means they are able to utilize a much broader habitat than zebra mussels. In addition, quagga mussels are able to not only colonize to hard surfaces but they can also colonize in soft surfaces such as sandy lake bottoms (Benson 2010). Reports show the invasion of zebra mussels and quagga mussels occurred within a decade of each other; unfortunately meaning there has not been enough time and resources to gain a full understanding of their specific effects.

OBJECTIVES

The purpose of this thesis was to determine the effect of two species of dreissenid mussels, zebra and quagga mussels, on the benthic invertebrate community of Lake Simcoe, Ontario. This was accomplished by counting benthic samples from 2017 and comparing them to data collected from 1982, 1983, 1986, 1993, 2008 and 2009. The years 1982, 1983, 1986 describe baseline data and the conditions of the lake without dreissenid mussels present. The years 1994 and 2008 were dominated by zebra mussels. In 2009 a shift occurred, whereby dominance from zebra mussels shifted towards quagga mussels, which were the only dreissenid present in 2017. This thesis investigates specifically how each of these dreissenid mussels has affected benthic community structure differently. It also investigates prior and post conditions of Lake Simcoe health based on research published from local authorities in order to fully understand abundance of the aquatic organisms and how they have changed over time.

HYPOTHESIS

Because zebra mussels affect the shallower regions of the Lake Simcoe and were essentially replaced by the quagga mussel in 2017, and the quagga mussel has greater system wide effects on the benthic species of Chironomids, Gastropods, Plecypoda, Oligochaetes and Amphipods causing great population declines, I therefore hypothesize that quagga mussels will affect the benthic invertebrate community differently than when zebra mussels were the dominant mussel species in the lake.

METHODS

Sampling

The sampling for this study was mainly conducted by the Ontario Ministry of Natural Resources and Forestry over the last 40 years. In addition, counts from Victoria Langen's thesis was used for the 2017 data (Langen 2017), with the remainder of the samples from this event being enumerated and included as part of this project and is summarized here. Data from both studies were provided by Dr. Rennie for analysis. Samples were collected in Lake Simcoe along a fixed transect during 1982, 1983, 1986, 1993, 2008, 2009, and 2017. The transect started at Sibbald Point Provincial park and continued towards an Ontario long term monitoring station K45 (Evans et al. 2011). Six depths were sampled along the transect, corresponding to 5, 10, 15, 20, 25, and 30 meter depths. Most samples were taken in late summer, but in 1986 the samples were taken in late March. Samples were taken with a 15.24 cm Ekman dredge or petit-Ponar with the same sampling area. Only the organisms retained on a 500 µm sieve were examined in this analysis. Retained organisms were either preserved in a 10% buffered formalin or were frozen for later analysis. A range of 3-7 replicates were collected at each site. Remaining samples for 2017 that were not counted or enumerated previously were processed as described below.

Sorting, Counting and Measurement

Samples were brought back to the lab where they were sorted and counted by broad taxonomic groups (typically by order) and then returned to the preservative. Frozen samples were thawed and enumerated; tissues were either then collected for stable isotopes analysis, or discarded (Langen 2019). Common taxa included Chironomidae, Gastropoda, zebra mussel (*Dreissena polymorpha*), quagga mussel (*Dreissena bugensis*), Oligochaetes, Plecypoda, and Nematoda. Shelled organisms were counted if the organism was recently living (i.e., contained tissues). Shells with no associated tissues were not counted and were discarded.

In my initial examination of the data, there seemed to be a possible error in the species count of gastropods in 1993. It is possible that the technician conducting the counts at that time may have tallied all shells rather than just the ones with tissues inside. This was suspected as 1993 gastropods counts were extremely high, unlike any other taxa that year, and were orders of magnitude greater than any other observed count in any other year. As such, the 1993 gastropod counts were removed from further analysis.

<u>Analysis of Data</u>

The data were imported into Microsoft Access and a database was created. Queries to extract means and standard deviations were conducted based on year, common site, site, depth, and species present. Multiple queries were run to determine the total densities, as well as densities of specific taxa (i.e., Chironomidae, Gastropoda, Zebra mussel (*Dreissena polymorpha*), Quagga mussel (*Dreissena bugensis*), Oligochaetes, Plecypoda, and Nematoda). Results of queries were exported into Microsoft Excel. Data were presented as mean abundance plus or minus 1 standard error (SE), and overall trends were examined visually, with particular attention to changes in patters around the establishment of zebra mussels in the mid- 1990’s (presented here as 2008/09 data) versus when quagga mussels were the dominant mussel (i.e., in 2017).

RESULTS

All Invertebrates

The total density of benthic invertebrates declined over the study period. The most pronounced declines in invertebrate density were found in the 5- and 30-meter depths in 2017 compared to the start of the study in 1980, whereas invertebrate densities 15-meter depth stayed relatively constant from 1980 to 2017. The pre-invasion invertebrate densities at all depths hardly differed from each other. Due to the lack of the omitted 1997 data, it is hard to observe the initial impact of the zebra mussel invasions. However, the 2008 to 2009 data highlighted that the quagga invasion resulted in the largest and fastest drop in invertebrate densities over the entire study. Moreover, in 2008 and 2009, the zebra mussel was the dominant species, thereby emphasizing the shift in dominance towards quagga mussels seen later. Post quagga mussel invasion, there was a leveling off of invertebrate densities to post invasion averages at the 10-, 15- and 20-meter depths as those are the preferred quagga mussel depths (Figure 1).

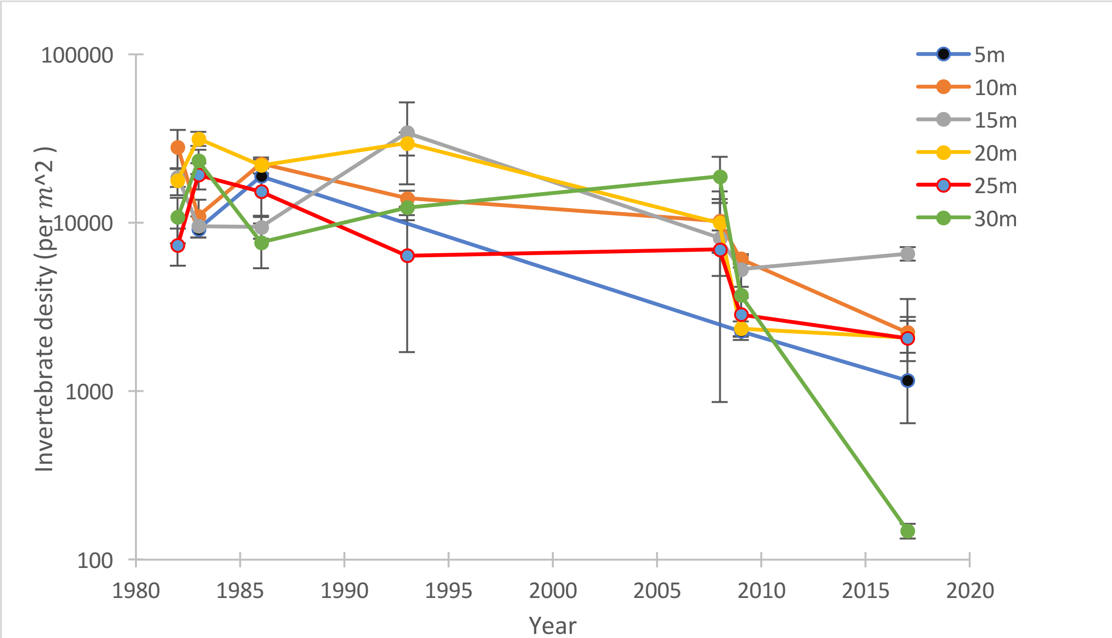

Figure 1. Total benthic invertebrate density found at 5-30m sites in Lake Simcoe, modeling the changes over a period of 40 years from 1980 to 2017. Note y-axis is a log scale. Error bars are ±1 standard error.

Dreissenid Mussels

Before 1994 there was no record of post-veliger dreissenid mussels in Lake Simcoe (Evans et al 2017). Zebra mussels invaded around 1994, demonstrated by an increase in density from 1993- 2008 especially in the 5-, 10-, and 15-meter sites (Figure 2). In 2017, zebra mussels were not found in any samples in Lake Simcoe, around the time of quagga mussel establishment. Zebra mussels in the remaining sites (20, 25, and 30m) did not increase at all and densities stayed low in these regions.

Pre-invasion there was no record of quagga mussels in Lake Simcoe at all. They had become more established by 2009 as shown by a huge jump in density at all depths at that time. The biggest depths to increase was found at the 15- and 25-meter sites, deeper than the preferred zebra mussel depths (Figure 3). In 2009, quagga mussels became the dominant species in Lake Simcoe, making the zebra mussel population almost non-existent by 2017. In 2017, the quagga mussel population soared, reaching extremely high densities that were more than over double that of 2009.

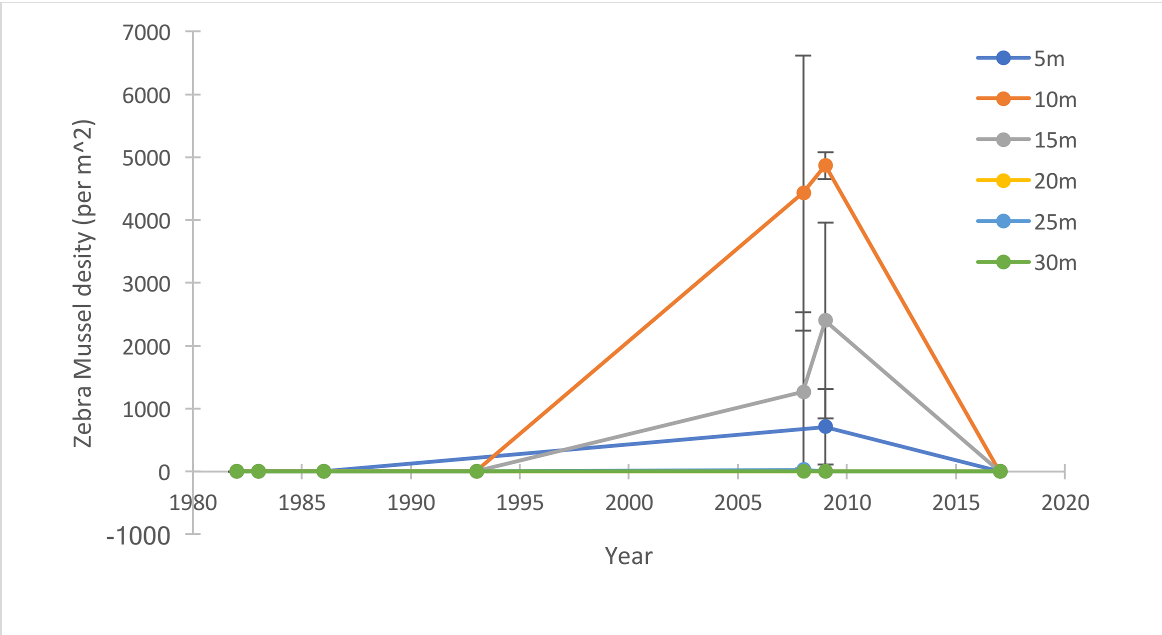

Figure 2. Changes in zebra mussel densities for the 5-30 meter depths over a period of 40 years in Lake Simcoe. Error bars are ±1 standard error.

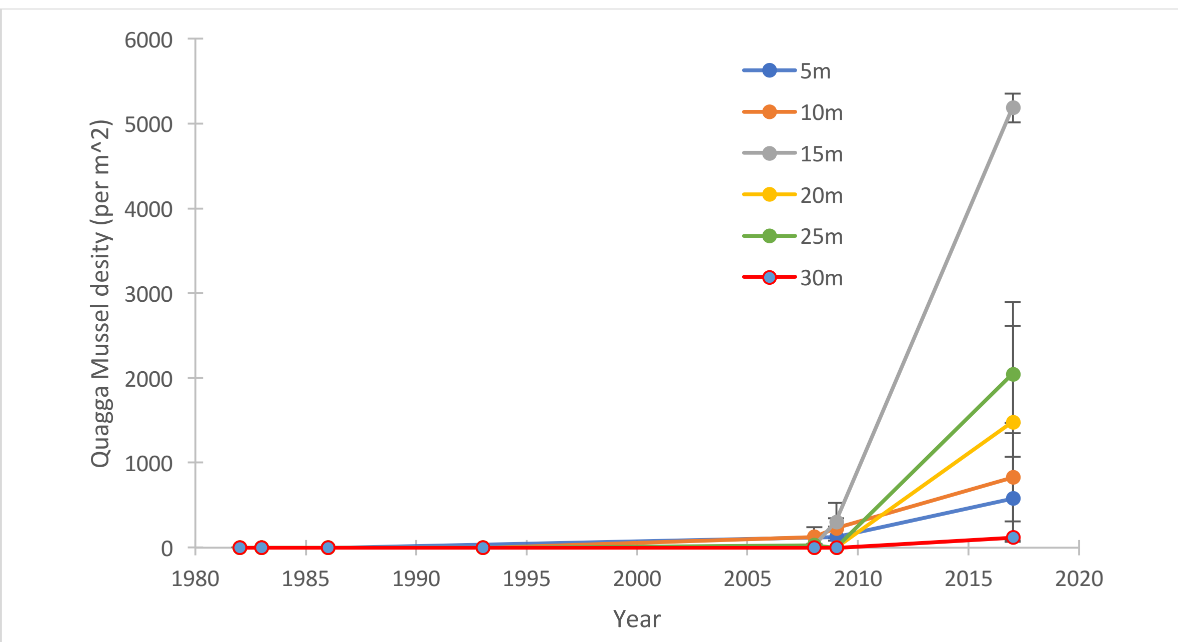

Figure 3. Changes in quagga mussel densities for the 5-30 meter depths over a period of 40 years in Lake Simcoe. Error bars are ±1 standard error.

<u>Native Benthic Invertebrates Densities</u>

Pre-invasion, benthic invertebrates, showed relatively high densities for all species examined in depth (i.e., chromomids, amphipods, gastropods, oligochaetes and plecypoda). Over the entire time period under investigation, chironomids experienced the biggest changes from 2009 to 2017. There was a major shift in the preferred sites and an overall decline in chironomids, suggesting the quagga mussel invasion was the largest factor for the disruption of their distribution. Amphipods experienced huge declines around the late 1980's, suggesting the zebra mussels were more of a factor in causing their declines than the quagga mussel. Compared to the 1980's, in 2009 the amphipods experienced declines but not to the same extent. Gastropod populations actually increased in the 5- and 10-meter sites over the timeframe of the zebra mussel invasion, whereas their population plummeted after 2009 when quaggas began their establishment. Major changes for oligochaetes in the form of populations declines started in 1985. Oligochate populations steadily decreased since that time and through the invasions of both dreissenid species. The quagga mussel invasion appeared to have further influenced these declines, especially in 2009, where the oligochaete population reached undetectable numbers. The plecypoda population stayed relatively constant during the zebra mussel invasion time period and did not experience declines. However, the plecypoda population decreased greatly to the point of non-detection during the quagga invasion.

Amphipods and gastropods showed the lowest initial density in 1980 and their densities were more unpredictable over time. Pre-invasion densities of chironomids and plecypoda had the highest density in the 10- and 15-meter sites (Figures 4 and 8), whereas oligochaetes had the highest densities in the 20- and 30-meter sites (Figure 7). Except for amphipods, all taxa pre-invasion had similar densities for all sites. Amphipods had extremely high densities at the 5-meter site possibly due to a counting error (Figure 5). The general trend for all species post invasion was a decrease in density. Amphipods, gastropods, oligochaetes, and plecypoda all experienced severe declines in the year 2009, following the quagga mussel invasion (Figures 5, 6, 7, 8). Chironomids species experienced more of a population depth shift as their density changed from the 20- and 30-meter sites to higher densities in the 5- and 10-meter sites (Figure 4).

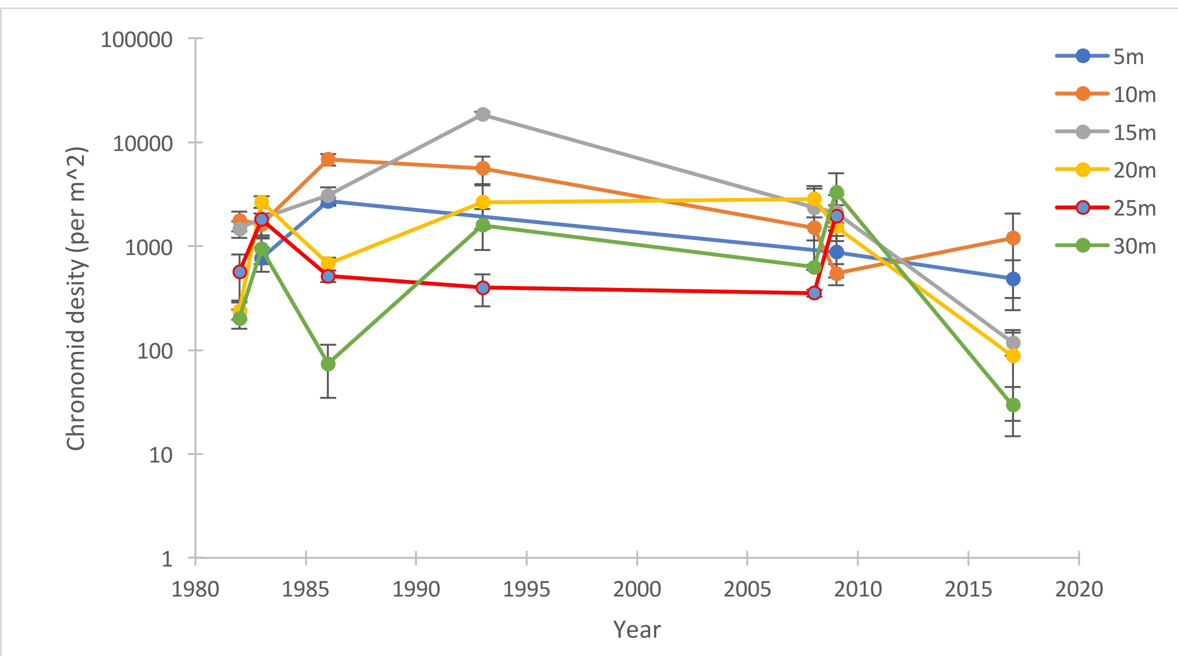

Figure 4. Changes in chironomid densities over 40 years from 1980-2017 compared to depths ranging from 5-30 meters. Note y-axis is a log scale. Error bars are ±1 standard error.

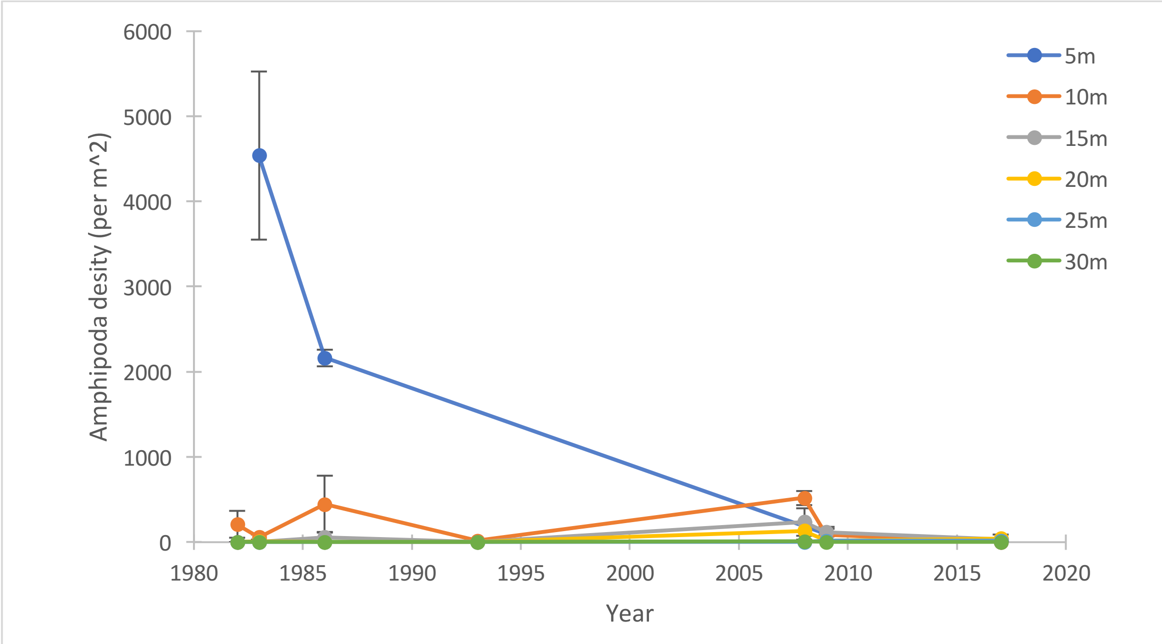

Figure 5. Changes in amphipod density from depths of 5-30 meters over a period of 40 years from 1980-2017. Error bars are ±1 standard error.

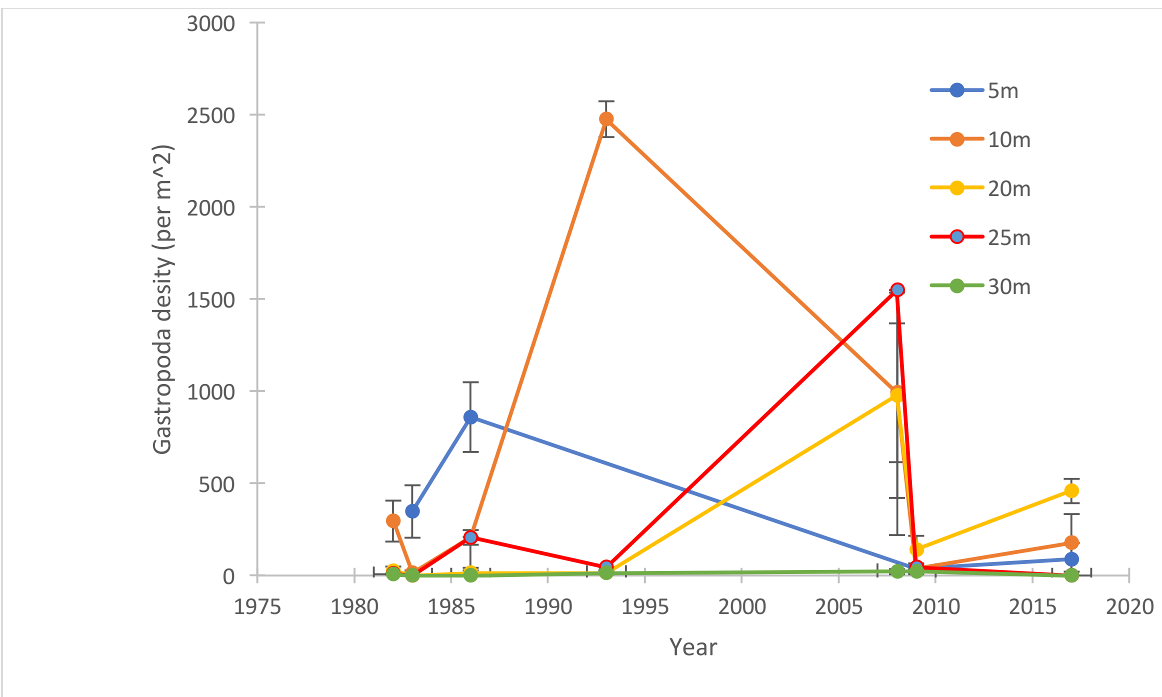

Figure 6. Changes in gastropod density over 40 years from 1980 to 2017 at each depth from 5-30 meters. Error bars are ±1 standard error.

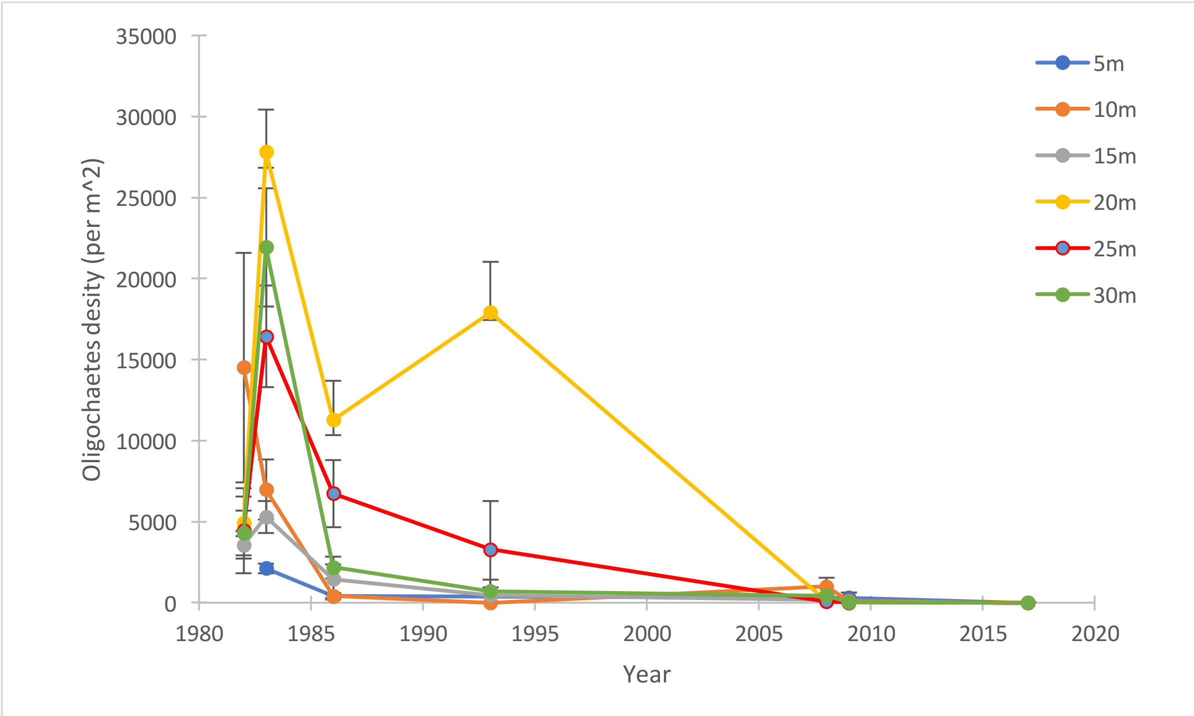

Figure 7. Changes in oligochaetes density at each depth ranging from 5-30 meters over a period of 40 years from 1980-2017. Error bars are ±1 standard error.

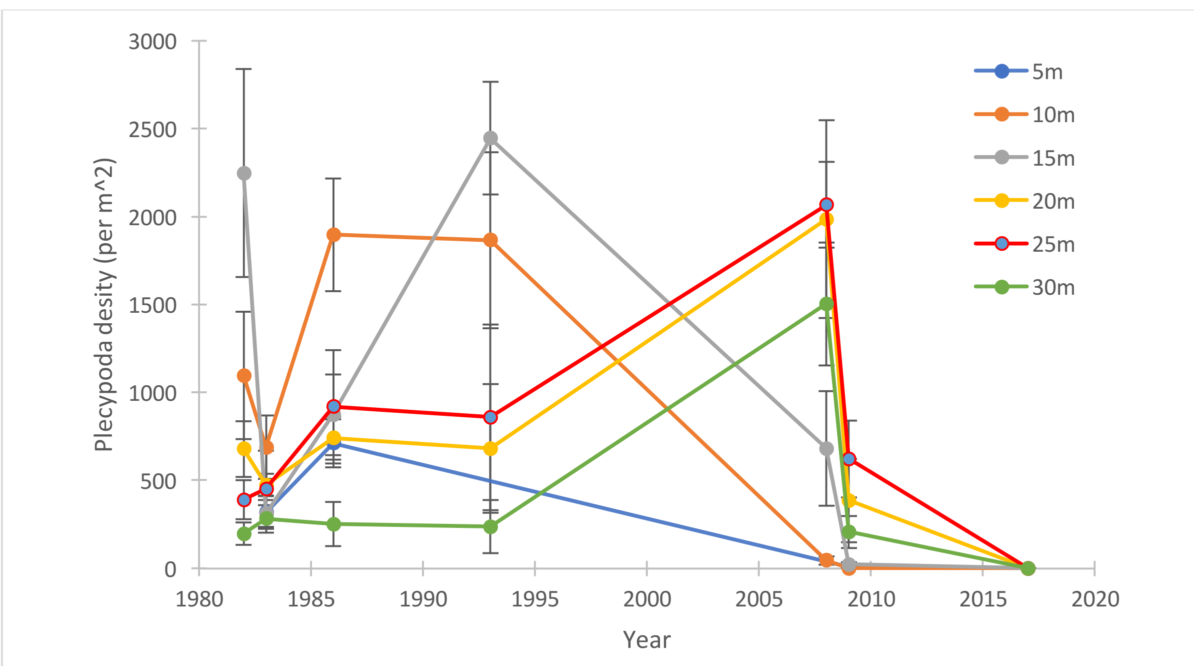

Figure 8. Changes in plecypoda density at each depth ranging from 5-30 meters over a period of 40 years from 1980-2017. Error bars are ±1 standard error.

DISCUSSION

My results indicate that abrupt changes to benthic invertebrate density appear to have been brought on by the invasion of quagga mussels from 2008 to 2009. An enormous decrease in chironomid, gastropod, plecypoda, oligochaete and amphipod densities was observed starting in 2008, especially in the 10-, 15-meter sites. The overall benthic invertebrate density stayed relatively constant up until 2008, and then density decreased rapidly between 2008 and 2009, and then further declined from 2009 to 2017, particularly in the 5- and 30-meter sites. Zebra mussels invaded Lake Simcoe between 1993 and 2008, indicated by a spike in density from the years 1993 to 2008, primarily at the 10- and 15-meter sites. Zebra mussel populations reached their highest densities in 2009 but then declined as quagga mussels took over the lake bottom. The quagga mussel became established in 2008, preferring the deeper sites of 15 to 25 meters. Amphipods, oligochaetes, and plecypoda were completely absent from the 2017 samples. Chironomids and gastropods experienced similar declines effects but their populations managed to be sustained at very low levels. These results are consistent with studies done by Jimenez et al. (2011) that found a low abundance of isopods, amphipods, and gastropods once dreissenid mussels were apparent. The study in this thesis built on those results to demonstrate the further impacts of quagga mussels establishing in the lake at high densities, namely, the apparent elimination of zebra mussels and the further decline of benthic invertebrates.

The loss of many important benthic invertebrates has resulted in immense changes to Lake Simcoe's fisheries, valued to over an estimated value over 50 million dollars (Evans et al. 1996). Lake whitefish are one of the primary catches in Lake Simcoe and the upper Great Lakes but their population in these regions have seen decreased health and decreased individual growth over the last 2 decades (Rennie et al. 2012). Lake whitefish are benthic foragers and primarily rely on soft-bodied and deeper water species such as chironomids, oligochaetes and sphaeriids. With the near extinction of these species due to dreissenids, the whitefish are having to switch their diet to more nearshore hard-bodied organisms such as the dreissenid mussel itself (Rennie et al. 2013). The dreissenid species, with its hard shell, is a costlier energy food source and the result is a decline in lake whitefish growth (Rennie et al. 2012).

Gastropods and chironomids managed to slightly recover their population levels in 2017, following the quagga mussel invasions. Dreissenid mussels facilitated the success of gastropods by increasing lake bottom complexity and increasing food supply. The mussel colonies form biological ‘islands’ that provide refuge and food resources for gastropods (Bially and MacIssac 2000). Chronomids experienced the same facilitation but were more responsive to the additional food source rather than the habitat creation. In the littoral regions with increased light penetration and nutrients released by dreissenids, higher algal growth is created, and the gastropods and chironomids use the added food source.

In 1993, gastropods increased by several orders of magnitude, resulting in extremely high densities for that year. This was likely the result of inconsistency in counting methods, specifically by including gastropods with empty shells in counts rather than gastropods with soft body parts only. In order to accurately represent the gastropod data, the results from 1993 were removed so the data did not influence the analysis of other sample years.

As for the sampling methods, the sampling devices utilized to make the sediment hauls were used inconsistently. Either the Ekman dredge or the petit-Ponar benthic sampler were used, depending on the sample year. However, it is unlikely that the use of different sampling tools affected the results as they collect the same sediment, resulting in similar estimates of community composition and invertebrate density (Elliot and Drake 1981). Also, this study reported densities per m^2, which corrected for minor differences in sampling areas between devices. Furthermore, the presence of mussels in later sample years strongly dictated a general switch from Eckman to Ponar, because the Eckman dredge commonly would jam and not close. With its heavier doors, the Ponar sampler was the only device that would get decent samples as it crushed any mussels that got stuck in the jaws, whereas they would get stuck in the Eckman jaws and the sample would be lost because of one mussel keeping the doors open when bringing samples to the surface.

Lake Simcoe has previously struggled with water quality. Swimming advisories are constantly posted and E. coli is commonly present in the lake, leading to outbreaks. With adequate time Lake Simcoe could have adapted, but with the rapid invasions of zebra and quagga musses, the lake wasn't able to adapt and the result was decreased water quality (Winter et al. 2002). These dreissenid mussels cause increased lake water clarity and, in turn, increase benthic algal production and the depth at which it can occur, resulting in more nutrients being present at deeper depths. The loss of many important benthic invertebrates has altered the oxygen levels present in the lake; chironomid head capsules are consistent with the findings of hypolimnetic O_2 concentrations meaning the head capsules are altering the depths oxygen is present and causing it to be non-cycling static water (Rennie and Evans 2012). Furthermore, the profundal benthos, the deepest zone, were also affected by these invasive dreisssenid mussels through water quality changes, particularly in declines in P (phosphorus) and Chl (chlorine) concentrations causing low oxygen presence and the constituent species to become hypoxic.

The findings of this study can be used to evaluate the effects of dreissenid mussels on Lake Simcoe, and how these invasive species affected the water quality of the lake order to improve it. A study like this one provides insight to how invasive dreissenids mussels have altered the benthic invertebrates of Lake Simcoe and what steps need to be taken to restore the health of the lake back to pre-invasion levels.

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