Dreissenid Mussels and Large Lakes: Effects on Littoral Ecology

by

Tedy Ozersky

A thesis
presented to the University of Waterloo
in fulfillment of the
thesis requirement for the degree of
Doctor of Philosophy
in
Biology

Waterloo, Ontario, Canada, 2010

AUTHOR'S DECLARATION

I hereby declare that I am the sole author of this thesis. This is a true copy of the thesis, including any required final revisions, as accepted by my examiners.

I understand that my thesis may be made electronically available to the public.

Abstract

Invasive organisms are one of the major threats to the ecological integrity of aquatic systems in the 21st century. Among the most notorious and important aquatic invasive organisms are the dreissenid mussels, *Dreissena polymorpha* and *D. rostriformis bugensis*, which having originated in the Ponto-Caspian region are now common in many parts of Europe and North America. Dreissenids have large impacts on many aspects of lentic ecosystem functioning, the sum of which is thought to lead to the translocation of biological production from the pelagic to the littoral zones of lakes. In this thesis I explore the effects of dreissenids on the nearshore zones of large lakes, investigate the mechanisms by which dreissenids couple the pelagic and nearshore zones of lakes and attempt to elucidate the factors affecting the strength of the dreissenid-mediated connection between the pelagic and littoral zones.

The effects of invasive organisms on an aquatic ecosystem will depend, in part, on the distribution and biomass of the invasive organisms in the system. In chapter 2 I present the results of a lake-wide survey of the distribution of invasive dreissenid mussels in Lake Simcoe, Ontario and discuss some of the factors that shape their distribution pattern in the lake. Dreissenid biomass averaged 27.2 (±24.3 SD) g shell-free dry mass (SFDM)/m^2 in the main basin of Lake Simcoe and 12.4 (±16.9 SD) g SFDM/m^2 in macrophyte-dominated Cook's Bay. I argue that water movement is an important determinant of dreissenid distribution, both through catastrophic disturbance in shallow water and through non-catastrophic effects on substrate distribution and possibly food supply rates. In areas of dense macrophyte growth, mussel abundance was shown to be associated with that of preferred macrophyte taxa, in particular with that of *Ceratophyllum demersum*. I used the results of my survey and the relationships between environmental variables and dreissenid biomass to estimate the total biomass of dreissenids in Lake Simcoe: 12,000 tonnes SFDM. Most of the dreissenid biomass in Lake Simcoe was concentrated in the nearshore zone, where dreissenids would have maximal impacts on littoral biological production.

One of the effects of the dreissenid invasion into the Laurentian Great Lakes appears to be a resurgence in the abundance of the nuisance alga *Cladophora glomerata* which experienced a marked decline following phosphorus abatement in the late 1970s and early 1980s. A subsidy of bioavailable phosphorus excreted by dreissenid mussels could be an important mechanism facilitating the growth of *C. glomerata*. In chapter 3, I describe a survey of dreissenid distribution and abundance followed by *in situ* experiments designed to measure dreissenid phosphorus excretion rates. Average dreissenid

mussel abundance in our study area was 3674 (±2233 SD) individuals/m^2, with an average biomass of 52.2 (±29.0 SD) g of shell free dry mass/m^2. The mussels excreted bioavailable soluble reactive phosphorus (SRP) at an average rate of 7.0 μg SRP/g shell free dry mass/hour, contributing about 11 tonnes of SRP to the study area over the *C. glomerata* growing season. Dreissenids appear to be an important source of recycled bioavailable phosphorus to the littoral zone, potentially supplying more soluble reactive phosphorus to the study area than local watercourses and waste water treatment plants, and more phosphorus than is required to sustain local *C. glomerata* growth.

Dreissenid establishment in many systems coincides with increases in the abundance and diversity of littoral benthic invertebrates and with changes to community composition of the benthos. Currently, there is a lack of long-term studies of the impact of dreissenid mussels on hard-substrate inhabiting littoral benthos. In chapter 4 I compare the littoral benthos of Lake Simcoe, Ontario just prior, and 14 years following the establishment of dreissenids in the lake. Densities of non-dreissenid invertebrates on hard substrata increased by nearly 50 times, from an average of 367.9 (±460.8 SD) individuals/m^2 in 1993 to an average of 16,706.4 (±10,204.5 SD) individuals/m^2 in 2008. The taxonomic diversity of the benthos increased significantly. The distribution of benthic organisms also changed; the numerical abundance of benthos has become more even across depths and sites, as has community composition. I suggest that in addition to increasing resource availability to benthic organisms dreissenids have also caused a homogenization of the littoral habitat by increasing the evenness of the distribution of food and habitat resources. The changes in the littoral benthic community in Lake Simcoe likely have wide-ranging implications to higher trophic levels and the cycling of energy in the lake.

In addition to impacting nutrient cycling and the benthic invertebrate communities of littoral zones, dreissenid mussels can have large effects on food webs and energy cycling. In chapter 5 I used stable isotope analysis of pre- and post-dreissenid components of the nearshore food web of Lake Simcoe, Ontario to determine how dreissenids affected food sources and energy flow in the littoral zone of Lake Simcoe. Results suggest that the post-dreissenid food web relies about equally on two energy sources: dreissenid biodeposits (redirected pelagic primary production) and littoral benthic primary producers. Although the relative importance of pelagic and benthic primary production to benthic organisms has not changed much following dreissenid establishment, the absolute importance of both increased considerably in the post-dreissenid littoral zone: the large increase in invertebrate biomass that followed dreissenid establishment means that the amount of both pelagic and benthic primary production needed to sustain post-dreissenid organisms had to increase considerably. The

results of this chapter suggest that dreissenids increase the availability to food to littoral organisms by redirecting pelagic primary production to the benthos and by stimulating littoral benthic primary production. The impacts of dreissenids on littoral benthic organisms probably have large effects on littoral and pelagic fish communities of lakes.

Dreissenid mussels translocate biological production to the benthos by stimulating benthic primary production through nutrient excretion and increases in water clarity, by increasing habitat availability for benthic organisms and by biodepositing pelagic material that becomes available to benthic organisms and the fish that feed on them. I argue that hydrodynamic factors are important in controlling the strength of the dreissenid-mediated pelagic-littoral connection in lakes. Because hydrodynamics relate to lake size, a relationship between lake size and the ability of dreissenids to translocate production the littoral zone can be postulated, where dreissenid effects are maximal in intermediate-sized lakes.

Acknowledgements

Drs. David R. Barton and Robert E. Hecky have my deep gratitude for their guidance, support, criticism, and supervision over the last few years. I also thank Drs. Stephanie Guildford, Ralph Smith and William Taylor for serving on my committee and for providing invaluable advice and guidance. Drs. Michael Stone and Edward Mills provided important insights and comments on an earlier draft of this thesis. Dr. David O. Evans inspired me to work on the benthic community and nearshore food web of Lake Simcoe and deserves thanks for the insight and logistical support he provided.

The help of my friends and fellow members of UWAEG must also be acknowledged. Andrew Bolyachevets, Dr. David Depew, Jenna Disch, Joel Harrison, Dr. Scott Higgins, Adam Houben, Jennifer Hood, Vicky Jackson, Dr. Sairah Malkin, Ryan Scott, Dr. Greg Silsbe, Tyrell Worrall and others provided advice, moral support, help in the field in and in the lab; all that in addition to being wonderful drinking companions. Dr. Sairah Malkin deserves special thanks for introducing me to the joys of field work and setting me on the path to graduate studies in aquatic ecology.

I must acknowledge the help of numerous lab and field technicians without whose assistance little of the work presented in this thesis would have been possible. Eric Dunford, Lin Lee, Simona Lenard, Dylan Pallett, Jessica Pang, Lee Pinnel, and others toiled in the shadows, counting bugs, filtering water and grinding samples. I would like to express my gratitude to Jake LaRose and others at the Lake Simcoe Fisheries Assessment Unit for providing my colleagues and me with a base of operations on Lake Simcoe. I would also like to acknowledge the help and patience of the staff at the University of Waterloo Environmental Isotope Lab.

Finally, I must thank my family, who supported me through the sometimes difficult times as a grad student morally, and at times financially.

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Chapter 1
General Introduction

1.1 Introductory remarks

When non-biologists ask me what I study and I mention zebra mussels I often get nods of recognition and complaints about cutting their feet on "the little bastards" last year at the cottage. The zebra mussel (*Dreissena polymorpha*) and its cousin the quagga mussel (*D. rostriformis bugensis*) are two of the most familiar and recognizable invasive organisms in the Great Lakes region and, as their spread continues, in many other parts of North America. The notoriety of dreissenids is related to the severity of their impacts on ecosystems: from water clarity to phytoplankton community composition to fish yields, dreissenids can affect numerous aspects of the aquatic environment. A conceptual understanding of the way dreissenid mussels affect invaded lentic ecosystems is coagulating around the central idea that *dreissenids translocate biological production from the pelagic realm to the littoral benthos of lakes* (Vanderploeg et al. 2002, Mills et al. 2003, Hecky et al. 2004, Higgins and Vander Zanden 2010). Working within this conceptual framework, my PhD thesis explores the way dreissenid mussels affect the ecological relationships in the nearshore areas of large lakes.

1.2 Dreissenid invasion history and autecology

Dreissenids are thought to have evolved in ancient Lake Pannon during the late Miocene period, more than 10 million years ago (Müller et al. 1999). In modern times their native range included the brackish and freshwater drainages of the Black, Azov and Caspian seas (May et al. 2006). Dreissenids began their range expansion in the 18th century, which was facilitated by the construction of shipping canals among various water bodies in the Ponto-Caspian area and Europe. By the 19th century dreissenids made their way to the Thames estuary, and many other water bodies throughout Europe (Astanei et al. 2005).

In 1988 adult *D. polymorpha* were discovered in Lake St. Clair (Hebert et al. 1989), and in 1991 a second dreissenid species, *D. rostriformis bugensis* was found in the Erie Canal and in Lake Ontario (Mills et al. 1996). Both dreissenids are thought to have been introduced as planktonic veligers in the ballast water of transoceanic shipping vessels, zebra mussels likely arriving from North European ports, and quagga mussels from the Black Sea (Brown and Stepien 2010). Since their initial introduction in the lower Laurentian Great Lakes dreissenids have spread to all five of the Great

Lakes, and many interconnecting waterways including the Mississippi River. In 2007 quagga mussels were discovered in Lake Mead, Nevada, and now occur in a number of watersheds in the south-western United States (Stokstad 2007).

Dreissenids are unique among freshwater bivalves in having a planktonic larval stage and the ability to attach to hard substrates by means of a byssus. These two traits are thought to play an important role in the invasiveness of dreissenids. Planktonic larvae can remain in the water column for up to a month (Sprung 1993) and are able travel large distances with water currents and in the ballast tanks of ships. Adult dreissenids are somewhat dessication resistant and can be transported between water bodies attached to the hulls of towed boats, on anchors, buoys and even on scientific equipment (Carlton 1993). Dreissenids are astoundingly fecund, with females producing up to a million eggs in one spawning event (Sprung 1993), and can be very abundant: settled mussels can reach densities of 50,000-150,000/m2 in the early stages on an invasion (eg. Dermott et al. 1993, Evans et al. in press).

Zebra and quagga mussels display some difference in habitat preference. While both species appear to prefer hard substrates, quagga mussels are able to colonize softer, silty substrates, and consequently are more common in deeper portions of lakes (Mills et al. 1996). When both species occur in the same system, over time quagga mussels are often able to out compete and replace zebra mussels. Initially, the two species partition the habitat, with zebra mussels being more common in shallow water, and quagga mussels occurring more frequently in deep water, but eventually quagga mussels displace zebra mussels even in shallow water. This has been observed in Europe (reviewed in Mills et al. 1996), as well as in many North American aquatic systems (Mills et al. 1999; Wilson et al. 2006, Patterson et al. 2005, Ricciardi and Whoriskey, 2004). Faster growth rates at low food concentrations is one of the factors thought to favour quagga mussels over zebra mussels (Stoeckmann 2003).

Dreissenid mussels are filter feeders, capable of filtering bacteria, algae, and small zooplankton in the size range of 0.4–1200 µm from the water column (Sprung and Rose 1988, Cotner et al. 1995, Lavrentyev et al. 1995, Horgan and Mills 1997). Dreissenids not only filter a wide range of particle sizes, but are capable of filtering a large volume of water. Estimates of filtration rates vary, ranging from 4 ml/individual/h to upwards of 200 ml/individual/ h, resulting in substantial filtering potential for large populations of dreissenids (Bunt et al. 1993, Reeders et al. 1993, Horgan and Mills 1997, Roditi et al. 1997). Regardless of clearance rates, it has long been realized that the ability of dreissenids and other mussels to filter particles from the water column strongly depends on

hydrodynamic factors (eg. Izvekova and Lvova-Katchanova 1972, Frechette et al. 1989). Because dreissenids are benthic organisms they rely on water mixing to replenish the supplies of edible particles near the bottom, and their ability to affect the phytoplankton is highest in mixed water columns (Ackerman et al. 2001, Edwards et al. 2005).

Material that is removed from the water column by dreissenids has a number of possible fates. Material that is not ingested is rejected as mucous-bound pseudofeces. Material that has been ingested can either be used to support metabolism, or excreted as feces and dissolved waste. Deposition rates, and the properties of feces and pseudofeces (biodeposits) have been examined by a number of investigators. Biodeposits consist of a mixture of digested and live phytoplankton, organic detritus and mineral particles (Izvekova and Lvova-Katchanova 1972, Roditi et al. 1997, Naddafi et al. 2007). Estimates of deposition rates show that dreissenid deposits can contribute significantly to the flux of material to the benthos, and together with the bacteria inhabiting them can be a significant food source to some benthic organisms (Izvekova and Lvova-Katchanova 1972, Gergs et al. 2009).

1.3 Dreissenid impacts on ecosystems:

Because of their filter-feeding mode of life, and their ability to attain very high densities on appropriate substrates, dreissenids can have large impacts on many facets of the aquatic environment. Perhaps most apparent are effects of dreissenids on the plankton. By removing a large quantity of phytoplankton from the water, dreissenids can increase water clarity, and alter the community composition of the phytoplankton. Increases in water clarity are reported from numerous dreissenid invaded systems, as are reductions in seston and chlorophyll concentrations and in algal biovolume (Leach 1993, Budd et al. 2001, Eimers et al. 2005, Higgins and Vander Zanden 2010). Increased water clarity enables primary production to occur at greater depths, leading to increases in the production of benthic algae and macrophytes (Pillsbury et al. 2002, Higgins 2005a, Zhu et al. 2006, Depew et al. in press).

The enhancement of benthic primary producers by dreissenids occurs not only through changes in water clarity but also through changes in nutrient cycling. Large populations of dreissenid mussels excrete dissolved nutrients at ecologically significant rates, potentially supplying limiting nutrients to benthic primary producers (Arnott and Vanni 1996, James et al. 2001, Conroy et al. 2005). Stewart et al. (1998) convincingly demonstrated that dreissenids can increase benthic primary production on a local scale, most likely though the excretion of dissolved nutrients. Particulate dreissenid biodeposits may also increase the nutrient content of sediments, fertilizing macrophyte

growth. Experiments in marine systems demonstrated that mussels can fertilize the growth of sea grasses (Reusch et al. 1994, Peterson and Heck 2001), although Zhu et al. (2007) found no fertilizing effect of dreissenids on macrophytes in Oneida Lake.

In addition to impacting pelagic and benthic primary producers, dreissenids have large effects on benthic invertebrates. Many studies and meta-analyses indicate that dreissenids enhance the production of littoral benthos, while negatively affecting the abundance of profundal benthos (Stewart and Hynes 1994, Dermott and Kerec 1997, Karatayev et al. 1997, Ricciardi et al. 1997, Bially and MacIsaac 2000, Lozano et al. 2001, Mayer et al. 2002, Ward and Ricciardi 2007, Higgins and Vander Zanden 2010; Jimenez et al. 2010). It is thought that the enhancement of littoral benthos occurs due to two factors. Dreissenids enhance food availability by biodepositing edible material and increasing the production of benthic algae. Dreissenids also increase the availability of habitat for benthic organisms among the shells of living mussels and in the shell deposits of dead mussels (Botts et al. 1996, Ricciardi et al. 1997, Stewart et al. 1998). The negative impacts of dreissenids on profundal benthos are less well understood, but it is thought that reduction in phytoplankton biomass and competition between dreissenids and other benthos for settling phytoplankton are responsible (Dermott and Kerec 1997, Higgins and Vander Zanden 2010).

Clearly, the impacts of dreissenids on various components of aquatic ecosystems have large consequences for the entire food web and for higher trophic levels. Many of the impacts of dreissenids on food webs can be viewed as the result of shifting patterns of biological production, with simultaneous enhancement in littoral areas and reductions in pelagic and profundal areas (Higgins and Vander Zanden 2010). The enhanced production of algae and invertebrates in nearshore areas has been associated with increases in the production of littoral fish species in Eastern European lakes (Karatayev et al. 1997) and in experimental ponds in North America (Thayer et al. 1997). Bioenergetics modeling and studies on the distribution and diet of pelagic fish suggest that dreissenids have led to reductions in the body condition and growth of some pelagic fish and increased their reliance on nearshore resources (Pothoven et al. 2001, Pothoven and Madenjian 2008, Rennie et al. 2009).

1.4 Structure and objectives of the thesis:

This thesis takes a multi-directional approach to exploring the effects of dreissenid mussels on the nearshore ecology of large lakes, focusing mainly on Lake Simcoe, Ontario, and to a lesser degree on Lake Ontario. The core of the thesis consists of four data chapters (chapters 2-5), each

written as an independent study. At the time of thesis submission chapters 2 and 3 have been published in the Journal of Great Lakes Research and chapter 4 has been submitted for publication in the Journal of the North American Benthological Society. The overall aims of this thesis were to describe and quantify how dreissenid mussels affect nutrient cycling, biological production and food web structure in the littoral zones of large lakes. For the purposes of this thesis I define the littoral zone as the nearshore area of a lake, where sufficient light reaches the lake bottom to maintain net primary production.

The effects of dreissenids on an ecosystem will depend in part on their distribution and abundance in the system. In chapter 2 I set out to describe the distribution of dreissenid mussels in Lake Simcoe, Ontario, and to determine which environmental parameters are important in determining dreissenid distributions. It is well know that substrate composition is an important determinant of dreissenid distribution (e.g. Mellina and Rasmussen 1994, Wilson et al. 2006), but the impacts of water movement on dreissenids are not well described. I used a video-based method to survey dreissenids on simple substrates such as rock, sand or silt, and ponar sampling in areas of dense macrophyte growth to describe relationships between dreissenid biomass, substrate composition, water movement and macrophyte community composition. The results of this study will improve our understanding of dreissenid- environment interactions and are the first published demonstration that water movement is an important determinant of dreissenid distribution of a whole-lake scale.

Excretion of dissolved nutrients by dreissenids has been measured in a number of lab studies (Arnott and Vanni 1996, Conroy et al. 2005), but field estimates of dreissenid phosphorus excretion are rare. Chapter 3 details a study designed to measure the *in situ* excretion of dissolved phosphorus by dreissenids in the nearshore of Lake Ontario. I used benthic microcosms to measure dreissenid excretion rates, and conducted a video-based survey of dreissenid biomass distribution in a portion of the lake nearshore which enabled me to estimate the excretion rates of the entire dreissenid population in my study area. To determine the importance of dreissenid excreted phosphorus to the study area I estimated the contribution of land based point- and non-point sources of phosphorus in the study area. Finally, with the help of Dr. Sairah Malkin, an estimate of phosphorus demand by benthic primary producers was made. This enabled me to compare dreissenids as a source of phosphorus to watershed phosphorus contributions to phosphorus demand by primary producers, and to gain a better understanding into the role of dreissenids in nearshore nutrient cycling.

While it is known that dreissenids enhance the production of nearshore invertebrates (Ward and Ricciardi 2007, Higgins and Vander Zanden 2010), few studies have examined the long term effects of dreissenids on hard-substrate inhabiting littoral benthos. Chapter 4 describes such a study. Dr. David Evans of the Ministry of Natural Resources conducted a detailed survey of the littoral macroinvertebrate community in Lake Simcoe just prior to dreissenid establishment, and I repeated his survey in 2008, fourteen years following dreissenid establishment. In both years sampling was conducted at four different sites and three different depths at each site. This enabled me to determine whether dreissenid impacts on the benthos vary spatially and with depth, another novel aspect of this study.

Chapter 5 explores the effects of dreissenids on the nearshore food web of Lake Simcoe. A number of authors have suggested that dreissenids could increase the contribution of pelagic carbon to littoral benthos (Izvekova and Lvova-Katchanova 1972, Gergs et al. 2009), but there are no studies examining the changes to the benthic food web associated with dreissenid establishment. The objectives of this chapter were to describe feeding relationships in the pre- and post-dreissenid littoral food webs on Lake Simcoe and to determine whether dreissenids increase the reliance of the benthic food web on redirected pelagic carbon. I used stable isotope analysis of pre- and post-dreissenid benthic organisms to evaluate the effects of dreissenids on carbon sources and feeding relationships in the benthos and to test the effect of using different mixing model and trophic level estimation methods on food web reconstruction. In Chapter 6 I summarize the results of chapters 2–5, and propose that the strength of the dreissenid-mediated pelagic-littoral connection strongly depends on hydrodynamic factors and lake size.

Chapter 2
Effects of Water Movement on the Distribution of Invasive Dreissenid Mussels in Lake Simcoe, Ontario

2.1 Introduction

The ability of invasive dreissenid mussels *(Dreissena polymorpha* and *D. rostriformis bugensis*) to attain very high biomass in some systems and consequently affect many important aspects of their environment has led to them being labeled "keystone species" (Vanderploeg et al. 2002), "ecosystem engineers" (Hecky et al. 2004, Sousa et al. 2009) and even "keystone engineers" (Gergs, 2009). Dreissenids can impact numerous facets of the aquatic environment including water clarity (e.g., Lowe and Pillsbury 1995, Eimers et al. 2005), nutrient dynamics (Hecky et al. 2004, Conroy et al. 2005), pelagic and benthic production (Johannsson et al. 2000, Vanderploeg et al. 2002), food web and community structure (Bially and MacIsaac 2000, Mills et al. 2003), sediment accumulation and distribution patterns (Howell et al. 1996, Klerks et al. 1996), and the accumulation and distribution of toxic substances (Howell et al. 1996). The magnitude and spatial extent of these effects will depend, in large part, on the abundance and distribution attained by dreissenids in the system.

Previous studies have identified a number of environmental parameters that can affect dreissenid distribution and abundance. These parameters include, among others, salinity and calcium concentration (Mellina and Rasmussen 1994, Mills et al. 1996), temperature (Mitchell et al. 1996), availability of suitable substrate (Mellina and Rasmussen 1994, Patterson et al. 2005, Wilson et al. 2006) and predation pressure (Barton et al. 2005, Lederer et al. 2006). Despite the recognition that physical disturbance by water movement is an important force structuring the distribution of mussels in marine systems (Sousa 1985, Hunt and Scheibling 2001, Westerbom and Jattu 2006) as well as that of some macrobenthos in freshwater systems (Barton and Carter 1982), little research has been done on the role of disturbance in structuring dreissenid mussel populations in freshwater. To my knowledge only two studies have explicitly examined the role of disturbance by surface waves on dreissenid mussel distribution. In a study of one site in Lake Erie, MacIssac (1996) found that dreissenids were more common in deeper water and on larger rocks where they would be more protected from physical disturbance by waves. Similarly, Bially and MacIsaac (2000) found that

larger colonies in deeper water were less vulnerable to destruction by water movement in a study of dreissenid colonies on soft substrates in Lake Erie. As far as I am are aware, no system-scale studies of the effects of physical disturbance by water movement on dreissenid distributions have been published to date.

I undertook a survey of dreissenid mussels in Lake Simcoe, Ontario, in order to estimate their lake-wide abundance and describe and quantify the effects of several key environmental parameters on their distribution. I expected that the most important factor affecting dreissenid distribution would be the availability of hard substrata (Mellina and Rasmussen 1994, Jones and Ricciardi 2005) but that local abundances could also be affected by exposure to wave action (MacIsaac 1996, Bially and MacIssac 2000). Dreissenids are capable of an epiphytic existence, settling on and attaching to macrophytes (e.g., Diggins et al. 2004), so I anticipated that mussel abundances may be related to macrophyte distribution in parts of Lake Simcoe where vascular plants are abundant. The results of this study will be important to understanding the effects of dreissenids on the Lake Simcoe ecosystem, as well as in any future modeling efforts which integrate physical and biological processes in Lake Simcoe.

2.2 Materials and Methods

2.2.1 Study site

Lake Simcoe is the largest inland lake in southern Ontario with an area of 722 km^2, mean depth of 14.2 m and maximum depth of 42 m (Young et al. 2010). The extensive littoral zone of Lake Simcoe is dominated by rocky substrates with some sandy areas as well as areas of dense macrophyte growth and finer sediments. Soft sediments predominate at depths greater than about 8–9 m (Rawson 1930). The lake consists of a roughly square oligo-mesotrophic main basin and two large bays: the deep and oligo-mesotrophic Kempenfelt Bay, and the relatively shallow, macrophyte dominated, mesotrophic Cook's Bay (Fig. 2.1). The main basin has a number of islands, the two largest of which are Georgina and Thorah Islands (15 km^2 and 6 km^2, respectively). The proximity of Lake Simcoe to the Toronto metropolitan area makes it a popular recreational site, with a large (>$200 million/year) sports fishery, in part supported by intensive stocking programs (Young et al. 2010).

Lake Simcoe experienced a number of invasions by exotic species over the last century, with dreissenid mussels being among the most recent. Zebra mussels (*D. polymorpha*) were probably introduced into the lake in 1991 and were well established by 1996 (Evans et al. in press). Quagga

mussels (*D. rostriformis bugensis*) were first detected in 2004, but so far appear to be significantly less abundant than zebra mussels (personal observation). Dreissenids are suspected of contributing to a number of recent changes in Lake Simcoe; decreased algal biovolume, increased water transparency, increased biomass and production of macrophytes, changes in benthic communities and changes in nutrient dynamics have all been linked with the establishment of dreissenids (Eimers et al. 2005, Depew et al. 2010, Jimenez et al. 2010, Winter et al. 2010, Guildford et al. unpublished).

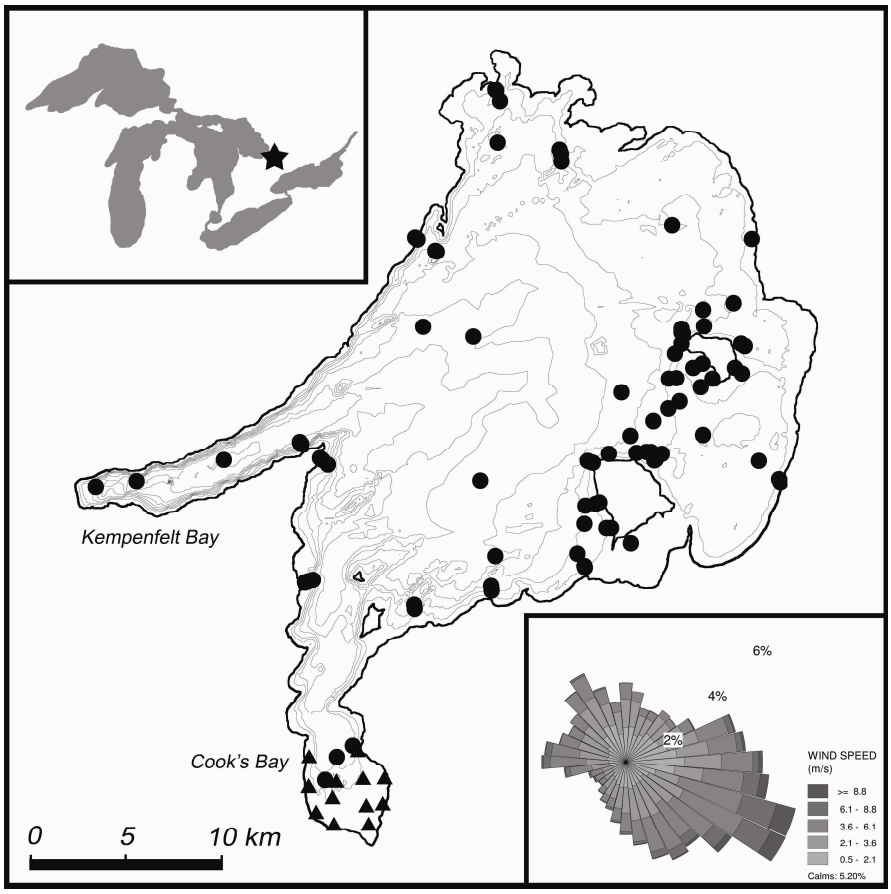

Figure 2.1: Map and location of Lake Simcoe with sampling sites and 5-m contour lines shown. Circles represent video survey sites, triangles represent sites surveyed with Ponar. The relative location of Lake Simcoe is represented by star in top inset. Bottom right inset shows a wind rose for Lake Simcoe, based on 2006–2008 meteorological data, with 'petals' pointing in the direction in which wind blows.

2.2.2 Estimation of mussel biomass

I used a video-based method to assess mussel distribution and biomass in the main basin of Lake Simcoe and in Kempenfelt Bay. Dreissenid percent cover was determined from underwater video recordings, and a percent cover-dreissenid biomass regression was used to estimate mussel biomass in video recordings. Video sampling offers a fast and economical way of surveying mussel distributions on relatively simple substrates (Custer and Custer 1997, Ozersky et al. 2009), but cannot be used to survey mussels attached to macrophytic vegetation. Since macrophytes are common in the nearshore of Cook's Bay, I sampled mussels and macrophytes in that portion of the lake using a Ponar grab.

Main Basin and Kempenfelt Bay

Mussel surveys were conducted over a number of sampling trips during the summers of 2006, 2007 and 2008. Six sites were sampled in May 2006, and another 20 in August 2006, all in the vicinity of Georgina and Thorah Islands. Nine sites were sampled in May 2007 and another 52 sites were sampled in October 2007; these were distributed throughout the main basin of the lake. Sites where heavy periphyton growth inhibited analysis of video images in October 2007 were re-sampled in September 2008. Examination of the results showed no evidence of differences in dreissenid biomass between years, so data from all three survey years were combined for analysis. Of the 87 sites visited, 22 were at a depth of 2 m, 22 were at a depth of 5 m, 29 were at a depth of 10 m, and 14 ranged in depth from 12 to 42 m.

The same sampling procedure was followed on each sampling date. A Splashcam underwater video camera (Ocean Systems, Everett, WA) connected to a DVD recorder was used to film the lake bottom from a boat. The camera was mounted in an aluminum frame such that an area of ~0.041 m^2 was filmed when the camera frame was resting on the bottom. Upon arrival at a sampling site, the depth and the site coordinates were recorded and the tethered frame was lowered until it touched bottom. The camera and frame were repeatedly raised and lowered to capture a number of separate "video quadrats" (Fig. 2.2) of the lake bottom at each sampling location.

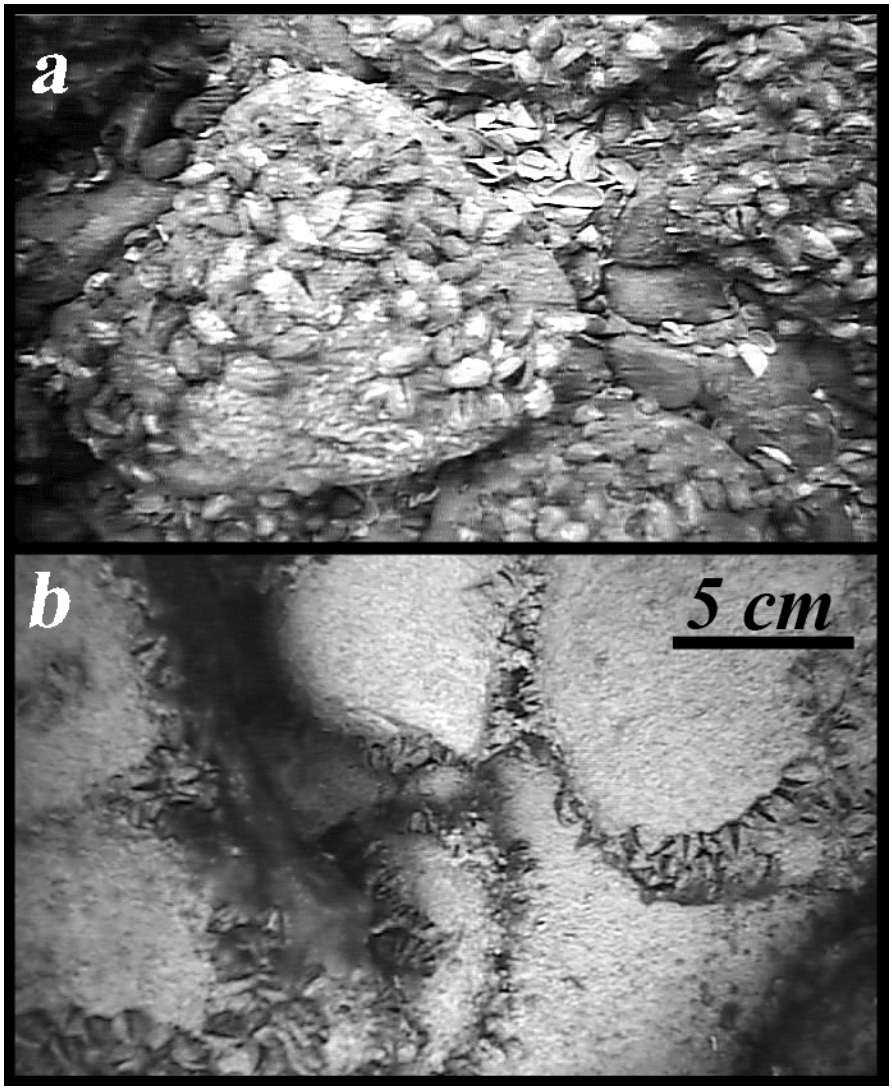

Figure 2.2: Video quadrats from 2-m sites with two different depth adjusted exposure (DAE) levels a) Grape Island site, DAE=8.4 b) Blackbird Point site, DAE=27.2.

The video footage from each site was converted into digital images by capturing video stills of non-overlapping quadrats not obstructed by disturbed sediment or macrophytes while the camera frame was resting on the bottom. Three to five randomly selected still images from each sampling site were analyzed using Adobe Photoshop CS2, version 9.0 (Adobe Systems, San Jose, CA). The areas covered by dreissenids in each image were delineated and coloured bright red, and the proportion of red pixels in the image was determined from a colour histogram. The proportion of red pixels in each image represents dreissenid percent cover which was converted to dreissenid biomass (see below). I

also used the video footage to classify the substrate in each quadrat as silt, sand, rock (which generally consisted of cobble and pebble), or mixed rock and silt.

To convert percent dreissenid cover from the video images to estimates of dreissenid biomass, a percent cover-biomass relationship was developed. Video groundtruthing was carried out on August 10, 2006 at Sibbald Point Provincial Park (44º 20' 09.5" N, 79º 19' 34.5" W) at a depth of ~ 2 m. Calibration of the video technique at greater depths was impossible due to recent legislative restrictions on scientific diving in the province of Ontario imposed by the Ontario Ministry of Labour. Substrate at the site consisted primarily of cobble and boulder with some pebble. Ten quadrats spanning a wide range of dreissenid percent cover were filmed and all mussels from each quadrat were harvested by a skin diver using an airlift sampler (Barton and Hynes, 1978). Upon return to the lab the dreissenid percent cover in each video quadrat was determined as described above. Mussels physically harvested from each quadrat were counted and shell length was measured with electronic calipers to the nearest 0.1 mm. Seventy-three individuals ranging in size from 5.0 to 24.6 mm were dried at 60ºC for 48 hours, and weighed before and after soft tissues were removed from the shells. The relationship between shell length and soft tissue mass was used to construct a power function between shell length (mm) and dreissenid biomass (g), expressed as shell-free dry mass (SFDM):

$$\text{SFDM}=0.000014\times\text{Shell length}^{2.31},\ R^2=0.92$$

This relationship was used to calculate dreissenid biomass for each of the harvested calibration quadrats. Percent cover determined from video analysis of calibration quadrats was regressed against dreissenid biomass determined for each calibration quadrat. The resulting relationship was used to convert percent cover determined from video analysis to dreissenid biomass for the survey quadrats (see results section).

Cook's Bay

A petite Ponar grab (sampling area=0.0231 m^2) was used to obtain triplicate samples of mussels and macrophytes at 13 sites, ranging in depth from 1 to 5 m on August 9, 2006. The contents of each grab were placed in a 250-µm aperture net and washed to remove fine sediment. Mussels and macrophytes were removed to separate plastic bags and placed on ice until they could be frozen upon return to the lab. Plants were identified to genus or species and recorded in order of their relative abundance in the sample. The plant material was then rinsed, dried at 60ºC for 48 hours and weighed to determine dry mass. Frozen mussels were thawed, measured with electronic calipers to the nearest 0.1 mm and their biomass was estimated using the relationship between shell length and SFDM.

2.2.3 Site exposure determination

The wind exposure (and hence the degree of potential disturbance by water movement) of all sampling sites at depths ≤10 m was determined from wind records and fetch. Records of wind speed and direction during 2006–2008 were obtained from the National Climate Data and Information Archive (Environment Canada, http://climate.weatheroffice.ec.gc.ca/) for the Barrie-Oro meteorological station (44º 26' 60.0" N, 79º 32' 60.0" W). A wind-rose diagram showing the distribution of wind speed and direction is presented as an inset in Fig. 2.1. I chose to restrict analysis to the strongest 10% of winds (wind speed >6.1 m/s), reasoning that strong winds would be most important in creating physical disturbance and structuring mussel distributions. To parameterize wind exposure I divided the sum of wind speeds blowing along 20º compass intervals by the sum of wind speeds blowing from all directions to obtain an index of relative wind exposure from each direction. The fetch across water was determined for each sampling site using ArcView 3.2 GIS software (ESRI, Redlands, CA). A clear acetate sheet with 18 lines representing compass directions matching those for which relative wind exposure was determined was taped to a computer screen and centered over an individual site. The fetch from each site to the nearest shoreline (mainland or island) was measured along 18 compass directions to the nearest 100 m. For nearshore sites (less than 500 m from shore), fetch was not measured within 30º parallel to the shoreline on each side of the site, since winds blowing parallel (or nearly parallel) to land are much less important in creating waves and disturbance than winds blowing more directly toward land.

Total wind exposure for each site was estimated by multiplying the square root of fetch along each of the measured compass directions by the relative wind exposure along that direction and summing the resulting estimate of wind exposure from each measured compass direction. This transformation was applied because wave energy and height are proportional to the square root of fetch (Wetzel 2001). To account for diminishing wave energy at increasing depth I calculated the Depth Adjusted Exposure (DAE) for each site by dividing the total wind exposure of each site by site depth squared. I squared the depth of the site since wave energy is dampened proportionally to depth squared (Wetzel 2001). This method of parameterizing wind exposure integrates the frequency and the speed of winds from each particular direction across open water as well as the effect of depth on exposure. Variations of this method for estimating wind exposure have been used in both freshwater and marine studies (e.g., Barton and Carter 1982, Westerbom and Jattu 2006). As can be expected, DAE values generally decreased with depth, and were higher in the main basin than in Cook's Bay because of shorter fetch in Cook's Bay. At each depth, sites were bimodally distributed in terms of

DAE; sites on southeastern shores tended to have higher DAE values than sites on northwestern shores owing to the prevailing north-western winds in the region.

2.2.4 Lake-wide biomass estimate

Lake-wide dreissenid biomass was estimated by extrapolating biomass estimates by depth and substratum, using the results of video-sampling in the main basin and in Kempenfelt Bay and Ponar sampling in Cook's Bay. A digitized bathymetric map of Lake Simcoe (excluding Cook's Bay) was used to estimate the areas of lake-bottom between 0–3.5 m, 3.5–8 m, 8–12 m, 12–20 m and 20–42 m. Dreissenid biomass differed among substrata so totals for each depth interval were calculated from the average dreissenid biomass in each substratum/depth interval, weighted by the frequencies of different substrata at our sampling sites. Because dreissenid biomass varied significantly with DAE at 2-m depths (see results section), the biomass calculation for the 0–3.5-m interval was further weighed for DAE. The shoreline of the lake was divided into 27 segments and the DAE for the center of each shoreline segment was measured in the same way as for the sampling sites. The average dreissenid biomass (g/m^2) was calculated for each segment based on its DAE value and the DAE-dreissenid biomass regression on rock substrates for the 2-m sites:

$$SFDM=60.82-(1.80\times DAE),\ R^2=0.56$$

Total dreissenid biomass for the 0–3.5-m depth interval was calculated by multiplying the dreissenid biomass/m^2 by the area of each shoreline segment and summing the values for all segments. Sand supported low dreissenid biomass, and dominated 9.2% of quadrats at 2-m depths. The biomass estimate was adjusted to account for sand sites by assuming 9.2% of the lake bottom in the 0–3.5-m interval was sandy. In Cook's Bay I used average biomass estimates from macrophyte dominated sites for the 0–8-m depth interval, and average biomass estimates from 10-m sites for the deeper portions of the bay where macrophytes were not found.

2.2.5 Statistical analyses

Because depth, substrate type and exposure are all related, but depth and substrate type are categorical variables whereas exposure is a continuous variable, I chose to assess the effects of these factors on dreissenid biomass separately. Dreissenid biomass was not normally distributed and could not be transformed to approximate normality, making the use of non-parametric tests necessary. Parametric tests were used where assumptions of normality and equal variance were met. Comparisons of multiple groups were carried out using Kruskal-Wallis one-way non-parametric

ANOVAs, followed by Dunn's post-hoc tests. T-tests were used where two groups meeting the assumptions of normality and equal variance were being compared. Simple linear regressions were used to examine the relationship between dreissenid biomass and DAE at 2, 5 and 10-m depths. The association between depth, macrophyte dry mass and dreissenid biomass in Cook's Bay was assessed using Spearman's rank correlation analysis. All statistical analyses were carried out using SigmaPlot 11.0 for Windows (Systat Software Inc., Chicago, IL).

2.3 Results

2.3.1 Mussel distribution and biomass

Main basin and Kempenfelt Bay

Video estimates of the percent cover of dreissenids in calibration quadrats ranged from 18.3 to 87.6%. Measured dreissenid biomass in these quadrats ranged from 9.2 to 48.0 g/m^2. Average mussel length in calibration quadrats was 13.0 mm, and average biomass per mussel was 0.0066 g SFDM. A linear relationship between percent cover and dreissenid biomass (g/m^2) fitted to the data (dreissenid biomass=0.75×(percent cover)) explained 85.7% of the variation (Fig. 2.3). This equation was used to convert percent cover as determined from video sampling to dreissenid biomass.

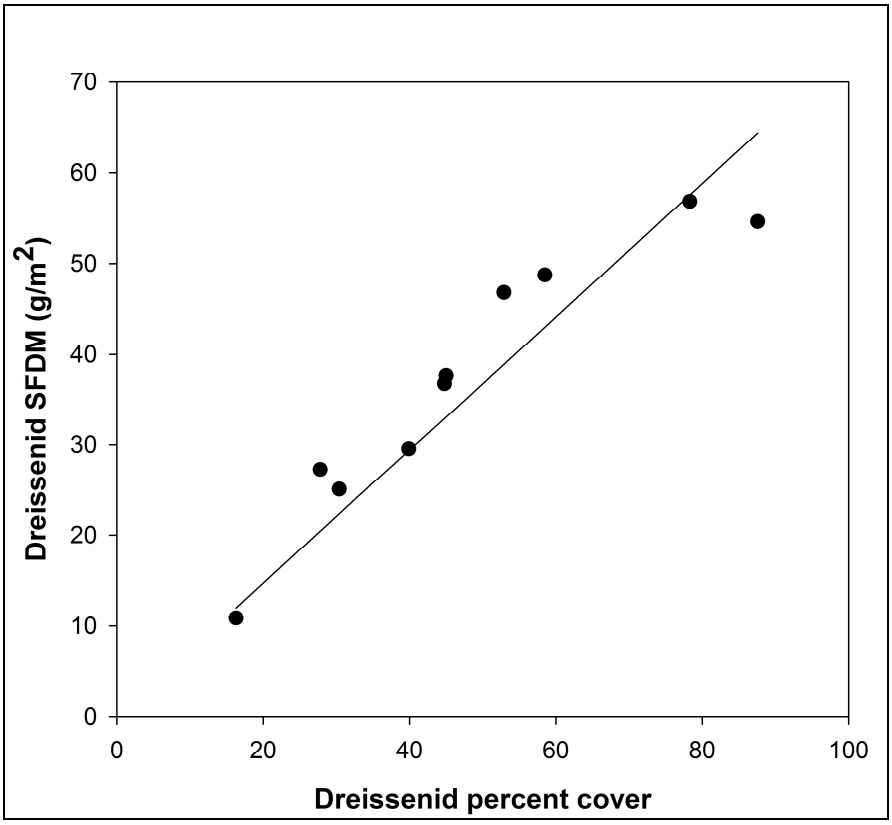

Figure 2.3: Results of video method calibration, showing relationship between dreissenid percent cover (as determined from video) and harvested dreissenid biomass (as shell free dry mass (SFDM) (g/m^2)).

Estimated dreissenid biomass averaged 27.2 g/m^2 (±24.3 SD), with a maximum of 75.3 g/m^2, and varied significantly with depth (Kruskal-Wallis one-way non-parametric ANOVA, $H_{4, 82}$=22.78, p<0.001) (Fig. 2.4a). Mean site mussel biomass was greatest at depths of 5 m and smallest at depths >20 m, but the differences were significant only between the >20 m depth category and the three depth categories ≤10 m (Dunn's test). Mussel biomass also differed on substrata of different textures. Quadrat biomass values (as opposed to site biomass means) from all depth strata were used to evaluate the relationship between substrate type and dreissenid biomass because more than one type of substratum was encountered at some sites. Rock and rock/silt quadrats supported significantly greater ($H_{3, 418}$=102.55, p<0.001) dreissenid biomass than did sand or silt (Fig. 2.4b).

The substratum was primarily rock at shallower sites; silt became increasingly important as depth increased and sand was most common at intermediate depths (Fig. 2.4c). To test the interactions between depth, substratum and mussel biomass with this unbalanced distribution of

samples, I conducted a series of Kruskal-Wallis one-way non-parametric ANOVAs on quadrat dreissenid biomass, comparing individual types of substratum across different depths. Dreissenid biomass differed among depths on rock substrates and was significantly lower at 2 m than at 5 or 10 m ($H_{2, 198}$=23.96, p<0.001). Sand supported more mussel biomass at 10 m than at 2 or 5 m ($H_{2, 30}$=11.94, p=0.003). Dreissenid biomass appeared to be similar on mixed rock/silt substrata at depths of 5 and 10 m but this could not be tested because only two quadrats with rock/silt were sampled at 5 m. Dreissenid biomass declined with increasing depth in quadrats on silt substrata, with significant differences among all depth strata ($H_{2, 163}$=70.85, p<0.001).

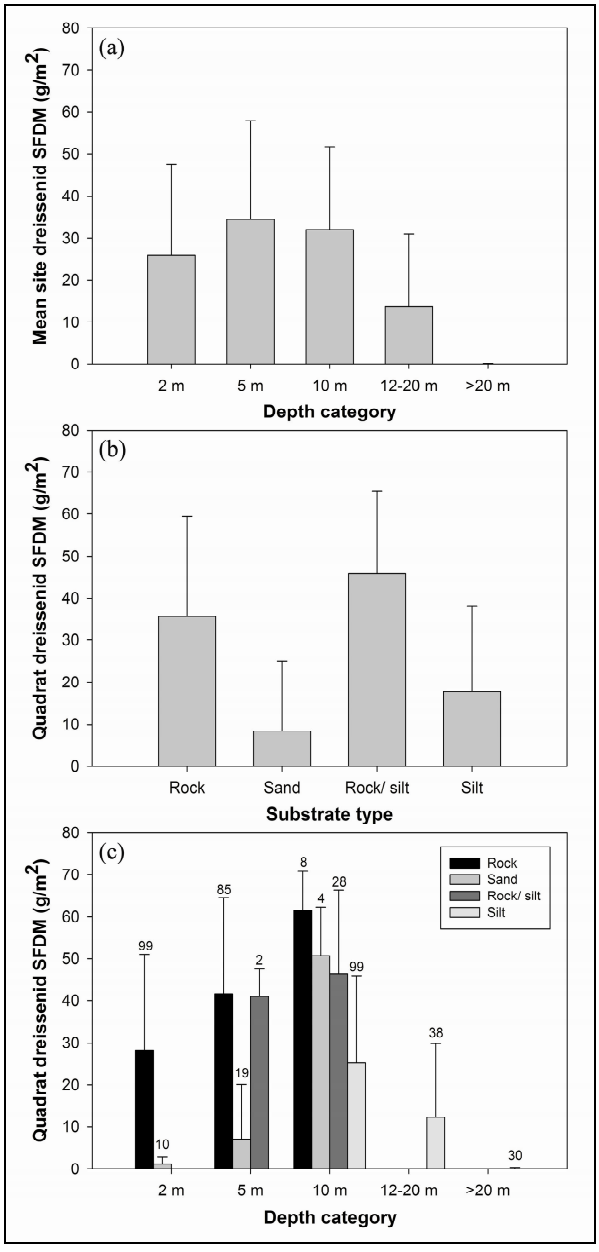

Figure 2.4: Dreissenid biomass expressed as shell free dry mass (SFDM) (g/m^2) in the main basin and Kempenfelt Bay of Lake Simcoe: a) mean site dreissenid biomass in five depth categories; b) quadrat dreissenid biomass from all depth strata in four substrate categories; c) quadrat dreissenid biomass by substrate type in five different depth categories. Numbers above bars show number of quadrats in each substrate category. Error bars represent one standard deviation about the mean.

Simple linear regressions were used to examine the relationship between DAE and mean site dreissenid biomass at 2, 5 and 10-m depths (Fig. 2.5). I confined regression analysis to rocky sites at 2 and 5-m depths, and to sites that contained at least some rock at 10-m depth. I also excluded one 2-m site that was dominated by fine gravel, reasoning that at shallow depths fine gravel is unstable and behaves similarly to sand. This was done to remove the confounding effects of substrate type on dreissenid biomass and focus solely on the effects of DAE on the most dreissenid-preferred substrates. There was a significant negative relationship between mean site dreissenid biomass and DAE at rocky sites at 2-m depths (R^2=0.56, p<0.001), and a negative, but not significant, relationship at 5-m depths (R^2=0.15, p=0.11). Mean site dreissenid biomass showed a positive, non-significant relationship to DAE at 10-m depths (R^2=0.14, p=0.18).

Substrate distribution also seems to be related to DAE. Sand, which supported very low mussel mass at 2 and 5-m sites was restricted to sites of intermediate DAE values (Fig 5a, 5b). Sites at 10 m which contained hard substrate in addition to silt tended to be slightly but not significantly more exposed (one-tailed independent samples t-test, t_{27}=1.69, p=0.051) and supported more dreissenid SFDM (t_{27}=2.16, p=0.02) than sites where the substratum was only silt (Fig. 2.5c).

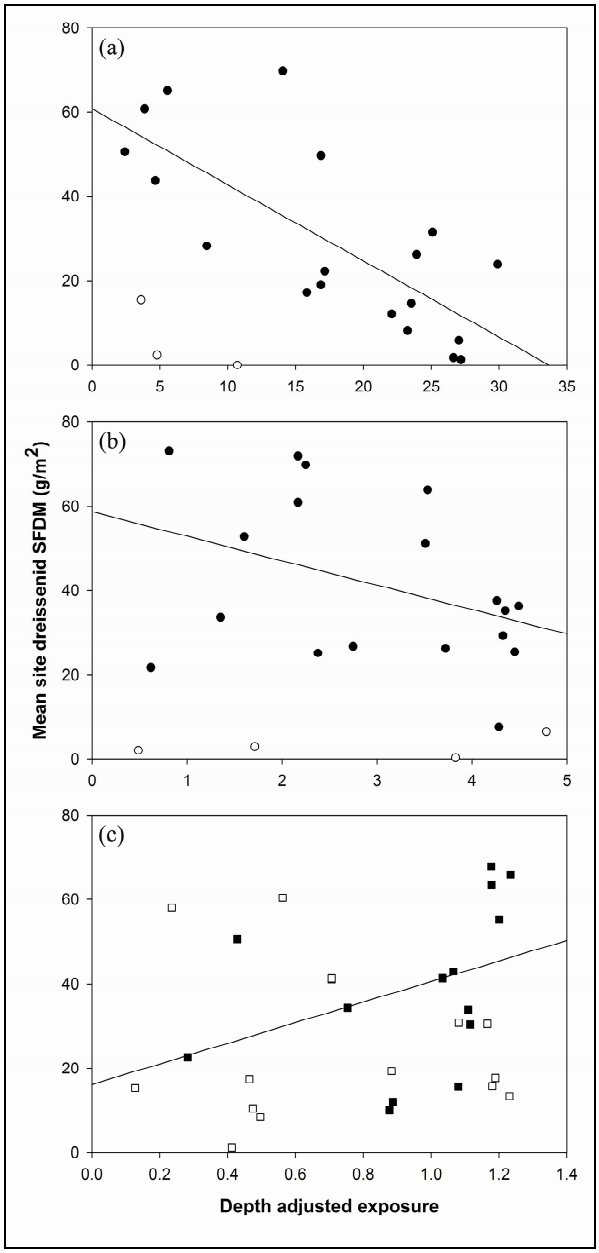

Figure 2.5: Mean site dreissenid biomass expressed as shell free dry mass (SFDM) (g/m^2) in the main basin and Kempenfelt Bay of Lake Simcoe plotted against disturbance expressed as Depth Adjusted Exposure (DAE) at: a) 2-m sites; b) 5-m sites; c) 10-m sites. Note that the scale of the x-axes changes to accommodate the range of DAE values at different depths. Filled circles represent rock dominated sites. Empty circles represent sand dominated sites. Filled squares represent sites dominated by mixed rock/silt substrates. Empty squares represent silt dominated sites.

Cook's Bay

The macrophyte community in Cook's Bay was fairly heterogeneous; I commonly found two or more macrophyte taxa in individual Ponar samples. *Ceratophyllum demersum*, *Vallisneria americana* and *Potamogeton* spp. were most common and frequently dominant; *Chara* spp., *Elodea canadensis* and *Myriophyllum spicatum* were frequently collected but rarely dominated the flora of a site. Macrophyte biomass ranged from 11.7 to 982.1 g dry mass/m^2, and averaged 362.6 g dry mass/m^2 (±266.2 SD). Spearman's rank correlation test showed that macrophyte biomass was significantly and negatively associated with depth (r_s=-0.62, p=0.01).

Mussel SFDM in Cook's Bay ranged from 0 to 69.8 g/m^2 (mean=12.4 g/m^2±16.9 SD) and did not vary systematically with depth. Average mussel size was 11.65 mm, and average biomass per mussel was 0.0059 g SFDM. Neither plant mass nor mussel biomass varied significantly with DAE in Cook's Bay. The ratio between dreissenid SFDM and plant dry mass was compared among samples dominated by the three most common macrophyte taxa (Fig. 2.6). The ratio of mussel to plant biomass assesses the suitability of each plant taxa as dreissenid substrate while accounting for differences in plant biomass among samples and for differences in plant morphology. The few samples dominated by *Chara* spp., *E. canadensis* and *M. spicatum* were excluded from the analysis because of low sample size. *C. demersum* supported significantly greater mussel mass per gram of plant dry mass than either *V. americana* or *Potamogeton* spp. ($H_{2, 26}$=18.37, df=2, p=0.0001).

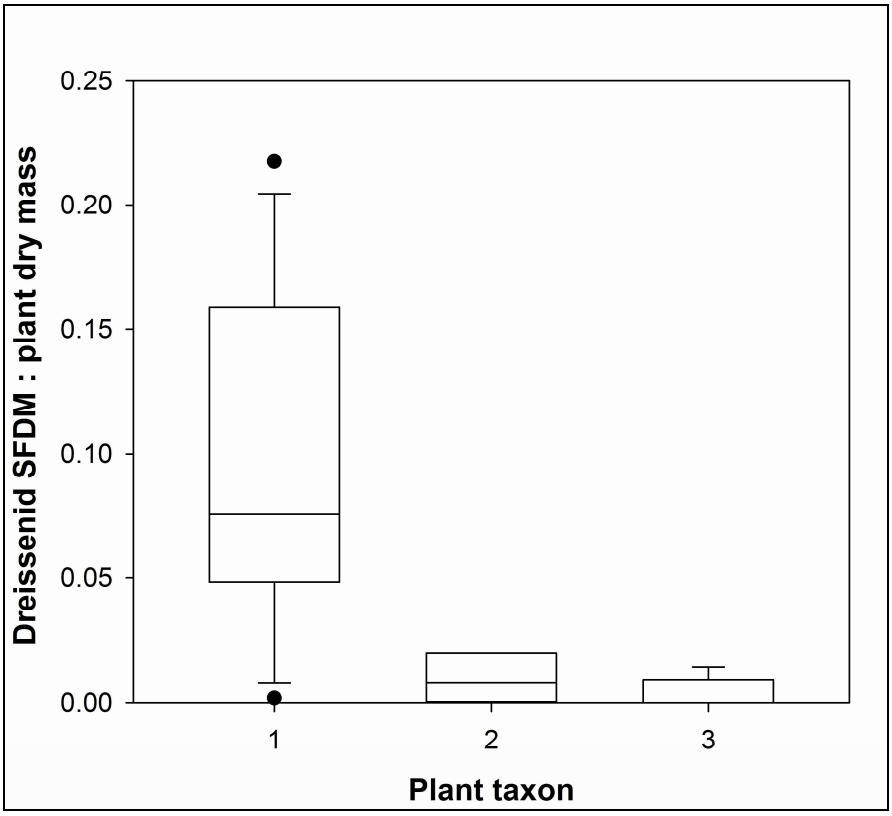

Figure 2.6: Ratio of dreissenid biomass (expressed as shell free dry mass (SFDM) (g/m^2)) to total plant dry mass (g/m^2) in samples dominated by the three most common macrophyte taxa in Cook's Bay, Lake Simcoe. 1=*Ceratophyllum demersum*, 2=*Potamogeton* spp., 3=*Vallisneria americana*.

2.3.2 Lake-wide biomass estimate

I estimated that there was a total of 12,000 tonnes of dreissenid SFDM in Lake Simcoe based on the results of our surveys in the summers of 2006, 2007 and 2008. Cook's Bay accounted for 3.5% of the total dreissenid biomass, a little less than its areal contribution to the lake (5.6%). In the main basin and in Kempenfelt Bay 25.6% of total dreissenid biomass was estimated to be in the 0–3.5-m interval (11.6% of lake area), and 32.1% of dreissenid biomass in the 3.5–8-m depth interval (15.1% of lake area). Only 0.1% of dreissenid mass was estimated to be at depths greater than 20 m (~34% of lake area) (Table 2.1). Assigning a precise error value to the biomass estimate is complicated by error propagation and my use of percent cover to biomass and exposure to biomass regressions in the final estimate. Considering the variability in dreissenid biomass at different depths and on different substrates (Fig. 2.4), the error of the biomass estimate may be large.

Table 2.1: Results of lake-wide biomass estimate, showing total dreissenid biomass as well as the percent of total dreissenid biomass encountered in different depth strata in the main basin and Kempenfelt Bay and in Cook's Bay.

Depth interval (m)	Area (km^2)	Percent of total lake area	Dreissenid biomass in depth interval (tonnes)	Percent of total dreissenid biomass
Main basin and Kempenfelt Bay				
0–3.5	83	11.6	3013	25.4
3.5–8	109	15.1	3815	32.1
8–12	91	12.7	2837	23.9
12–20	147	20.5	1787	15.1
20–42	250	34.6	11	0.1
Cook's Bay				
0–8	23	3.1	278	2.3
8–12	18	2.5	139	1.2

2.4 Discussion

This study represents the first published demonstration of the role of catastrophic physical disturbance in structuring dreissenid mussel distributions on a system-wide scale. MacIsaac (1996) demonstrated that wave disturbance can be important at the site-scale on hard substrates and Bially and MacIssac (2000) showed that wave action can destroy dreissenid colonies on soft substrates along an exposed stretch of shoreline. My results show that dreissenid biomass in Lake Simcoe is significantly affected by water movement, substratum type and depth. All three factors are related: wave disturbance decreases exponentially with depth, and the composition of the substratum is largely controlled by the disturbance regime as well as by the local geology and topography. Shallow, exposed areas in Lake Simcoe are dominated by rocky substrata, but as depth increases and exposure decreases, finer sediments accumulate and eventually dominate the lake bottom. Because of the relationship between substrate and disturbance we can speak of non-catastrophic and catastrophic effects of water movement on dreissenids. I define catastrophic effects as the actual destruction of mussels by disturbance, and non-catastrophic effects as indirect consequences of disturbance on mussels through control of substrate distribution and food supply rates.

Catastrophic effects are most apparent in shallow water where disturbance by waves and ice scour is greatest and mussels can be crushed by floating ice or rolling rocks (MacIsaac 1996). Shallow sites that are sheltered from the prevailing winds support greater dreissenid biomass than sites that are more exposed. The pattern of substrate colonization also differs between sheltered and exposed sites. Whereas at low exposure sites mussels were covering most of the substrate, at high

exposure sites mussels were mostly confined to the crevices between rocks where they would presumably be more protected from disturbance (Fig. 2.2). The likelihood of catastrophic disturbance decreases rapidly with increasing depth, as indicated by the weakly negative (statistically insignificant) relationship between dreissenid biomass and disturbance at 5-m sites. My observations regarding catastrophic disturbance in shallow water are consistent with reports of catastrophic impacts of wave action on dreissenid mussels in Lake Erie (MacIsaac 1996, Bially and MacIsaac 2000) and marine mussels in Nova Scotia (Hunt and Scheibling 2001).

The non-catastrophic effects of water movement can be observed in all parts of the lake, and are probably more important than catastrophic effects in structuring the lake-wide distribution of dreissenids in Lake Simcoe. For example, the effects of water movement on substrate distribution can be seen as non-catastrophic effects and play an important role in determining the distribution of dreissenids in the system. Enhancement of food supply to dreissenids can also be seen as a non-catastrophic effect of water movement; the weakly positive relationship between dreissenid biomass and DAE on mixed rock and silt substrates at 10-m depths is consistent with increased rates of food supply to mussels through more water movement at more exposed sites (Edwards et al. 2005). Westerbom and Jattu (2006) found that mussel biomass in the North Baltic peaked at intermediate disturbance levels which they attributed to enhanced rates of food and gas delivery to the mussels. The effects of disturbance by water movement on substrate distribution and hence dreissenids can also be seen at 10-m depths. Sites that contained rock in addition to silt supported higher dreissenid biomass than sites containing only silt, and tended to occur at higher DAE levels. I classified all substrate finer than sand as silt but it is likely that at greater depths and lower disturbance levels even finer substrates such as clay and marl commonly occur. Decreasing particle size in combination with low food supply rates at greater depths are likely responsible for the decreasing dreissenid biomass seen at depths below 10 m.

Dreissenid biomass in Lake Simcoe varied widely among and within sites. The average mussel biomass in the main basin of Lake Simcoe and in Kempenfelt Bay (27.2 g SFDM/m^2) was similar to that reported from Lake Erie in 2002 (24.7 g SFDM/m^2) by Patterson et al. (2005) based on ponar grabs and air-lift samples collected by divers. Dreissenid biomass on hard substrates in the main basin and in Kempenfelt Bay (35.7 g SFDM/m^2) was lower than that the 52.2 g SFDM/m^2 found during a video survey of a portion of Lake Ontario shoreline in 2006 (Ozersky et al. 2009) and that reported from a diving survey of the Canadian shoreline of Lake Ontario by Wilson et al. (2006) (86.9 g SFDM/m^2). While it appears that dreissenid biomass in Lake Simcoe is similar to that in Lake Erie,

but lower than in Lake Ontario, comparison between Lakes Simcoe, Erie and Ontario is complicated by the dominance of quagga mussels in the latter two lakes, by differences in substrate distribution and by methodological differences between the various surveys.

The use of video sampling to survey dreissenid distribution in the main basin and Kempenfelt Bay of Lake Simcoe enabled me to collect and process a large amount of information about the distribution of dreissenid mussels relatively rapidly and inexpensively. Similar techniques have been used to survey dreissenid mussel distribution patterns and biomass in the Laurentian Great Lakes (Custer and Custer 1997, Coakley et al. 1997, Bially and MacIsaac 2000). Despite these advantages, there are several potential sources of error associated with converting dreissenid percent cover from a video image to dreissenid biomass. For example, in particularly dense populations dreissenids can grow on top of one another; Coakley et al. (1997) found it necessary to apply a correction factor of about 10X to estimate areal abundance during the early phase of colonization of Lake Erie when the active layer of mussels was 4 cm thick. My calibration suggests that this was not necessary in Lake Simcoe during 2006–2008, more than 10 yr after dreissenids became established. Dreissenid mussels often attach to the underside of rocks as well as to the sides and overhangs of large boulders where they would not be seen in video images. This should not be a major source of error in Lake Simcoe where stones larger than cobbles are relatively rare. Finally, I was only able to calibrate the video method on structurally complex substrata in the nearshore, so my estimates of dreissenid mass on finer particles in deeper water may be somewhat inflated. The problems of the video-based approach notwithstanding, I feel that it provides a convenient and reasonably accurate tool for estimating biomass over large areas and if anything, provides a conservative estimate of biomass.

In Cook's Bay, *C. demersum* appears to support more mussel biomass per gram plant mass than the other two most common macrophyte taxa in my samples: *Potamogeton* spp. and *V. americana*. Other studies have noted similar patterns. For example, Lewandowski and Ozimek (1997) found greater numbers of dreissenids on macrophytes that were perennial and had rigid and complex leaf structure (such as *C. demersum*) than on macrophytes that were annual and had simple leaf structure (such as *Potamogeton mucronatus*). Diggins et al. (2004) reported large numbers of dreissenids on *C. demersum* and very low numbers on *V. americana*. Zhu et al. (2007) also found few mussels on *V. americana*. A recent survey has shown that *C. demersum, V. americana* and *Potamogeton* spp. have different distributions in Cook's Bay, with *C. demersum* mainly found at intermediate depths and *V. americana* and *Potamogeton* spp. occurring more commonly in shallow

areas (Stantec 2007). It seems probable that mussel distribution in Cook's Bay would be related to the distribution of preferred macrophyte species such as *C. demersum*.

The Ponar sampler used in Cook's Bay may not adequately sample tall, canopy-forming macrophyte taxa, potentially leading to underestimation of plant and mussel biomass in this study. A recent, detailed survey of macrophyte distribution and biomass in Cook's Bay showed good correlation between Ponar samples and diver collected quadrats, and yielded an average plant biomass of 233 g dry mass/m^2 (Stantec 2007), similar to my estimate of 362 g dry mass/m^2. The results of the Stantec (2007) survey suggest that my estimates of macrophyte and mussel biomass obtained from Ponar samples are not unrealistic, and may be slightly inflated.

A number of recent changes occurring in Lake Simcoe make it likely that the biomass and distribution of dreissenids in the lake will change in the future. For example, the round goby (*Neogobius melanostomus*) has recently invaded Lake Simcoe but at the time of our survey was confined to a small area at the south of the lake (Jake LaRose, Lake Simcoe Fisheries Assessment Unit, personal communication). This fish is a voracious predator on dreissenids and significantly reduced the abundance of dreissenids in Lake Erie (Barton et al. 2005) and Lake Michigan (Lederer et al. 2006). If the population dynamics of round goby in Lake Simcoe follow the same trajectory observed in Lake Erie, a substantial reduction in the abundance of mussels in the nearshore zone could be expected. Given the abundance of potential predators of round goby (e.g., yellow perch, smallmouth bass) in the littoral zone of Lake Simcoe, densities and impacts of round gobies may be more limited than in parts of the lower Great Lakes. The recent invasion of Lake Simcoe by rusty crayfish (*Orconectes rusticus*) may also affect future dreissenid distributions in the lake. Rusty crayfish are more aggressive than native crayfish species, and could force native species to rely more heavily on dreissenids, which are generally a less preferred food source (Love and Savino 1993, Stewart at al. 1998).

The profundal zone (depths>20 m) of Lake Simcoe encompasses nearly 35% of the lake area, but supported only 0.1% of the total dreissenid biomass. Quagga mussels were first found in Lake Simcoe in 2004 (Jake LaRose, Lake Simcoe Fisheries Assessment Unit, personal communication). They have replaced the initially dominant zebra mussels in Lakes Erie (Patterson et al. 2005) and Ontario (Wilson et al. 2006), and are increasing in relative abundance in Lake Huron (Nalepa et al. 2007). Quagga mussels are more tolerant of soft substrates, low temperatures and food limitation (Mills et al. 1996, Baldwin et al. 2002, Stoeckman 2003), and in the future might be expected to colonize the deeper parts of Lake Simcoe to a greater extent than zebra mussels.

In summary, I show that depth, exposure to wave disturbance, substrate availability, and the interactions among these factors are important in shaping dreissenid mussel distribution in the main basin of Lake Simcoe. At shallow depths, high levels of water movement ensure that the lake bottom is dominated by rocky substrate, and substrate availability is rarely limiting to dreissenids. At these shallow depths catastrophic disturbances are most important in structuring dreissenid distribution. Areas of intermediate depth where exposure is high enough to maintain an abundance of hard substrate but not high enough to disturb mussels support the highest dreissenid biomass in Lake Simcoe. At greater depths where substrate and food availability becomes limiting, water movement may increase the availability of both, facilitating dreissenid establishment and growth. I did not see a direct link between disturbance and dreissenid distribution in Cook's Bay where the distribution of different macrophyte taxa appears to be more important. More research is needed to explore the relationships between physical disturbance and dreissenid mussels across a wider range of disturbance regimes and substrate types.

Chapter 3
Dreissenid Phosphorus Excretion Can sustain C. glomerata Growth Along a Portion of Lake Ontario Shoreline

3.1 Introduction

Water quality and ecosystem functioning of the Laurentian Great Lakes are facing a number of major challenges, among the most important of which are the effects of the invasion by the exotic zebra mussel *Dreissena polymorpha* and its congener the quagga mussel *D. bugensis*. Several major ecological consequences of the dreissenid invasion are well recognized in the literature, including the collapse of native unionid mussel populations through fouling, a decrease in phytoplankton biomass and changes in nearshore optical properties through intensive filtration, and physical restructuring of the benthic environment (reviewed in Vanderploeg et al. 2002). Dreissenid mussel abundance has also been shown to be positively correlated with the presence of the nuisance filamentous green macroalga *Cladophora* (Wilson et al. 2006), and dreissenid mussels have been charged with driving a resurgence of this macroalga in the lower Great Lakes (Higgins et al. 2008). Although some questions regarding the taxonomic identity of *Cladophora* in the Great Lakes remain, recent phylogenetic evidence indicates that *Cladophora glomerata* is the only species of *Cladophora* in the Laurentian Great Lakes (Ross 2006, Muller et al. unpublished).

Dreissenid mussels may be increasing the prevalence of *C. glomerata* in the lower Great Lakes through a number of mechanisms. Due to their high filter feeding capacity, and possibly their demand for Ca^{2+} reducing the frequency of whiting events, establishment of large dreissenid mussel populations has been associated with increases in water clarity (Lowe and Pillsbury 1995, Eimers et al. 2005, Barbiero et al. 2006), enhancing the growth of *C. glomerata* at previously light-limited depths (Higgins et al. 2005a, Higgins et al. 2006, Malkin et al. 2008). Dreissenids may also be facilitating the areal expansion of *C. glomerata* in the Great Lakes through an increase in the availability of hard substrate for algal attachment (Vanderploeg et al. 2002). Dreissenids, especially quagga mussels, are able to colonize soft substrates (Bially and MacIsaac 2000, Beekly et al. 2004) where they form extensive areas covered in shell material from living and dead mussels (Coakley et al. 1997). *C. glomerata* is restricted to hard substrates, including mollusk shells (Dodds and Gudder 1992, Wilson et al. 2006). Consequently, the expansion of quagga mussels onto soft substrate in littoral zones provides additional habitat for *C. glomerata* growth. Finally, by filtering suspended

particulate matter and voiding or excreting feces, pseudofeces and dissolved nutrients, dreissenid mussels may be redirecting nutrients from the pelagia to the benthos, potentially leading to eutrophication of the nearshore benthic environment. The nearshore shunt hypothesis proposes that dreissenid mussel beds increase the interception, retention and recycling of nutrients in the nearshore zone, benefiting *C. glomerata* though increased nutrient availability as well as improved water clarity (Hecky et al. 2004). *C. glomerata* has been shown to be P-limited in the Great Lakes (Auer and Canale 1982, Higgins et al. 2005b), so nutrients supplied via dreissenid mussels should lead to greater proliferation of the macroalgae.

The excretion rate of dissolved P by dreissenid mussels has previously been estimated in laboratory studies (Arnott and Vanni 1996, James et al. 2001, Conroy et al. 2005, Naddafi et al. 2008). Arnott and Vanni (1996) extrapolated their phosphorus excretion results using mussel biomass data from Lake Erie, showing phosphorus released by mussels to be more important than that from zooplankton, macrophytes, sediment or external sources. Conroy et al. (2005) estimated that phosphorus turn-over rates in Lake Erie increased by 25-30% following the invasion of dreissenids.

Laboratory studies of dreissenid P excretion may under- or over-estimate the actual contribution of P by dreissenids in natural systems. Previous lab studies of dreissenid excretion excluded the detritivore and microbial community associated with dreissenid beds, which have been shown to promote P release by remineralizing mussel feces and pseudo-feces (Prins and Smaal 1994). The laboratory studies by Arnott and Vanni (1996) and Conroy et al. (2005) used starved mussels, potentially resulting in lower excretion rates than for mussels feeding on their natural food sources. Finally, most studies have used mussels which could have been stressed by handling, sustained periods out of water and transport to the laboratory. I tried to avoid these potential confounding factors by measuring excretion *in situ* where unstressed mussels would be feeding on natural diets.

My objective was to compare the contribution of P recycled through the dreissenid community and the affiliated microflora and microfauna with local point and non-point sources of P in my study area. Additionally, I wanted to compare dreissenid and watershed P contributions with modeled P demand by *C. glomerata* (modeling done by Dr. Sairah Malkin) in the study area. I estimated the abundance of mussels in the nearshore zone (depths <12 m) through a video survey and measured the P excretion rate of dreissenid mussel populations *in situ* during the main *C. glomerata* growing season when macroalgal P demand is highest.

3.2 Material and Methods

3.2.1 Study site

The study was carried out along a portion of the northwestern shoreline of Lake Ontario, near the Town of Oakville in the Regional Municipality of Halton (Fig. 3.1). This site was chosen in part because Malkin *et al.* (2008) studied and modeled *C. glomerata* growth and abundance in the area. The Halton region shoreline is almost completely urbanized, with a number of watercourses, storm sewers and one wastewater treatment plant (WTP) discharging within the study area. The bottom substrate consists entirely of bedrock, boulder, cobble and pebble, with finer sediments at depths greater than about 25 meters. The dominance of hard substrates at depths <25 meters make the entire littoral zone a suitable habitat for both dreissenid mussels and *C. glomerata*. The substrate at the study area was covered by large numbers of dreissenid mussels (almost exclusively *D. bugensis*), with luxuriant mats of *C. glomerata* at depths shallower than 12m (personal observation). Phosphorus excretion experiments were performed near Oakville's Dingle Park (43^{o}26'39" N, 79^{o}39'49" W) at a mean depth of 1.5±0.25 meters (Fig. 3.1). Total mussel biomass, dreissenid phosphorus excretion and uptake of P by *C. glomerata* were modeled for an 8 km long stretch of Halton shoreline between 0 and 12 m depth; an area of approximately 10.4 km^2 (shaded area in Fig. 3.1).

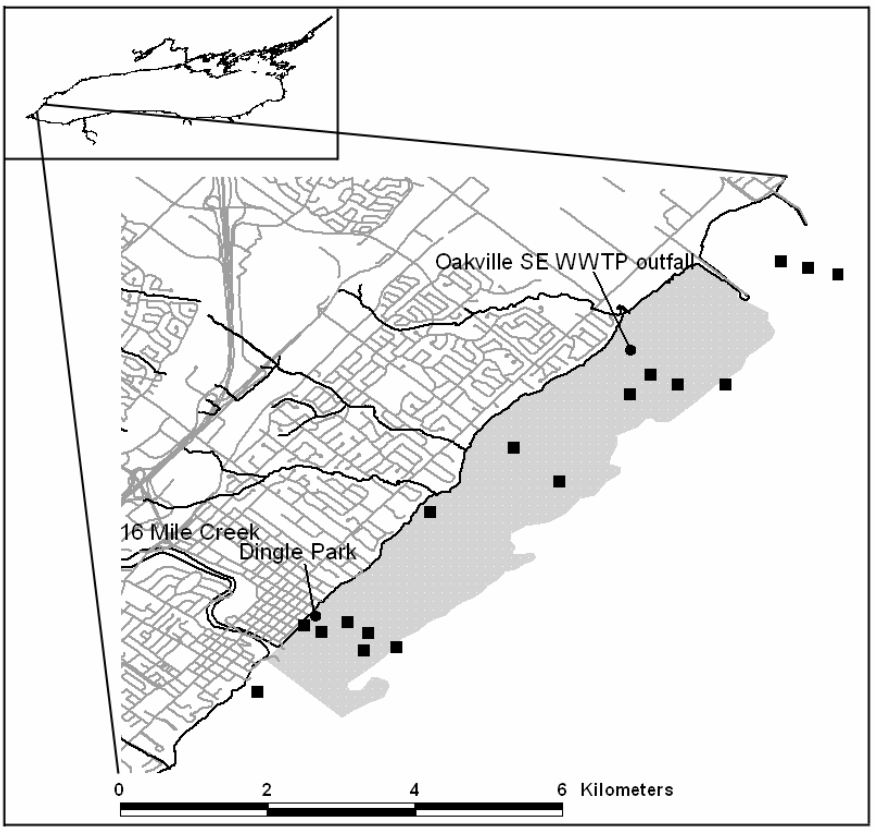

Figure 3.1: Map of study area, with mussel survey sites, phosphorus excretion experiment site and major outfalls shown. Shaded polygon shows the area where dreissenid P excretion and *C. glomerata* P uptake were modeled. Map created using ArcView GIS (version 3.2)

3.2.2 Biomass survey

The biomass survey was conducted along the Halton shoreline on two dates in the spring of 2006, when *C. glomerata* biomass was still low and consequently bottom visibility was unimpaired. On both dates a Splashcam underwater video camera (Ocean Systems, Everett, WA) connected to a VHS recorder was used to film the substrate. The camera was mounted on an aluminum frame so that an area of 0.0408 m^2 was filmed when the frame was resting on the bottom. Upon arrival to a sampling location, the GPS coordinates and depth of the station were recorded and the camera was used to film the lake bottom. At least three separate quadrats of 0.0408 m^2 each were filmed at every sampling site by lifting and lowering the camera in its frame to capture the separate quadrats. I sampled a total of 21 sites, ranging from 2 to 35 meters in depth.

The video footage from each sampling station was converted to Portable Network Graphics (PNG) image files, and analyzed in Adobe Photoshop CS2 (Version 9.0, 2005). The number of live

mussels per quadrat and the percentage of the quadrat covered by live mussels were determined for three quadrats from each sampling station. Mussels were deemed alive if they responded to the lowering of the camera and the associated current by reducing the gape width of their valves, as determined from the video recordings for each quadrat. Percent cover data were converted to shell free dry mass using a relationship between % cover and shell free dry mass developed on hard substrates in Lake Simcoe (Ontario), where I filmed and harvested mussels from 10 separate quadrats (Chapter 2):

SFDM (g/m^2)=0.97×(percent cover) (R^2=0.89, p<<0.05)

A continuous estimate of total biomass along the Halton shoreline was made by fitting a polynomial function to the depth versus biomass relationship using data from 17 sites at 2, 5, 10 and 15 meters (Equation 1) (SPSS 15.0). Sites at greater depths sampled only once (e.g. 20, 25, 30, 35 meter depth) were excluded from analysis, but generally supported mussel densities similar to those found at 10 and 15 meters.

(1) Dreissenid biomass at depth (x)=$0.0669x^3–2.6134x^2+31.76x–50.879$

(R^2= 0.75, p<<0.05)

Equation (1) was used to determine the total dreissenid biomass at 1-meter depth intervals within the study area, based on bathymetric maps of the area (Virden et al. 2000). Because equation (1) predicts negative biomass in the 0–1 meter depth interval, the average values from the 1–2 meter interval were used to calculate the biomass in the 0–1 meter interval where mussel densities were quite low. I report dreissenid biomass down to a depth of 12 meters because little *C. glomerata* growth was observed below this depth (Malkin et al. 2008). I also chose to limit our biomass projection to 12 m because I was interested in measuring mussel P contribution into the mixed layer (since P excreted below the mixed layer would not be available to *C. glomerata*) and the depth of the mixed layer was never shallower than 12 m during the course of our study (D. Depew, personal communication).

Figure 3.2: Photograph of incubation chamber used in phosphorus excretion experiments. In addition to the stirring paddle the lid contains two sampling ports.

3.2.3 Phosphorus Excretion Measurements:

Phosphorus excretion measurements were made using 1.8 L clear acrylic chambers, which consisted of a cylindrical body (25 cm tall, 10 cm diameter) with a neoprene skirt at the bottom (Fig. 3.2). The neoprene skirt ensured a tight seal against the substrate when a ring-shaped flexible sock filled with lead shot was fitted around the bottom of the chamber. A clear acrylic movable piston with

two sampling ports and a rubber gasket fit into the top of the chamber. A hand operated stirring paddle was also fitted through the top piston to allow gentle stirring before water sampling through the sampling ports. Clear chambers were used to ensure phosphorus uptake by phytoplankton and periphyton was maintained during incubations (Reigman et al. 2000, Litchman et al. 2004), as well as to minimize disturbance of dreissenids (Morton 1969), making our results close to net daytime nutrient uptake and excretion rates. A snorkeller collected triplicate water samples approximately 20 cm above the lake bottom, then deployed four incubation chambers over mussel encrusted rock, three chambers over naturally mussel-free rock, and three chambers separated from the substrate by a sealed plastic barrier and so containing only lake water. Any *C. glomerata* present on the mussels or rocks was carefully removed prior to enclosure by trimming with scissors. This experimental design allowed the estimation of phosphorus excretion rates by mussels and the associated biota, as well as phosphorus release and uptake by benthic biofilm not associated with mussels (detritus, periphyton, microbiota and invertebrates) and phytoplankton. The top pistons were inserted into each chamber at the start of the incubation period, separating the contents of each chamber from outside water. After two hours of incubation, water in the chambers was sampled though one of the sampling ports. All mussels enclosed by the chambers were harvested into a collection bag using a scraper for biomass determination. Shell free dry mass was determined from a relationship between mussel shell length and tissue weight. To derive the shell length to dry mass relationship, mussels from the incubation site were dried at 60ºC for at least 48 h, measured using electronic calipers to the nearest 0.1 mm, and then weighed to determine their mass with and without the shell. Shell free dry mass (SFDM) of mussels in the chambers ranged from 0.04 to 0.41 g, which translates to 5.1–52.3 g SFDM/m^2, biomass values typical of our study area. Water samples were analyzed for soluble reactive phosphorus (SRP) concentration using the stannous chloride colourimetric method (APHA, 1998) on a CARY 100 spectrophotometer (Varian systems, Palo Alto, CA). Phosphorus excretion incubations were conducted on June 12, June 21, July 5 and July 19 of 2006, a period marked by high *C. glomerata* biomass.

Phosphorus values obtained in excretion experiments were converted to biomass- specific mussel excretion rates for each date as follows. The average final SRP concentrations in all chambers deployed over mussel-free substrate (containing biofilm and phytoplankton) was subtracted from the final concentration in each chamber deployed over mussels (containing mussels, biofilm and phytoplankton). The subtraction was done to correct the effect that phytoplankton and periphyton in chambers containing mussels might have on P dynamics, and allow us to estimate net rates of mussel

excretion alone. The net change in SRP due to mussels in each chamber was divided by the shell free dry mass of mussels in the chamber and incubation time to yield biomass-specific phosphorus excretion rates. The average excretion rate across all dates was combined with our video measurements of biomass between 0 and 12 m to estimate the dreissenid-mediated flux of phosphorus along the Oakville shoreline.

The effect of biofilm on P dynamics was calculated by subtracting the average final SRP concentration in chambers containing only water (separated from the substrate) from the final SRP concentration in each chamber deployed over mussel free substrate, with the difference representing change due to biofilm. The effect of phytoplankton on P dynamics was calculated by subtracting average initial SRP concentration in the water from the final SRP concentration in chambers containing only water (separated from the substrate).

3.2.4 P supply from catchment sources

Nutrient loading to Lake Ontario from Sixteen Mile Creek (formerly known as Oakville Creek) was calculated from daily measurements of discharge and monthly water samples. Water discharge was recorded hourly by Water Services of Canada (WSC) on the two main arms of the creek, at Milton (43°30'50" N, 79°52'47" W) and at Omagh (43°29'56" N, 79°46'36" W), using gauge-type recorders. The sum of the discharge at these two sites captures most of the water that flows into Lake Ontario from Sixteen Mile Creek. Discharge data was available for the years 1964 to 2005. Total phosphorus concentrations in Sixteen-Mile Creek was monitored by the Ontario Ministry of the Environment (MoE) at a station adjacent to the river mouth (Station 06006300102; 43°26'34" N, 79°40'16" W) at approximately monthly intervals throughout the year from 1964 to the present. These data were maintained by the Provincial Water Quality Monitoring Network (PWQMN), a branch of the MoE. Samples were analyzed colourimetrically using a Technicon AutoAnalyzer (Ministry of Environment 2007*a*, *b*).

Because nutrient management programs came into effect in the early 1970s, and because of potential land use changes over the past 4 decades, the dataset was narrowed to the period encompassing 1991 through to the last year for which data was available: 2005. Total P and SRP loading was calculated as a product of TP and SRP concentration on a given day and mean daily discharge (as the sum of the discharge from the two arms) on the same day (Sigmaplot version 8). It was found that the relationships between discharge and loading were best described by the following functions:

(2) TP Loading=36.368×discharge$^{1.4255}$ (R^2 = 0.8625)

(3) SRP Loading=5.2651×discharge$^{1.6464}$ (R^2 = 0.7875)

where loading is mg P/s and discharge is m^3/s.

Daily loading was then computed using the loading-discharge function and the measured daily discharge for the most recent years available in the database, 2004 and 2005. Loading from 2004 and 2005 was calculated because of large differences in rainfall and consequently P loading between the two years (Malkin et al. 2008), which allowed me to compare dreissenid P excretion with a wide range of watershed P loading.

Loading of P from Oakville Southeast Wastewater Treatment Plant, the second major source of P to the study area was obtained from a report prepared by The Regional Municipality of Halton, Environmental Services (Regional Municipality of Halton 2008). Data from 2007 were used since they were readily available, and because there is no reason to believe loadings from this plant vary significantly between years. Loadings of phosphorus from three minor watercourses entering our study area (Joshua's Creek, Wedgewood Creek, Morrison Creek) and storm sewers were estimated from figures in a report prepared for the Lake Ontario Shoreline Algae Action Committee (LOSAAC) by Aquafor Beech Limited (2005). I had to rely on visually estimating loading from figures in the report because no raw data were available. The report relies on a combination of field measurements of discharge and nutrient concentrations and on data from the Water Survey of Canada (WSC), the Provincial Water Quality Monitoring Network (PWQMN) and other external sources.

3.2.5 P demand by C. glomerata

The uptake rate of P by C. glomerata was estimated using model-predicted daily estimates of *C. glomerata* biomass and biweekly measurements of *C. glomerata* P content. *C. glomerata* biomass and growth were simulated at daily time steps using the *Cladophora* growth model (CGM; Canale and Auer 1982; Higgins et al. 2005b) The structure, calibration and validation for the CGM for our study site are described elsewhere (Malkin et al. 2008). Essentially, the CGM simulates attached biomass accrual based on predictions of daytime biomass-specific net primary production, nighttime respiration, and mechanical or other loss processes. The biomass-specific metabolic rates were predicted based on growth constrained by P content, daily light dose, temperature, and density-dependent self-shading. Model simulations were calibrated and validated against 2 years of independently measured *C. glomerata* biomass in harvested quadrats.

C. glomerata P content was measured approximately every 2 weeks using samples collected by a snorkeller throughout the growing season. From these discrete measurements, daily P content was calculated by linear interpolation. Samples were collected in triplicate from 2 m depth, cleaned to remove debris and dried at 60^{o}C for a minimum of 24 hours. Dried *C. glomerata* samples were then combusted at 450^{o}C for 1 hour and subsequently autoclaved for 30 minutes in distilled water with 4% potassium persulphate solution added to a final concentration of 0.16%. Following this digestion procedure, orthophosphate was measured spectrophotometrically using the molybdate blue method (APHA 1998). Depth-specific estimates of P content of *C. glomerata* were calculated as an exponential function of depth, using the equations presented in Malkin et al. (2008).

The rate of P uptake by *C. glomerata* (g P/m^2/d) was calculated as the product of daily simulated *C. glomerata* biomass per area (g DM/m^2), depth-specific simulated *C. glomerata* growth (per day), and depth-specific P content of *C. glomerata* (g P/g DM). The concentration of P sequestered by *C. glomerata* was calculated per depth contour down to 12 m, based on the nearshore slope of the Oakville area, estimated from bathymetric maps (Virden et al. 2000)

3.3 Results and Discussion

3.3.1 Dreissenid distribution and biomass

The study site supported an average abundance of 3,674 mussels/m^2 (±2,233 SD), an average percent cover of 53.5%, and an average biomass of approximately 52.2 g SFDM/m^2 (±29.0 SD). Depth appeared to be the most important variable affecting mussel density, with very low density and biomass in shallower water and higher density and biomass in deeper water (Fig. 3.3). Mussel density averaged only 95 mussels/m^2 (biomass = 2.7 g SFDM/m^2) at 2 m stations, and increased with depth to 4,586 mussels/m^2 (biomass = 71.0 g SFDM/m^2) at depths of 10 to 12 m. The low mussel abundance observed at 2 m stations is most likely caused by the combined effects of ice scour in the winter, when mussels not hidden in cracks and crevices are displaced by moving ice, and strong wave action during storms in the ice-free season. The greatest variability in dreissenid biomass was found at 5 m stations where the lowest densities were generally found on flat, smooth bedrock. At this depth there is likely a lesser impact of ice scouring, but disturbance by surface waves may still limit mussel colonization and survival on substrates that afford little protection from wave action.

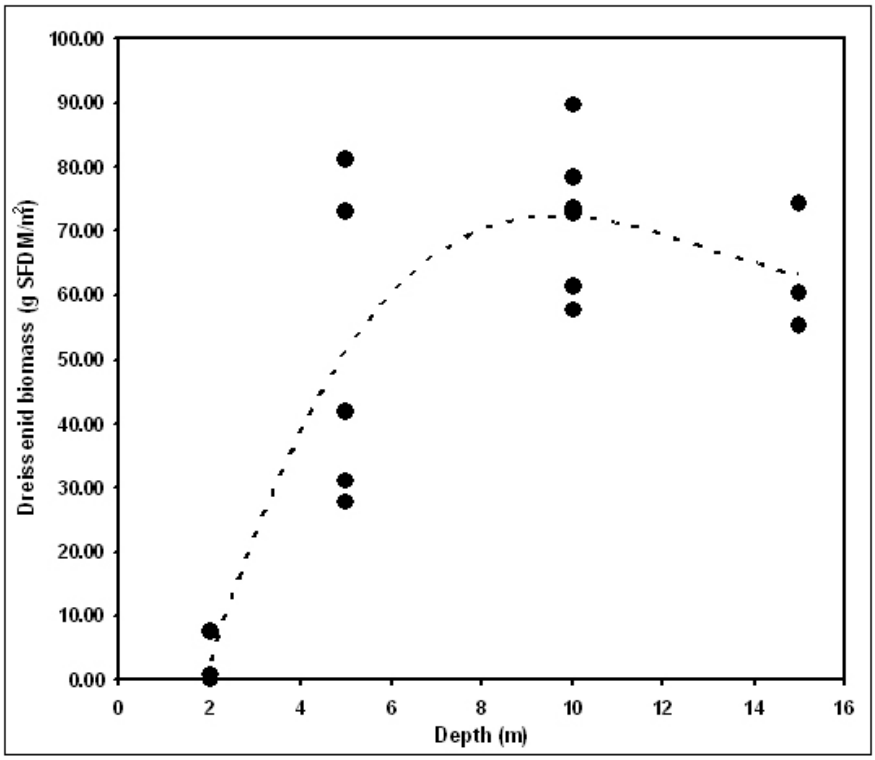

Figure 3.3: Average dreissenid SFDM (g/m^2) measured at different depths along the Halton shoreline. Dashed line represents equation (1).

The biomass of quagga mussels in the study area is comparable to that measured in recent surveys in Lake Erie and Lake Ontario. In a 2002 survey Patterson et al. (2005) found an average dreissenid biomass of 67.9 g SFDM/m^2 between the depth of 0 and 15 meters in Lake Erie's hard substrate-dominated eastern basin. While the average biomass found by Patterson et al. (2005) is very similar to the average biomass found at my study site (52.2 g SFDM/m^2), the biomass at shallow water sites was much higher in Lake Erie in 2002 than in Lake Ontario in 2006: 58.1 vs. 2.7 g SFDM/m^2. Barton (unpublished data) surveyed mussel abundance and biomass in Lake Erie's eastern basin in 2004, using an airlift to sample hard substrate sites. He found low biomass at 2 m sites (0.9 g SFDM/m^2), and higher biomass at greater depth: 24.7 g SFDM/m^2 at 6 m, and 41.0 g SFDM /m^2 at 10 m. These biomass values are somewhat lower than in my study area along the northwestern shoreline of Lake Ontario, but seem to follow a similar pattern of increasing dreissenid biomass with increasing depth. Barton et al. (2005) attributed the decline in dreissenid abundance observed in Lake Erie's eastern basin between 2002 and 2004 to predation by round gobies. Wilson et al. (2006) conducted an

extensive survey of the Canadian shore of Lake Ontario, reporting lower mussel biomass at 5 meters than at 20 meters, as well as lower biomass on soft compared to hard substrates. They reported a lakewide average percent cover of 60.5% (±38.3 SD) and 86.9 g SFDM/m^2, compared to the 53.5% (±28.9 SD) and 52.2 g SFDM/m^2, found in my study area. One of the reasons the percent cover and biomass numbers found in this study are lower than those described by Wilson et al. (2006) could be the inclusion of 2 m sites in my survey, which tended to support very low mussel densities.

It is important to recognize that, unlike the abovementioned studies where mussels were actually harvested to determine biomass, I used a video based technique to estimate dreissenid mussel biomass. The use of a video-based method may result in underestimation of mussel biomass because mussels may not grow in a single layer, and because mussels may grow on the underside of rocks, where they can not be seen on video. Despite these drawbacks, it appears that percent cover correlates well with dreissenid biomass where examined. Custer and Custer (1993) found a strong linear relationship (R^2= 0.96) between dreissenid percent cover determined from video and biomass determined by harvesting the filmed quadrats. Wilson et al. (2006) also found a significant, albeit weaker correlation (R^2=0.77) between diver estimated percent cover and dreissenid biomass (K. Wilson, personal communication). Finally, the relationship between percent cover and biomass that was used to estimate biomass in this study, derived from ground-truthing in Lake Simcoe on substrates similar to those encountered at our study site in Lake Ontario, shows a strong relationship between percent cover determined from video and actual biomass (R^2= 0.89). I believe that the video-based method provides a reasonable, conservative estimate of actual biomass, while significantly speeding up data collection and processing.

3.3.2 Phosphorus excretion

Water column SRP concentration at the depth of the incubation chambers ranged from 0.9 µg/L to 2.8 µg/L and averaged 1.9 µg/L (±0.4 µg/LSD) across all dates (Fig. 3.4). Following a two hour incubation, SRP levels in chambers containing mussels increased on all experimental dates, with values ranging from 1.9 µg/L to 4.2 µg/L, and an average of 3.0 µg/L (±0.8 µg/L). The increase in SRP concentrations in mussel-containing chambers compared to incubations on mussel-free rock was statistically significant on June 12, 2006 (independent two-sample t-test, df=4, 2-tailed, t=5.58, p<0.05). SRP concentrations in chambers deployed over mussel-free substrate increased on three of four sampling dates relative to treatments containing only water by an average of 0.5 µg/L (±0.6 µg/L). The increase was statistically significant on July 19, 2006 (independent two-sample t-test,

df=4, 2-tailed, *t*=4.619, *p*<0.05). The increase in SRP concentrations over mussel-free rock relative to treatments containing only water and sealed from the substrate indicates that substrate-associated biofilm served as a net source of SRP in our experiments. Final SRP concentrations in chambers that excluded the bottom substrate decreased on all dates except July 5, 2006 relative to initial conditions by an average of 0.5 µg/L (±0.6 µg/L). The net decrease in chambers excluding the bottom substrate is likely the result of SRP uptake by phytoplankton in these chambers during the incubation period. Table 3.1 summarizes the net change in SRP concentrations in the different incubation treatments on all four dates sampled. The low SRP release rates by both mussels and substrate on June 21 and July 5 may have been a result of low water temperatures caused by upwelling events which are common along this shoreline (Table 3.1). In addition to the low water temperatures on June 21, the lack of a significant change in SRP levels in the mussel containing chambers could be explained by the low mussel biomass included in all chambers on that date.

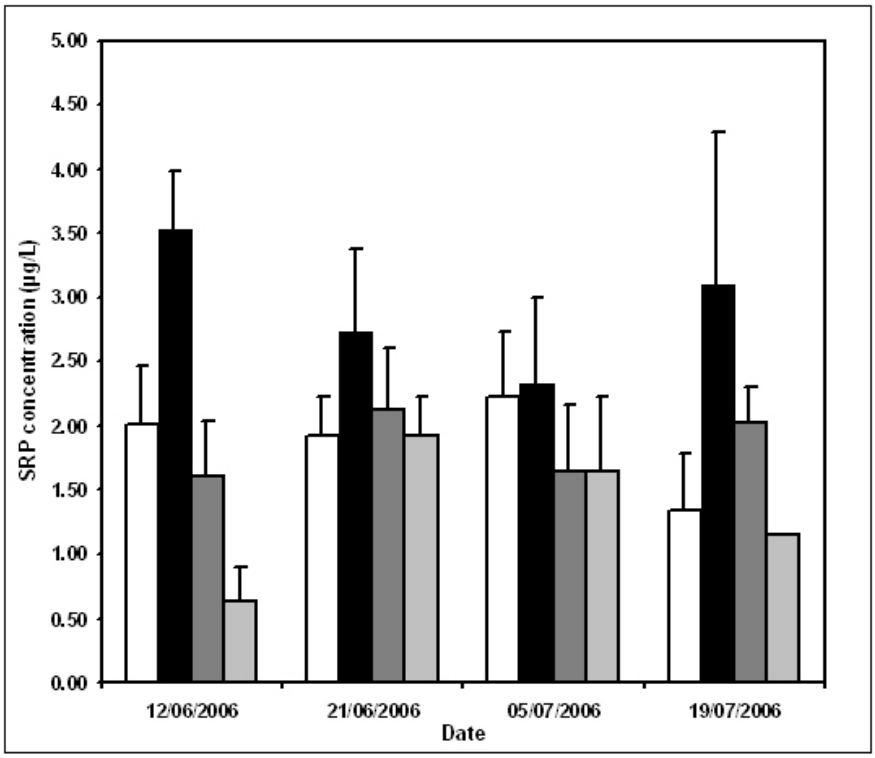

Figure 3.4: SRP (µg/L) at the start of 2 hour incubations (white bars) and following a 2 hour incubation over mussel-encrusted rock (black bars), mussel free rock (dark gray bars), and in chambers containing only water (light gray bars). Error bars represent one standard deviation about the mean.

Table 3.1: Water temperature on incubation dates, average mussel biomass in mussel containing chambers, and the net mean effect of mussels, substrate associated biofilm and plankton on SRP concentrations in incubation chambers during the course of a two hour incubation. Positive numbers indicate SRP addition, negative numbers indicate uptake of SRP. Numbers marked with an asterisk indicate a significant change in SRP concentration at the $p<0.05$ level.

Date	Water temperature (ºC)	Average mussel biomass in mussel containing chambers (g SFDM)	Net effect of mussels (µg SRP/g SFDM/h)	Net effect of biofilm (µg SRP/h)	Net effect of plankton (µg SRP/h)
June 12, 06	14	0.24	8.2*	0.9	-1.3
June 21, 06	9	0.09	11.2	0.2	0.00
July 05, 06	8	0.23	2.6	0.00	-0.5
July 19, 06	16	0.22	6.1	0.3*	-0.4

A direct comparison of P excretion rates obtained in this study with the few other studies which measured dreissenid excretion rates is complicated by a number of factors. Of the five other studies which report dissolved P excretion rates, four were laboratory studies (Arnott and Vanni 1996, James et al. 2001, Conroy et al. 2005, Naddafi et al. 2008), while the fifth is based on measured increases in SRP concentrations observed in the Seneca River following dreissenid establishment (Effler et al. 1997). In the experiments by Arnott and Vanni (1996) and Conroy et al. (2005) mussels may have been stressed by transport to the laboratory and sustained periods out of the water immediately prior to measurement of excretion rates. On the other hand, in the excretion experiment run by James et al. (2001) the mussels were allowed to acclimate to laboratory conditions for two weeks before excretion rates were measured; Naddafi et al. (2008) used a one day acclimation period. The length of the experiments also varied: Arnott and Vanni (1996) used two and six hour incubation periods, finding lower excretion rates for the six hour incubation, while Conroy et al. (2005) allowed their mussels to excrete for six hours, as did Naddafi et al. (2008). James et al. (2001) carried out a longer term experiment, where mussel excretion was measured over the course of two weeks. Additionally, in the two short term experiments, the mussels were placed into filtered water, starving the mussels for the duration of the trial, while James et al. (2001) 'fed' their mussels with unfiltered reservoir water. On the other hand, Naddafi et al. (2008) filtered the water used in incubation experiments through 100 µm mesh, removing most of the zooplankton, but not all potential mussel food. Finally, I studied quagga mussel excretion rates, while all other reported rates are for zebra mussels (with the exception of those by Conroy et al. (2005).

In addition to the aforementioned differences in methodology, the rates measured in the different studies may include P release and uptake processes other than mussel excretion. Arnott and Vanni (1996) carried out their excretion experiments in filtered water, and scrubbed their mussels to remove periphyton, ensuring that measured rates represent net excretion by the mussels and not gross

rates which include uptake by phytoplankton and periphyton. Conroy et al. (2005) also used filtered water, but did not report removing periphyton adhering to mussels; thus their rates include whatever effect periphyton had on P dynamics in the experimental chambers. Similarly, James et al. (2001) did not report removing periphyton from their mussels. James et al. (2001) kept their mussels in unfiltered water to allow them to feed, but corrected for possible phytoplankton P uptake by having control chambers with unfiltered water and no mussels. Naddafi et al. (2008) removed periphyton from their mussels, but included phytoplankton in incubation chambers, correcting for the effect of phytoplankton by including controls with phytoplankton but no mussels. The only other reported excretion rate comes from SRP measurements made in the Seneca River before and after the establishment of dreissenids (Effler et al. 1997). The rate estimated by Effler et al. (1997) was not obtained experimentally, and is therefore difficult to compare with the four laboratory studies.

Unlike the laboratory studies discussed above, I used mussels which had not been stressed by transport to the laboratory and handling. The mussels used in my trials were exposed to natural photoperiods, temperatures and food sources. Because this work was done *in situ* and since I was interested in the effects of mussel-associated microbiota, I could not filter the water inside the incubation chambers or fully remove the biofilm adhering to the mussels, so another way was needed to correct for the effect of phytoplankton and biofilm not associated with the mussels. I attempted to approximate net P release rates by dreissenids and the associated microbiota by measuring the P release and uptake rates of phytoplankton and biofilm in the absence of mussels, and then subtracting this rate from the gross rates of P release in chambers containing mussels and mussel associated biofilm, phytoplankton and biofilm associated with the substrate. Since phytoplankton biomass is probably lower (due to phytoplankton removal by mussels during the incubation) in mussel containing chambers than in chambers without mussels, my net rates should be considered conservative estimates. Another factor that could cause an underestimate of excretion rates by the mussels is the positive relationship between P concentration and P uptake rates by algae and bacteria (e.g. Bentzen and Taylor 1991). Because of the higher SRP concentrations in mussel-containing chambers, P uptake rates by periphyton, phytoplankton and bacteria could be higher than in control chambers deployed over mussel free substrate, and this would result in underestimation of mussel P excretion

Table 3.2: Mean dreissenid SRP excretion rates in µg SRP per gram SFDM per hour from this study and a number of other studies.

Study	Setting	Species	SRP excretion rate (µg/g SFDM/h)
This study	Field measurement	*D. bugensis*	7.0
Arnott and Vanni 1996	Lab measurement	*D. polymorpha*	13.75 - 31.58
Conroy et al. 2005 (based on Table 1)	Lab measurement	*D. bugensis*	6.83
		D. polymorpha	12.83
James et al. 2001	Lab measurement	*D. polymorpha*	3.08
Naddafi et al. 2008	Lab measurement	*D. polymorpha*	2.5 - 22.5
Effler et al. 1997	Field observation	*D. polymorpha*	5.62

Despite differences in methodology, the biomass-specific SRP excretion rates obtained in all studies are surprisingly similar (Table 3.2): rates obtained in this study are close to those reported for *D. bugensis* by Conroy et al. (2005). However, our rates are 2- 4.5 times lower than rates reported by Arnott and Vanni (1996) (Table 3.2), and more than 2 times higher than those found by James et al. (2001) for *D. polymorpha*. The wide range reported by Naddafi et al. (2008) encompasses many of the rates reported in other studies of dreissenid excretion. Although the order of magnitude similarity in the range of all five direct measurements of mussel P excretion suggests that laboratory studies could yield realistic excretion estimates, a side-by-side comparison using mussels from the same system would be needed to determine whether excretion results from laboratory and field studies are significantly different from each other.

3.3.3 Phosphorus supply to the nearshore by dreissenids

The results of this study suggest that dreissenid mussels and the biota closely associated with them can have large impacts on dissolved phosphorus cycling in the nearshore of Lake Ontario. The biomass survey indicated that there was a total of 530 tonnes of dreissenid SFDM along an 8 km stretch of Halton shoreline between the depths of 0 and 12 meters (shaded area in Fig 3.1). The average SRP excretion rate in the study area was 0.45 mg SRP/m^2/hour. Assuming this rate is constant throughout the diel cycle (24 hours), then I can estimate that a total of 11 tons of SRP are excreted by dreissenids from May to August, the main *C. glomerata* growing season (Malkin et al. 2008). Since dreissenid feeding activity and digestion follows a diel rhythm (Morton 1969), it appears likely that excretion rates are not uniform throughout the day. Further study is needed to determine how the diel rhythm of feeding and seasonal variation in food availability affect dreissenid excretion. Most digestion in dreissenids takes place during the quiescent period of the diel cycle when the shell valves are closed and filtering is minimal (Morton 1969), and dreissenids have been shown to excrete considerable amounts of SRP even when starving (James et al. 2001).

A comparison of modeled phosphorus uptake rates by *C. glomerata* with dreissenid excretion rates reveals that dreissenids in the 0–12 m depth zone are capable of excreting phosphorus in excess of the demand by *C. glomerata* during the early spring at all depths, and at all depths >3.5 m during peak demand (Fig. 3.5). Total SRP excretion by dreissenids in the mixed layer significantly exceeds the total P demand by *C. glomerata*, so excess phosphorus excreted by dreissenids at greater depths could still be available to *C. glomerata* at shallower depths. It is estimated that *C. glomerata* in the modeled area (Fig. 3.1) takes up 25 kg of P/day during peak P demand, while dreissenid mussels in the same area excreted 89 kg of recycled bioavailable SRP/day.

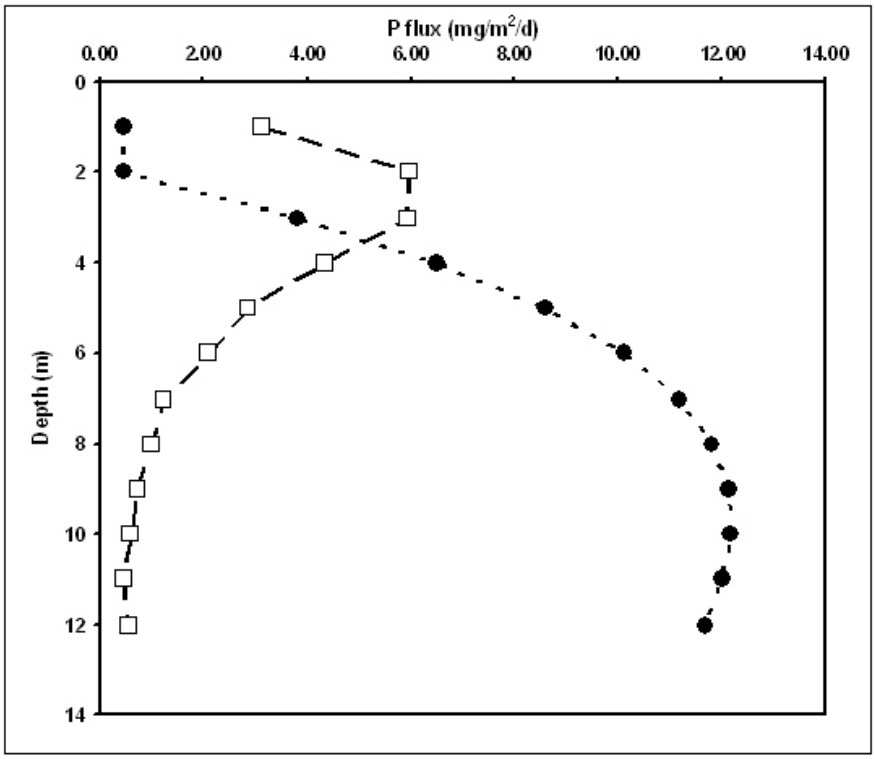

Figure 3.5: Phosphorus uptake rate by *C. glomerata* during peak uptake period as calculated by the CGM (clear squares) and phosphorus excretion rate by dreissenid mussels (solid circles).

Finally, I can compare bioavailable phosphorus regenerated from dreissenids with other known fluxes of phosphorus in the vicinity of the study area. In 2004-2005, Sixteen-Mile Creek supplied 5,300 to 7,200 kg of TP and 1,200 to 1,700 kg SRP/year, most of which entered Lake Ontario in early spring. Only 300-1,200 kg of TP and 50-250 kg of SRP were discharged from

Sixteen Mile Creek during the main *C. glomerata* growing season (May to August). The Oakville SE Wastewater Treatment Plant discharged 2,672 kg of TP in 2007, of which the vast majority (2,587 kg) was in readily bioavailable dissolved form, making the WTP the largest watershed source of SRP to the study area. This source contributed 690 kg of TP and 687 kg of SRP during the main *C. glomerata* growing season (Regional Municipality of Halton, 2008). The combined input of SRP from Sixteen-Mile Creek and the Oakville SE WTP equals between 6 and 7.6 kg SRP/day during the main *C. glomerata* growing season. Three smaller creeks (Joshua's Creek, Wedgewood Creek and Morrison Creek) contributed approximately 2000 kg of TP/year, while storm sewers were a relatively minor source, discharging just under 200 kg of TP/year (Aquafor Beech Limited 2005). Assuming that the proportion of TP to SRP in the water discharged by the three smaller tributaries and storm sewers is similar to that from Sixteen-Mile Creek, I can estimate their annual contributions to be 460 and 46 kg SRP, respectively. Unfortunately, phosphorus loading from the smaller creeks and storm sewers was reported as a single value for the entire year, making it difficult to say how much they contribute during the *C. glomerata* growing season. Phosphorus inputs from watershed sources and dreissenid inputs are summarized in Table 3.3.

Table 3.3: Annual total phosphorus (TP) and soluble reactive phosphorus (SRP) loading from watershed sources to study area and dreissenid P excretion (assuming mussel excretion only occurs for six months of the year).

Source	Annual TP load (kg)	Annual SRP load
Sixteen-Mile Creeek (based on 2004-2005 loading)	5,300-7,200	1,200-1,700
Oakville SE WWTP (based on 2007 loading)	2,672	2,587
Joshua's Creek, Wedgewood Creek, Morrison Creek (based on 2004-2005 loading)	~2000	~460
Storm sewers (based on 2004-2005 loading)	~200	~46
Dreissenid mussels (based on 2006 measurments)	---	16,000

The results of this study suggest that mussels could be recycling, and thus supplying, as much as 32,000 kg of bioavailable phosphorus to the study area annually. This is well in excess of all other sources, which supply between 10,170 and 12,070 kg TP/year, but is likely an overestimate because dreissenid phosphorus excretion rates are probably lower in the winter. However, even if mussel excretion rates were reduced to zero for six months of winter, the amount of bioavailable phosphorus released through dreissenid excretion would still be greater than the amount of TP supplied from watershed sources. More significantly, dreissenids supply considerably larger amounts of SRP than

watershed sources in this heavily urbanized study area: more than three times as much SRP is released by dreissenids (assuming no excretion for six months of the year) than is supplied from the watershed throughout the year. It is likely that dreissenids would provide an even greater proportion of bioavailable phosphorus along rural and natural shorelines compared to watershed sources, than along urbanized shorelines such as the one I studied, where numerous point sources of P loading occur.

Due to their large biomass and enormous filtering capacity, feeding and excretion by dreissenid mussels can have large impacts on the nearshore environment. Their filtration removes particles from the water and improves light transmission in the coastal zone, expanding the illuminated bottom area that can support *C. glomerata* growth. In this study, I have shown that dreissenids have a substantial effect on phosphorus cycling in the nearshore, in a sense representing a new source of SRP by efficiently recycling and increasing the rate of remineralization of phosphorus in the littoral zone of the Great Lakes. A number of important questions still remain. Results from this study and the CGM show that dreissenids supply more P than is needed to support local *C. glomerata* growth (except perhaps at the shallowest depths), but it is unknown how heavily *C. glomerata* actually relies on this P source. The variability of phosphorus excretion by dreissenids over the annual cycle is also unclear, as is the effect of depth on excretion rates. I used average excretion rates obtained in June and July at a depth of 1.5 meters and extrapolated across the summer season and down to a depth of 12 meters, making these results general approximations. This may not be unrealistic: results from Lake Simcoe show similar SRP excretion rates at 2, 5 and 10 m depth (Ozersky et al. unpublished). Finally, our understanding of post-dreissenid nearshore phosphorus dynamics would benefit from elucidating the source of the phosphorus recycled by mussels, specifically determining the proportion of P made available from offshore Lake Ontario compared to that contributed directly from the land catchment in the form of particulate organic matter. If much of the phosphorus recycled by dreissenids is brought to the nearshore by currents from the open lake in the form of phytoplankton and not from local watershed sources, then local reductions in nutrient inputs may not be sufficient to control growth of nuisance benthic algae. Even if watershed inputs in our study area were completely eliminated, dreissenids would still supply more than enough P to fuel the local nuisance growth of *C. glomerata* (assuming mussels recycle mostly offshore- derived P). If much of the P recycled by dreissenids comes via offshore phytoplankton, local action may not appreciably reduce local *C. glomerata* growth; lake-wide reductions in TP concentrations would be required. Such reductions would only be possible through coordinated action by different jurisdictions

around the lower Great Lakes, but lake-wide decreases in TP levels and primary productivity may not be feasible or even desirable due to the negative effect they might have on pelagic food webs and fisheries. Increased nearshore benthic primary productivity and nuisance *C. glomerata* growth brought about by dreissenid mussels may be a long- term feature of the post- dreissenid ecological landscape of the Great Lakes.

Chapter 4
Long-term Impacts of Invasive Dreissenid Mussels on the Littoral Benthos of a Large Lake

4.1 Introduction

Almost 25 years have passed since the dreissenid mussels *Dreissena polymorpha* and *D. rostriformis bugensis* invaded North American freshwaters. The colonization of North American aquatic ecosystems by these species has been associated with significant and often drastic changes to many aspects of the aquatic environment. One of the most consistently observed and significant effects attributed to dreissenids has been the translocation of primary and secondary production from the pelagic to the nearshore zone, a process that has been called "benthification" (Mills et al. 2003), or the "nearshore shunt" (Hecky et al. 2004). Benthic invertebrate communities have been particularly strongly affected by dreissenids, with most studies showing enhancement of the nearshore benthos (Stewart and Haynes 1994, Botts et al. 1996, Ricciardi et al. 1997, Bially and MacIsaac 2000, Ward and Ricciardi 2007), and more mixed impacts offshore (Lozano et al. 2001, Nalepa et al. 2003, Jimenez et al. in press).

Two dominant mechanisms are seen as responsible for the effects of dreissenids on nearshore benthic communities. Dreissenid mussels increase the surface area and complexity of both hard and soft substrates, creating additional habitat on and between mussel shells (Stewart et al. 1998). Dreissenids also increase the amount of food available to detritivores and grazers by depositing edible organic material (Izvekova and Lvova-Katchanova 1972, Gergs and Rothhaupt 2008) and potentially by stimulating benthic primary production through nutrient remineralization and increasing light availability by filtering and clearing the water column (Hecky et al. 2004, Malkin et al. 2008, Ozersky et al. 2009). Experimental studies show that both mechanisms (increased habitat complexity and food availability) are important, with the former likely playing a dominant role (Ricciardi et al. 1997, Stewart et al. 1998). Previous studies have identified a number of taxonomic groups as particularly likely to benefit from dreissenid establishment, most notably gammarid amphipods, oligochaetes, some gastropods, isopods and flatworms (Dermott et al.1992, Griffiths 1992, Stewart and Haynes 1994, Ricciardi et al. 1997, Stewart et al. 1998).

Despite two decades of study and the description of dominant mechanisms of impact as well as outcomes of dreissenid establishment on benthic communities, some gaps in knowledge remain. Chief among these is the paucity of long-term quantitative studies of dreissenid impacts on hard substrate nearshore communities. Most of the knowledge concerning dreissenid impact on hard substrate benthos comes from short-term studies using artificial substrates. While valuable, such studies only include habitat on and in between mussels while ignoring the potentially important habitat present in between individual rocks and in the frequently large deposits of mussel shell. I am aware of only one long-term, quantitative study of dreissenid impacts on natural hard substrates, repeated a number of times at two adjacent sites in Lake Ontario (Stewart and Haynes 1994, Haynes et al. 1999, Haynes et al. 2005). Another issue is that most studies have been carried out in only one location and at only one depth (but see Ricciardi et al. 1997), so extrapolation to different sites and depths is questionable.

The objective of this study is to evaluate the long-term effects of dreissenid establishment on the benthic fauna of rocky littoral substrata in a large inland lake. Quantitative, depth-stratified sampling of the benthos was carried out at four sites in Lake Simcoe, Ontario, just prior to establishment of dreissenids and again fifteen years after. I describe changes in the density and community composition of the benthos and present evidence that long-term *Dreissena* presence has led to "homogenization" and enhanced production of the benthic community across space and depth.

4.2 Materials and methods

4.2.1 Study site

Lake Simcoe is a large (722 km^2), oligo-mesotrophic lake, located in a predominantly agricultural (43% of catchment area) watershed in Southern Ontario (Fig. 4.1). Lake Simcoe has an extensive littoral zone with approximately 45–55% of the lake bottom area of the Main Basin located in the euphotic zone, i.e., depths <2.5 times Secchi depth or 16 m (D.O. Evans OMNR, unpublished data). The littoral zone is dominated by hard substrates such as boulder, cobble, and pebble with areas of sand and softer sediments in sheltered and deeper parts of the nearshore zone. Lake Simcoe supports a large recreational fishery of native cold-water species including primarily lake trout and lake whitefish, and cool- and warm-water species, such as yellow perch and smallmouth bass. Dreissenid mussel larvae were first observed in Lake Simcoe in 1993, but mussels did not appear in

the benthos until fall 1994 and were becoming well established in the lake by the winter of 1995–96 (Evans et al. in press). As of 2008 dreissenids were abundant throughout the littoral zone of the lake, attaining an average biomass of 27.2 g of shell-free dry mass in the main basin of the lake, with more than 80% of the biomass concentrated at depths <12 m (Chapter 2). Dreissenid establishment in Lake Simcoe has been linked to increased Secchi depth and decreased algal biovolume (Eimers et al. 2005), increased macrophyte biomass (Depew et al. 2010), altered nutrient dynamics (Guildford et al. unpublished) and decreases in the abundance of profundal benthos (Jimenez et al. 2010).

Four locations were sampled in this study: Sibbald and Blackbird Points in the south-central part of the lake, and Grape and Strawberry Islands in the north. Sibbald Point was the only mainland site sampled in this study. Substrate at all sites consisted predominantly of cobble, boulder and pebble with some patches of sand at 6 m depths in 1993. By 2008, these substrata were covered with living dreissenid mussels and spaces between rocks were filled with a large amount of deposited mussel shells and soft, fine-grained material. While substrate composition was generally similar among sites, the sites differed in the degree of exposure to currents and waves. Sibbald and Blackbird Points are relatively exposed to the prevailing north westerly winds, while Grape Island is the most protected site.

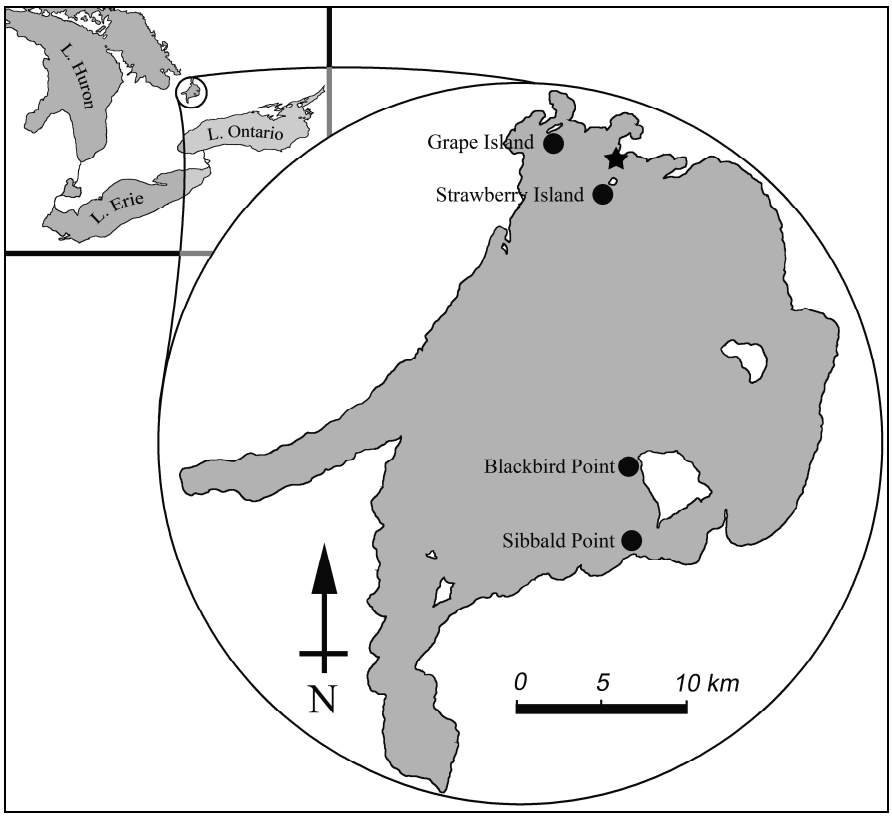

Figure 4.1: Map of Lake Simcoe in relation to Laurentian Great Lakes. Airlift sampling sites are marked with dark circles. McRae Point (Chapter 5) is marked with a star shape.

4.2.2 Sampling design

Benthic invertebrates were sampled in 1993, just prior to mussel establishment, and in 2008, fourteen years after mussel establishment. Four sites were sampled at three depths (2, 4 and 6 m) in both sampling years (Fig. 4.1). Benthic invertebrate sampling was carried out between August 25 and September 16 in 1993, and on September 20 and September 21 in 2008, using airlifts (Barton and Hynes 1978) operated by divers, with 500-µm nitex collection bags in 1993 and 375-µm nitex collection bags in 2008. The airlift was fed compressed air from the surface in 1993, and from a standard SCUBA tank in 2008. In both sampling years divers systemically "vacuumed" the substrate within randomly placed sampling quadrats, while removing and cleaning rocks by hand and using a scraper to a depth of 20 cm or until the underlying hard substrate was reached. Three or 4 replicate quadrats (0.25 m^2 in 1993, 0.0625 m^2 in 2008) were collected from each depth at each site in both

years; the smaller quadrat was used in 2008 because of the large amount of mussel shell material collected (2 to 4 L/sample).

Benthic samples were preserved in the field with 10% buffered formalin. Samples collected in 1993 were stored in formalin until 2008 when they were transferred to ethanol prior to sorting. Samples collected in 2008 were transferred to ethanol shortly after return to the lab. Samples were elutriated to separate lighter organic material from the heavier sand and mussel shells, and invertebrates were sorted from both fractions with the aid of a dissecting microscope. Some of the 2008 samples were subsampled by spreading the elutriated material evenly on a round surface, and then subdivided into 8 even slices. Two opposite slices were combined to make up a ¼ subsample. Benthic invertebrates in one replicate from each depth/site combination were identified to genus (Oligochaeta to family) and enumerated. Invertebrates in the remaining replicates were identified to a level between order and species (see appendix A). Although crayfish were frequently collected in 1993 and 2008 they are not included in the results of this study. I believe that the use of a smaller quadrat and sub-sampling in 2008 would have made comparisons between 1993 and 2008 difficult for such large and mobile animals.

4.2.3 Statistical analyses

Two-way ANOVA, followed by Holm-Sidak post-hoc tests, was used on Log_{10} (1993 numbers) or square root (2008 numbers) transformed densities to examine differences in total macroinvertebrate abundance between sites and depths in 1993 and 2008. I was unable to transform the 2008 data to meet the assumption of equality of variance, but decided to go ahead with the analysis because ANOVA is relatively robust against violation of this assumption, especially when the number of replicates in different treatments is equal or nearly equal as is the case here (Glass et al. 1972). Mann-Whitney U tests were used to compare the total and relative abundances of different taxonomic groups in 1993 and 2008. The Mann-Whitney test was also used to compare total average abundance in 1993 and 2008. Only taxa comprising at least 3% of any sample were included in the comparisons. Oribatid mites were also excluded because the mesh used in 1993 was too coarse to retain them if they were present.

Changes in community composition were analysed using multivariate statistics. Multidimensional scaling (MDS) of square root transformed abundances was used to visualize differences in community composition between sites and depths. Two-way analysis of similarity

(ANOSIM) tests were used to test for the significance of the differences in community composition between different sites and depths. Similarity of percentages (SIMPER) tests were used to determine the degree of dissimilarity among sites and depths and to identify the taxa contributing most to the dissimilarity (Clarke and Warwick, 2001). Cluster analysis on abundant and common taxa (present in at least 10% of samples and comprising at least 1% of abundance) was used on 2008 abundance data to identify taxa groupings. Non-multivariate analyses were carried out using SIGMAPLOT 11 (Systat Software Inc., Chicago), multivariate analyses were carried out using Primer v.6 (Primer-E Ltd. Plymouth, UK).

4.3 Results

4.3.1 Pre-dreissenid benthic community

The average density of benthic macroinvertebrates in 1993 was 367.9 (±71.1 SE) individuals/m^2. A total of 60 taxa was identified in the samples that were sorted to genus, with an average of 17.0 (±7.5 SD) taxa/sample. The benthic invertebrate community consisted primarily of Chironomidae (21.1%), Sphaeriidae (13.9%), Oligochaeta (11.2%), Hydrobiidae (9.6%), Heptageniidae (8.5%) and the amphipod *Hyalella azteca* (8.2%) (Table 4.1). Densities differed significantly among sites and depths (two-way ANOVA, and Holm-Sidak post-hoc tests). Total abundance declined with increasing depth at all sites. Strawberry Island yielded significantly more and Grape Island significantly fewer invertebrates than did the other two other sites (Fig. 4.2a, Appendix A).

An MDS plot of the pre-dreissenid community (Fig. 4.3a) grouped samples by site and depth, and these groupings were confirmed by a two-way ANOSIM test, which showed significant differences in community composition among all sites (global R=0.722, p=0.001) and all depths (global R=0.517, p=0.001). The percent dissimilarity between depths and sampling sites (based on average depth and site abundances) as well as the organisms contributing most to group dissimilarity were identified using the SIMPER test. Percent dissimilarity values between depths and sites are shown in table 4.2. Variations in the abundance of chironomids and Oligochaeta contributed most to dissimilarity among sites. *H. azteca* and chironomids contributed most to dissimilarity among depths,

Table 4.1: Average total abundance and percent composition (excluding *Dreissena* spp.) of benthic invertebrates in 1993 and 2008, with standard error is shown in brackets. Asterisks represent significant difference between 1993 and 2008 samples at α=0.05, and appear beside the significantly larger value.

	Abundance/m^2		Percent composition	
	1993	2008	1993	2008
Amphipoda				
H. azteca	40.3 (12.6)	2740.6 (451.1)*	8.2 (1.3)	16.7 (2)*
Gammarus sp.	5.3 (1.5)	1902.2 (320.6)*	1.1 (0.3)	10.9 (1.1)*
E. ischnus	0 (0)	1092.6 (296.9)*	0 (0)	5.1 (1.4)*
Crangonyx sp.	13.8 (4.5)	630.4 (147.8)*	3.9 (0.9)	3.2 (0.5)
Isopoda				
C. racovitzai	0.2 (0.1)	1614.2 (236.4)*	0.2 (0.2)	10.9 (1.3)*
Gastropoda				
Hydrobiidae	14.4 (3)	254.9 (48.3)*	9.6 (2.4)	1.5 (0.3)
Physidae	7.6 (1.6)	50.5 (10.1)*	2.4 (0.5)*	0.3 (0.1)
Planorbidae	0.1 (0.1)	134.8 (63.7)*	0.1 (0.1)	0.7 (0.3)*
Pleuroceridae	7.6 (2.5)*	0 (0)	2.5 (0.8)*	0 (0)
Ancylidae	0.4 (0.2)	485.7 (101.4)*	0.5 (0.3)	3.4 (0.7)*
Bivalva				
Sphaeriidae	32.6 (4.6)	91 (18)	13.9 (1.6)*	0.5 (0.1)
D. polymorpha	0 (0)	3322.5 (347.6)	- (-)	- (-)
D. bugensis	0 (0)	100.1 (16.5)	- (-)	- (-)
Unionidae	0.3 (0.2)	0 (0)	0.5 (0.4)	0 (0)
Insecta				
Chironomidae	106 (28.9)	3338.3 (485.2)*	21.1 (2.6)	20.4 (2.5)
Polycentropodidae	6.7 (1.6)	261 (52.4)*	1.4 (0.3)	2.3 (0.5)
Helicopsychidae	0 (0)	85 (53.3)*	0 (0)	0.3 (0.1)*
Leptoceridae	2 (0.5)	58 (23.2)	1 (0.4)	0.3 (0.1)
Hydroptilidae	0.3 (0.2)	21 (8.2)*	0.2 (0.2)	0.1 (0)
Hydropsychidae	0.6 (0.4)	0.7 (0.5)	0.1 (0.1)	0 (0)
Caenidae	1.6 (0.6)	18.8 (6.6)	0.2 (0.1)	0.1 (0)
Heptageniidae	35.5 (8.8)	55.8 (17.2)	8.5 (1.4)*	0.3 (0.1)
Ephemeridae	0.7 (0.3)	21.7 (8.1)*	0.2 (0.1)	0.2 (0.1)
Sialidae	0.1 (0.1)	12.4 (3.8)*	0.2 (0.2)	0.1 (0)*
Elmidae	14.5 (4.9)	92.8 (45.1)	3.7 (1.3)	0.6 (0.3)
Psephenidae	0.9 (0.4)*	0 (0)	0.4 (0.2)*	0 (0)
Acari				
Hydracarina	26.4 (14.1)	324.1 (73.1)*	6.6 (1.3)*	1.8 (0.3)
Worms				
Planariidae	0.8 (0.3)	404.3 (85.4)*	0.3 (0.2)	2.3 (0.4)*
Oligochaeta	43.7 (10.7)	2540.8 (309.3)*	11.2 (1.9)	15.4 (1.3)*
Hirudinea	1.5 (0.5)	49.4 (14.6)*	1.4 (1)	0.3 (0.1)*
Nematoda	3 (1.8)	312.2 (75.4)*	0.2 (0.1)	1.8 (0.4)*
Other	1 (0.3)	99.2 (45.5)*	0.2 (0.1)	0.5 (0.2)*
TOTAL	367.7 (71.1)	22192.4 (2529.5)*	100 (0)	100 (0)

with shallower depths yielding higher densities of both organisms. The greatest dissimilarity between depths was between 2- and 6-m sites, and Grape Island and Strawberry Island were the most dissimilar sites.

4.3.2 Changes associated with *Dreissena* and the Post-dreissenid benthic community

Considerable change in the abundance and community composition of the benthos occurred following the dreissenid invasion (Table 4.1). Both total invertebrate density (22,192.4 ± 2,529.5 SE individuals/m^2) (Mann-Whitney U test, $T_{42,45}$=903.0, p<<0.05) and richness (31.2 ± 6.4 SD taxa/sample) (two-sample independent t-test, t_{23}=-5.05, p<<0.05) were significantly greater in 2008 than in 1993. Average density of non-dreissenid invertebrates in 2008 was 16,706.4 (±1,571.2 SE) individuals/m^2. A total of 85 taxa were identified in the 2008 samples, including 3 recent introductions (*D. polymorpha*, *D. rostriformis bugensis* and the amphipod *Echinogammarus ischnus*) that contributed an average of 4515 individuals/m^2.

Densities of most groups of invertebrates were significantly greater in 2008 (Mann-Whitney U test, at a=0.05). Notable exceptions were Pleuroceridae, Unionidae and Psephenidae, none of which were collected in 2008; densities of Hydropsychidae were the same in both years; Sphaeriidae, Caenidae and Heptageniidae were more abundant in 2008, but not significantly so. Abundant taxa that were found only in 2008 included *D. polymorpha*, *D. rostriformis bugensis*, *Echinogammarus ischnus*, the caddisfly *Helicopsyche borealis* and the chironomids *Procladius* and *Cricotopus*.

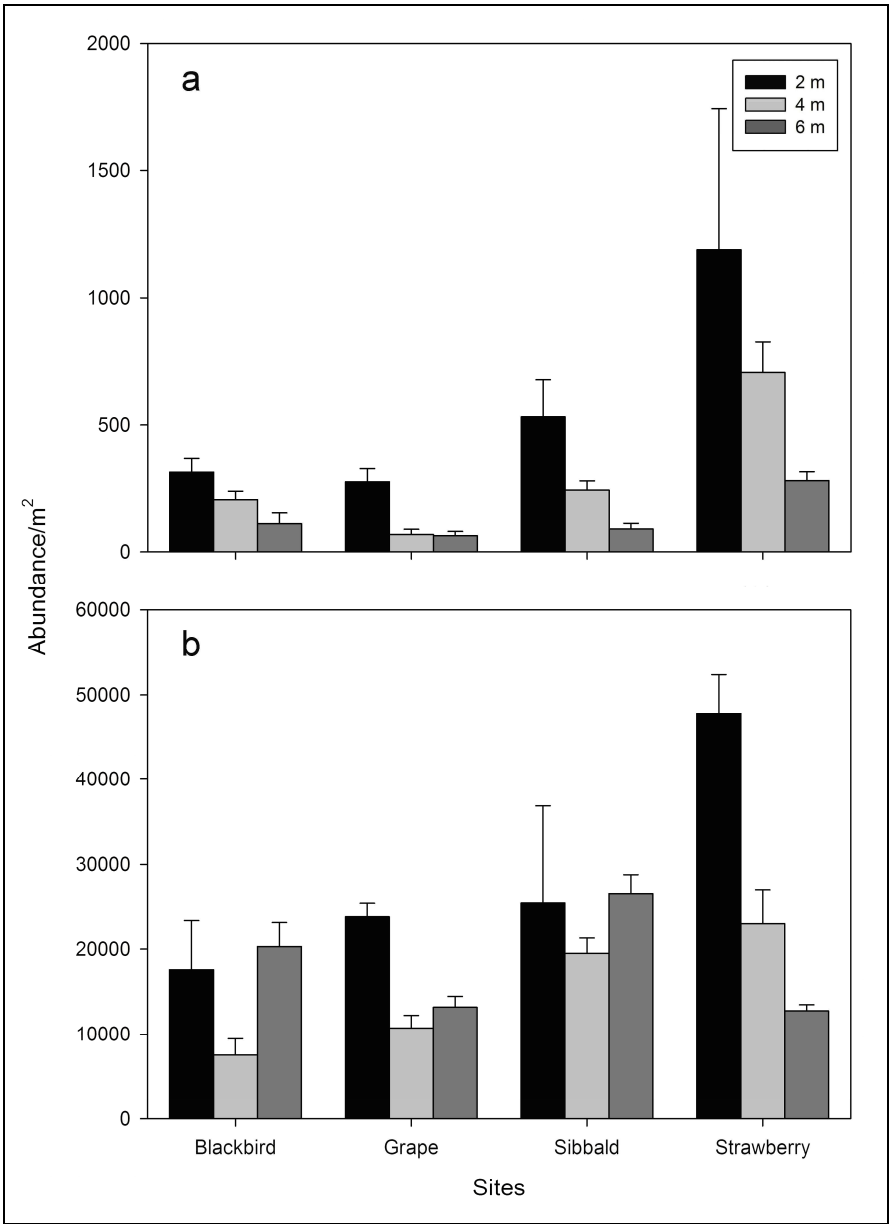

Figure 4.2: Average abundance of benthic invertebrates at 2, 4 and 6 m in 1993 (top panel) and 2008 (bottom panel) at four sampling sites. Note different scale of the y-axes.

A number of significant changes occurred in the relative composition of the benthos as well (Mann-Whitney U test, at a=0.05). The amphipods *H. azteca*, and *Gammarus* sp., the isopod *Caecidotea racovitzai*, planorbid snails, Ancylidae, *Sialis* and all worms (Planariidae, Oligochaeta, Hirudinea and Nematoda) increased in relative abundance. In contrast, Physidae, Sphaeriidae,

Heptageniidae and Hydracarina were relatively less abundant. ANOSIM tests on total invertebrate abundance as well as relative community composition show significant differences (R=0.941, p=0.001; R=0.77,p=0.001) between 1993 and 2008.

With the exception of *Dreissena*, in 2008 the benthic community was numerically dominated by Chironomidae (19.7%), *H. azteca* (16.1%), Oligochaeta (14.6%), *Gammarus* sp. (10.5%) and *C. racovitzai* (10.2%) (Table 4.1). Overall, *D. polymorpha* comprised 19.1% of benthic abundance, while *D. rostriformis bugensis* was considerably less abundant at 0.6% of the total. Although not included in analysis, small oribatid mites were very abundant in shallow water at Strawberry Island and occurred in low numbers at the other locations.

Table 4.2: Percent dissimilarity of benthic communities between pairs of depth and site groups as determined by SIMPER analysis. Comparisons are shown for the 1993 benthic community, the 2008 benthic community including dreissenids, and the 2008 community excluding dreissenids.

	Dissimilarity (%)		
Comparison	1993	2008 with *Dreissena*	2008 without *Dreissena*
2 vs. 4 m	44.7	34.52	38.38
2 vs. 6 m	56.05	44.31	48.73
4 vs. 6 m	48.29	37.92	42.62
Blackbird vs. Grape	57.26	38.77	43.68
Blackbird vs. Sibbald	47.64	43.11	49.41
Blackbird vs. Strawberry	53.97	38.50	43.93
Grape vs. Sibbald	57.64	40.57	43.87
Grape vs. Strawberry	64.1	39.90	44.46
Sibblad vs. Strawberry	46.6	43.33	48.10

Two-way ANOVA showed that invertebrate abundance differed significantly among depths ($F_{2, 44}$=10.59, p<0.05), and sampling sites ($F_{3, 44}$=7.10, p<0.05). There was significant interaction between the effects of sampling depth and sampling site ($F_{6, 44}$=4.71, p=0.001). Despite significant effects of depth and site, Holm-Sidak post-hoc tests showed that these differences were present across only a few comparisons, with relatively low abundance at 4 m at Blackbird Point and Grape Island and no differences between depths at Sibbald Point. Abundance at Strawberry Island at 2 m was highest among all sites and depths in both 1993 and 2008 and continued to show a decline in abundance with depth in both years. The most dramatic change from 1993 to 2008 was the increased abundance at 6 m across all sites, with average increases of 145 fold, and no differences among all sites at this depth.

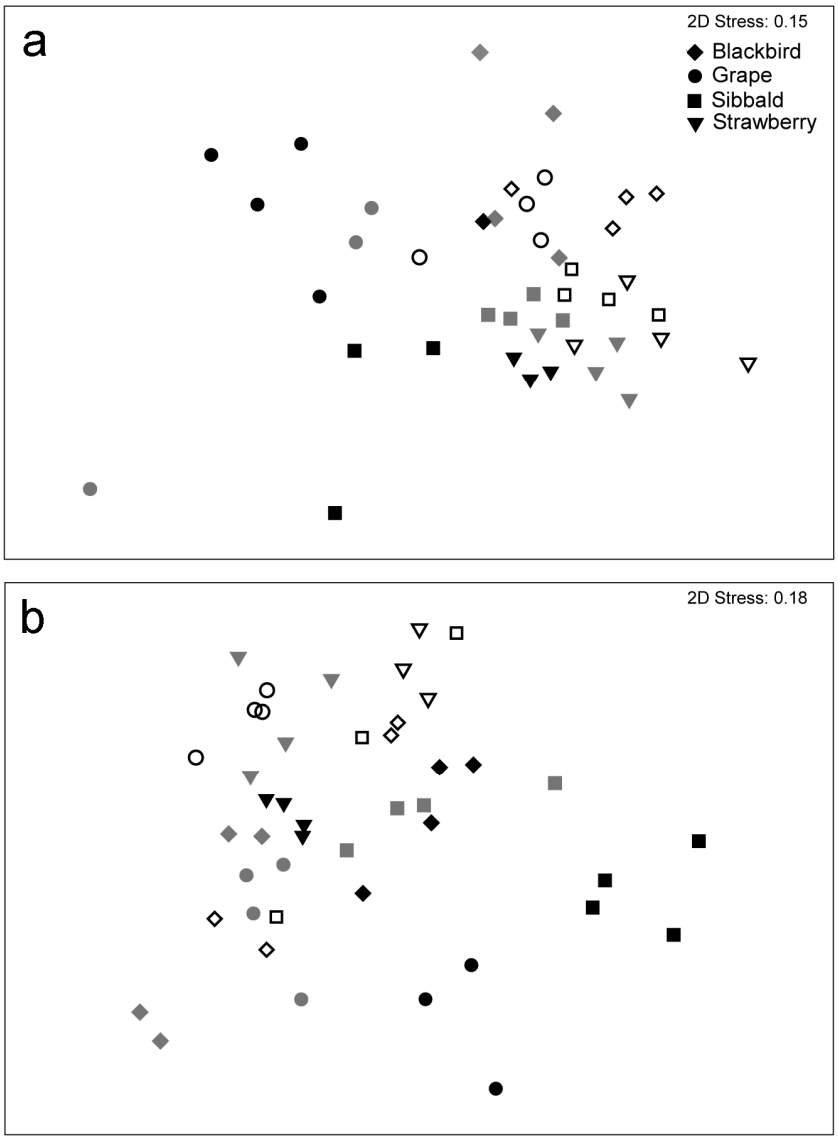

Figure 4.3: MDS of square root transformed invertebrate abundances in 1993 (top panel) and in 2008 (bottom panel). Empty symbols represent 2-m sampling quadrats, grey symbols represent 4-m quadrats and black symbols represent 6-m quadrats.

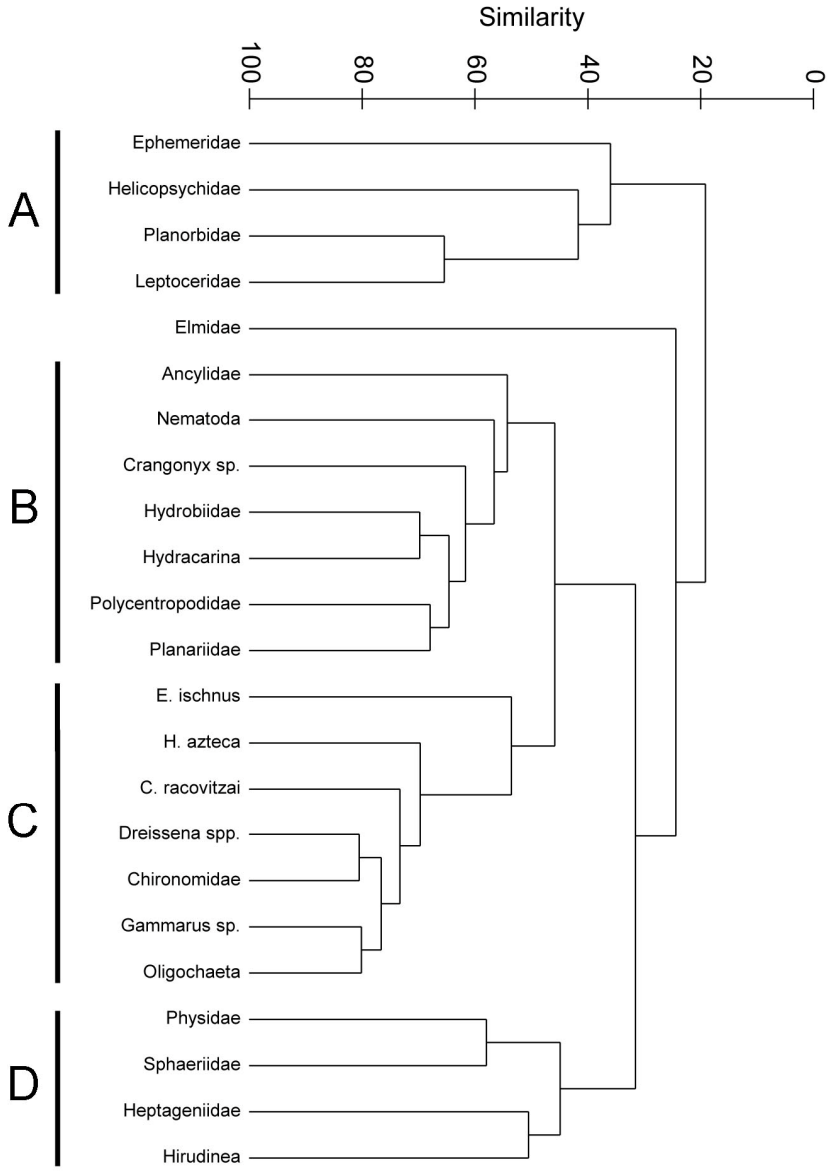

Figure 4.4: Hierarchical cluster analysis dendrogram of taxa similarity for 2008 data, based on square root transformed abundances. Letters represent clusters of taxa.

As in 1993, variations in the abundance of chironomids and oligochaetes were primarily responsible for differences among sites, although differences in the abundance of *H. azteca*, *C. racovitzai* and *E. ischnus* were also important. Differences in densities of *E. ischnus*, *H. azteca*, *Gammarus sp.* and chironomids contributed most to dissimilarity among depths. Amphipods were more common at shallow depths, whereas high chironomid densities were more typical of 6-m depths. Sibbald Point and Strawberry Island were determined to be the most dissimilar of the sites. Dissimilarity values between depths and sites decreased from 1993 to 2008 for almost all pair wise comparisons, regardless of the inclusion of dreissenids in SIMPER analysis (Table 4.2). Cluster analysis (Fig. 4.4) of common taxa (present in at least 10 percent of samples, and comprising at least 1% of total abundance in a sample) shows four distinct groups, with elmid beetles forming an apparent outlier. *Dreissena* spp., *H. azteca*, *E. ischnus*, *Gammarus* sp., chironomids and oligochaetes form a distinct group (cluster C). All of these taxa, with the exception of Chironomidae, have increased in proportional abundance following dreissenid introduction. Cluster A is 'farthest' from the dreissenid-associated community (cluster C) and includes organisms which do not constitute a large part of the benthos although some, like Planorbidae and Helicopsychidae increased in proportional abundance following dreissenid introduction. Cluster B includes a number of groups which increased in absolute abundance but not, with the exception of Ancylidae and Planariidae in proportional abundance. Finally, cluster D, with the exception of Hirudinea which increased slightly, includes organisms which decreased in relative abundance following dreissenid invasion.

4.4 Discussion

Considerable change has taken place in the littoral benthos of Lake Simcoe in the thirteen years following dreissenid establishment in the lake. An enormous increase in the total abundance of organisms, concordant with large compositional changes and increased taxonomic diversity, has resulted in a significantly altered benthic community. The distribution of benthic organisms across sites and depths has become more homogeneous. These changes to the benthic community occurred during a period when phosphorus inputs to the lake decreased slightly (Evans et al. 1995, Young et al. 2010) and suggest that dreissenid establishment in the lake caused substantial shifts in the flow of energy and material between the pelagic and benthic realms of Lake Simcoe.

Differences in the sampling methodology between 1993 and 2008 could potentially affect the results of this study. The finer mesh size used in 2008 could have led to retention of smaller

organisms and to higher perceived abundances and diversity in 2008. This is likely not the case since most of the organisms in 2008 were fairly large and would not have passed through a 500-µm mesh, with the possible exception of oribatid mites which were excluded from analysis. Different airlift designs were used in 1993 and 2008 but the presence of large pebbles in samples from both years suggests that both designs were similarly powerful and efficient in sampling macrobenthos. Overall, I believe that any effect on the results attributable to methodological differences would be minor relative to the effect of dreissenid mussels.

The littoral macroinvertebrate community of Lake Simcoe in 1993 was generally similar to that observed by Rawson (1930) in the mid 1920's, with chironomids, sphaeriid clams, amphipods and oligochaetes numerically dominating the community. At all four sampling sites macroinvertebrate density decreased with increasing depth, a finding I attribute to decreasing benthic primary productivity and lower food availability at greater depths. Average invertebrate abundance and community composition differed among sites, suggesting that the pre-dreissenid benthos was not spatially homogenous, with significant differences among locations in the lake. The substrate at all sites was generally similar, consisting of cobble, pebble and boulder so it would appear that factors other than substrate composition were responsible for the spatial differences in the pre-dreissenid macroinvertebrate community.

Significant change in both the total abundance and the relative composition of the benthos followed the dreissenid invasion of Lake Simcoe. Most striking was the magnitude of the increase in total macroinvertebrate abundance observed between 1993 and 2008. Large changes in the relative abundance of many organisms have also occurred. The proportions of detritivores and omnivores such as amphipods and isopods increased, while native filter-feeding sphaeriid clams declined in relative abundance and unionid mussels were absent from 2008 samples. The community composition observed by us in 2008 was similar to that described by Kilgour et al. (2008) from shallow and intermediate depths of the littoral zone of the lake in 2005, although invertebrate abundances were considerably higher in our study. The difference in abundance was likely due to differences is sampling methodology and substrate at the sampling sites; Kilgour et al. (2008) used kick and sweep sampling on hard substrates in shallow water and ponar sampling on deeper soft substrates. Despite differences in methodology and abundances, the results of both studies show that amphipods, isopods and chironomids are important components of the post-dreissenid littoral benthos in Lake Simcoe on both hard and soft substrates. An interesting difference in the results of our studies pertains to the amphipod community. Whereas Kilgour et al. (2008) found that *Gammarus lacustris* was the

dominant amphipod species in their samples, *H. azteca* was the most abundant amphipod in my samples, and *G. fasciatus* was the most abundant member of the *Gammarus* genus, with *G. lacustris* and *G. pseudolimneus* occasionally present. These differences may be due to the different substrate types sampled by me and Kilgour et al. (2008), or perhaps to interannual variation in the benthos.

Dreissenids modified not only the community composition of the benthos but also its depth distribution. Whereas in 1993 the density of benthic invertebrates decreased with increasing depth at all sampling sites, this was not the case in 2008. Invertebrate communities at different depths were also more similar in 2008 than in 1993, as indicated by percent similarity values. I suggest that dreissenids increased the evenness of resource distribution with depth in the littoral zone. By increasing water clarity and nutrient remineralization dreissenids likely enabled greater benthic primary production in deeper water, thereby increasing food availability to benthic grazers in deeper portions of the littoral zone. Dreissenids also deposit large amounts of organic-rich feces and pseudofeces, which with the bacteria that inhabit this material can provide a food resource to benthic omnivores and detritivores throughout the littoral zone (Izvekova and Lvova-Katchanova 1972; Gergs and Rothhaupt 2008).

In addition to increased community similarity across depth, community similarity among sites appeared to be greater in 2008 compared to 1993. When dreissenid mussels were included in SIMPER analyses the percent dissimilarity between all site groups was lower in 2008 than in 1993. Excluding dreissenids from the comparisons reveals a marginal increase in dissimilarity between two site pairs and substantial declines in dissimilarity between all other site pairs. Total invertebrate abundance has also become more even, with fewer significant among-site differences in abundance in 2008 compared to 1993. I suggest that dreissenid mussel establishment has led to a homogenization of benthic communities in the littoral zone of Lake Simcoe, perhaps by modifying the availability of habitat and food resources in similar ways across different parts of the littoral zone. With the above in mind, Strawberry Island and Sibbald Point supported the highest invertebrate abundances in both 1993 and 2008, although the differences between sites were not significant in 2008.

Despite increased similarity of benthic communities between sites, MDS and ANOSIM analyses show that significant differences in community composition between sites remain. For example Ancylidae were relatively scarce at Sibbald Point, but were relatively common at intermediate and deeper locations at the other sites. Elmid beetles were rarely found at most sites, but were not uncommon at Blackbird point. Oribatid mites were uncommon in most locations, but approached average densities of more than 20,000/m^2 at the 2-m Strawberry Island site. I interpret the

among-site differences to mean that the effects of dreissenid introduction can vary within a system and are modified by site specific factors. The variable effects of dreissenids on littoral benthos would be expected to be more apparent in large lakes having greater habitat diversity.

The benthic community at 6-m locations at Sibbald Point and Grape Island is distinct from that found at 6-m locations at the other two sampling sites and from that of the rest of the benthos (Fig. 4.3b). The 6-m sites at Sibbald Point and Grape Island are characterised by high abundance of chironomids, higher abundance of burrowing mayflies (Ephemeridae), and relatively lower abundance of isopods. I attribute those differences to the prevalence of soft (silt-like) substrate at those two stations. All 6-m stations were dominated by hard substrata in 1993 which suggests that either a different part of the site was sampled in 2008 or that the nature of the substrate changed from 1993 to 2008. I can not rule out the former possibility, although site coordinates were matched closely between years. Dreissenids increase sedimentation rates by active filtration and deposition (Howell et al. 1996, Klerks et al. 1996) and bivalve shell deposits could increase sediment accumulation by enhancing substrate roughness which would, in turn increase fine particle accumulation rates (Sousa et al. 2009). It is possible that over the 13 years of dreissenid presence in Lake Simcoe an encroachment of soft substrates has occurred into the deeper and less energetic portions of the littoral zone.

Results of cluster analysis suggest that amphipods, chironomids and oligochaetes form a species complex with dreissenid mussels. These organisms have been reported to increase in abundance following dreissenid establishment on hard substrata in other studies (Dermott et al. 1993, Stewart and Haynes 1994, Ricciardi et al. 1997, Ward and Ricciardi 2007), and probably benefit from direct spatial association with dreissenids by exploiting interstitial spaces between mussels shells and feeding on biodeposits. Other organisms that increased in absolute abundance, and sometimes in relative abundance formed separate clusters, and may include species that benefit from dreissenid presence indirectly, perhaps through increased benthic primary production or increases in their prey items. Species that decreased in abundance (with the exception of leeches) form a separate cluster, and may be negatively affected by dreissenid presence.

Comparison with literature

Increases in abundance and diversity of hard-substrate littoral benthos following dreissenid establishment have been noted in other studies. Dermott et al. (1992) noted that dreissenid presence significantly increased the abundance of many invertebrates in shallow rocky areas of Lake Erie.

Stewart and Haynes (1994) observed a large increase in the abundance of non-dreissenid invertebrates and an increase in taxonomic diversity following dreissenid establishment on hard substrates in the nearshore of Lake Ontario. They found that density of non-dreissenid invertebrates increased by almost an order of magnitude one to two years following dreissenid establishment, although the increase they observed was lower than seen in this study. In a survey of a number of shallow sites along the St. Lawrence River Ricciardi et al. (1997) found that invertebrate densities on rocks increased by 1.6 to 8.4 times from the early stages of dreissenid invasion to two years following the invasion.

Short-term studies conducted using artificial substrates also show consistent increases in the abundance of non-dreissenid macroinvertebrates in the presence of both living mussels and mussel shells glued to the substrata. Stewart et al. (1998) demonstrated that the presence of live mussels increased invertebrate densities on ceramic tiles by more than 6 times, while mussel shells increased densities by more than 4 times in Lake Erie. Comparable increases in invertebrate abundance were reported from a similar experiment conducted in the St. Lawrence River (Ricciardi et al. 1997). More modest increases were found in experiments in Lake Constance, where the presence of either mussel shells or living mussels caused a doubling in the densities of non-dreissenid macroinvertebrates on tiles (Mörtl and Rothhaupt 2003).

The responses of various taxonomic groups to dreissenid establishment in Lake Simcoe also show some parallels to that seen in other studies. Gammarid amphipods are often observed to benefit from dreissenid establishment and were among the groups that increased most in abundance in this study. Isopods, worms, chironomids and hydrobiid snails have been reported to benefit from dreissenid presence elsewhere (Dermott et al. 1993, Stewart and Haynes 1994, Ricciardi et al. 1997, Stewart et al. 1998, Mörtl and Rothhaupt 2003), and showed among the largest abundance increases in Lake Simcoe. Proportional decline in sphaeriid abundance in Lake Simcoe is similar to results from other dreissenid invaded systems. Pleurocerid snails, which were completely eliminated in this study, responded differently in different studies; Ricciardi et al. (1997) saw declines in their numbers, whereas Stewart and Hynes (1994) observed significant increases.

Overall, the increases in non-dreissenid invertebrate abundance in Lake Simcoe are the largest reported in studies of dreissenid impacts on hard substrata, while the community response was similar to that seen in other studies. The results of the only other published long-term study of dreissenid impacts on natural hard substrata (Stewart and Haynes 1994, Haynes et al. 1999, Haynes et al. 2005) differ significantly from mine. In the above studies non-dreissenid invertebrates initially

increased in abundance within one to two years following dreissenid establishment but then declined to pre-dreissenid densities within five years of dreissenid presence at the sites, and remained low nine years following. While I cannot comment on the trajectory of invertebrate densities between initial dreissenid establishment and 2008, densities of non-dreissenid invertebrates were exceptionally high thirteen years following dreissenid mussel establishment in the littoral zone of Lake Simcoe. The reasons behind the striking difference in the response of the littoral benthos between Lake Ontario and Lake Simcoe can not be resolved with our data, but I propose a few possible explanations. Haynes et al. (2005) attributed the declines in non-dreissenid invertebrate abundance to the decrease in the local abundances of *Dreissena*, suggesting that initial increases were linked to the presence of large numbers of dreissenid mussels. Dreissenids at our study sites were an order of magnitude more abundant in 2008 than in Lake Ontario in 1995 or in 1999. Zaiko et al. (2009) noted a dreissenid biomass threshold below which they observed little effect of dreissenid presence on other benthic fauna. Perhaps this biomass threshold was exceeded in the early stages of dreissenid colonization of parts of Lake Ontario, but as dreissenid abundance declined below this threshold other benthic organisms declined to pre-dreissenid levels. Mussel abundances in Lake Simcoe may have been sustained at a high level because of higher primary productivity (average open-lake TP in 2004–2008 ~14 µg/L; Young et al. 2010) than in Lake Ontario (average open-lake TP below 10 µg/L; Malkin et al. 2010) so Lake Simcoe could have a higher carrying capacity for filter-feeding dreissenids. Lake Simcoe might also provide a more stable thermal regime in the littoral zone throughout the growing season, being less subject to seiche and upwelling phenomena than Lake Ontario; Wilson et al. (2006) found a negative relationship between upwelling frequency and dreissenid abundance in Lake Ontario, so the structuring effects of dreissenids on benthic communities may be weaker in areas of frequent upwelling. Another factor that could contribute to the continued high invertebrate abundance in the littoral zone of Lake Simcoe is the fact that Lake Simcoe is smaller and less turbulent than Lake Ontario. It is conceivable that dreissenid shells accumulate to a greater extent in the nearshore zone of Lake Simcoe than they do in Lake Ontario, increasing habitat availability for nearshore benthos.

Ecological implications

A number of important changes have occurred in Lake Simcoe since the invasion of the lake by dreissenids. The abundance of profundal benthos has decreased (Jimenez et al. 2010), as has phytoplankton biovolume (Eimers et al. 2005). Depew et al. (2010) have shown that the biomass and areal coverage of macrophytes increased in Cook's Bay, a large mesotrophic embayment of the lake,

with little change in nutrient load, and this study has shown large increases in the abundance of littoral benthos. These observations are consistent with what has been termed "benthification"- the increased importance of benthic processes (Mills et al. 2003), or the "nearshore shunt hypothesis" - increased retention and recycling of nutrients and energy in the nearshore (at the expense of the pelagic and profundal zones) as a consequence of ecological engineering by dreissenids (Hecky et al. 2004).

Dreissenids can cause the translocation of biological activity and production to the nearshore through a number of mechanisms. Habitat modification by accumulation of living mussels and non-living shells likely plays an important role, providing increased habitat structure that captures and retains sediment and biodeposits and provides cover for other invertebrates. The presence of dreissenids has been shown to reduce fish predation on amphipods (Gonzalez and Downing 1999, Mayer et al. 2001) so dreissenids not only provide increased surface area for invertebrate colonization but interstitial spaces between mussel shells may also provide protection against predators. Dreissenid biodeposits could contribute to increased abundances of littoral benthos by providing an additional food source to benthic invertebrates. Dreissenids could also enhance resource availability to littoral invertebrates by stimulating benthic primary production. Increased light availability due to dreissenid filtration will increase the depth at which benthic algae can grow (Mayer et al. 2002, Malkin et al. 2008) and nutrient excretion by dreissenids can contribute to increases in benthic algal production. Stewart et al. (1998) found higher levels of benthic chl. *a* in the presence of living dreissenids, and Ozersky et al. (2009) showed that dreissenid excretion can meet phosphorus demand by benthic algae. Results of isotope analysis (Chapter 5) suggest that pelagic carbon (in the form of dreissenid mussel biodeposits) and benthic algal production are equally important in the post-dreissenid nearshore food web of Lake Simcoe, supporting the notion that dreissenids redirect pelagic carbon to the nearshore.

Increased abundance of littoral invertebrates could have implications for higher trophic levels in Lake Simcoe. If littoral benthivorous fish are food limited, the increased abundance of littoral benthos could lead to increased fish biomass and production as has been found in a number of lakes in the former USSR (Karatayev et al. 1997) and in experimental ponds in North America (Thayer et al. 1997). Conversely, increased protection from predation afforded by mussel shells could partially negate the potential positive effects of increased invertebrate abundance on fish (Mayer et al. 2001). Pelagic benthivores such as lake whitefish and piscivores such as lake trout could conceivably be affected either negatively or positively. The reduction in pelagic and profundal resources caused by

redirection of energy to the nearshore could reduce resource availability for these offshore, cold-water species. On the other hand, if lake trout and whitefish can modify their foraging behaviour to increase reliance on littoral resources they could benefit from enhanced littoral secondary productivity. In small inland lakes, lake trout have been shown to shift between predominately littoral and predominately pelagic feeding in response to invasion by bass (Vander Zanden et al. 1999), and lake whitefish in Lake Huron appear to rely more heavily on nearshore benthic production following dreissenid establishment (Rennie et al. 2009).

Conclusion

This study is unique in being one of the very few long-term studies of dreissenid effects on nearshore benthos to have examined multiple sites and depths. I observed a large increase in the abundance and diversity of littoral benthos at four widely geographically separate sites which I attribute to the dreissenid establishment in the system. My results agree with other studies in showing that *Dreissena* increases the abundance and diversity of many invertebrate groups, including amphipods, worms and some snails, reaffirming that dreissenids have similar impacts in different systems (Ward and Ricciardi 2007). However, I also show that the effects of *Dreissena* can be site and system specific. *Dreissena* has increased the evenness of invertebrate distribution and community similarity with depth and across sites in the littoral zone of Lake Simcoe. The increase in the availability of benthic prey could potentially benefit higher trophic levels if energy transfer from the benthos to fish is increased along with the abundance of the benthos. Dreissenid impacts on the littoral benthos of Lake Simcoe agree with the hypothesis that dreissenid translocate material and energy from the water column to the nearshore.

Chapter 5
Dreissenid Effects on the Littoral Food Web of Lake Simcoe: Evidence from Stable Isotopes

5.1 Intro

The establishment of invasive organisms in aquatic environments can have direct and indirect impacts on the structure and functioning of the ecosystem. Among the most important, but perhaps most difficult to quantify, are changes to food web structure and energy flow. A promising technique for untangling the complex effects of invasive organisms on food webs is the use of stable isotopes of carbon (^{13}C) and nitrogen (^{15}N). Generally, carbon isotope ratios are conserved between food sources and consumers, so the isotopic ratios of carbon can be used to elucidate energy sources of consumers when different food sources have distinct ratios of carbon isotopes (Peterson and Fry 1987; Hecky and Hesslein 1995). Unlike carbon, nitrogen isotopic composition changes with movement up the food web, becoming enriched in ^{15}N by an average of about 3.4 per mil (‰) with every trophic step. Consequently the nitrogen isotopic composition of members of the food web can be used to determine the trophic level of organisms if the nitrogen isotopic signature of the base of the food web is known (Minagawa and Wada, 1984; Post, 2002). The combined application of carbon and nitrogen stable isotopes can be used to detect the effects of invasive organisms on energy sources and trophic relationships in invaded systems. For example, using stable isotopes Vander Zanden et al. (1999) showed that invasion by smallmouth bass affected the flow of energy between the littoral and pelagic zones in Canadian lakes. Gorokhova et al. (2005) found that the invasive cladoceran *Cercopagis pengoi* increased the length of the pelagic food web in the Baltic Sea and Limén et al. (2005) used stable isotopes to examine food partitioning between native amphipods and the invasive *Echinogammarus ischnus* in Lake Erie.

The dreissenid mussels *Dreissena polymorpha* and *D. rostriformis bugensis* are notorious invasive organisms, whose effects on food webs are not fully understood. It is thought that dreissenids affect food webs by translocating energy and nutrients from the pelagic zones of lakes to the nearshore, and by competing with consumers for pelagic primary production (Mills et al. 2003, Hecky et al. 2004, Higgins and Vander Zanden 2010). Hecky et al. (2004) proposed the nearshore shunt hypothesis to explain some of the ways in which dreissenid mussels translocate energy and

nutrients to the nearshore. By filtering the water dreissenids increase water clarity and nearshore nutrient remineralization rates, leading to increased benthic primary production in the nearshore. Additionally, pelagic material filtered and sedimented (biodeposited) by dreissenids can become available to benthic consumers such as amphipods and chironomids (Izvekova and Lvova-Katchanova 1972; Gergs 2009). The result is increased resource availability to nearshore consumers at the expense of the pelagic food web.

Current understanding of dreissenid effects on food webs comes from hypothetical and numerical models (eg. Mills et al. 2003, Pothoven and Madenjian 2008), experimental ponds (Thayer et al. 1997), and studies of direct predation on dreissenids or of feeding on their biodeposits (French and Bur 1992, Custer and Custer 1996, Gergs 2009). Relatively few studies used stable isotopes to explore the effects of dreissenids on aquatic food webs. Results of these studies show that dreissenids are trophically flexible, can potentially compete with zooplankton for pelagic production, and that dreissenid deposits can form an important part of invertebrate diet (Mitchell et al. 1996, Szabo 2004, Garton et al. 2005, Limén et al. 2005, Gergs 2009, Campbell et al. 2009, Rennie et al. 2009). Campbell et al. (2009) have shown that by feeding on dreissenids, invasive round gobies can re-direct energy from dreissenids to littoral fish such as bass and perch. The study by Rennie et al. (2009) is unique among the above in adding a temporal dimension to the study of dreissenid impacts on food webs. They employed stable isotope analysis of pre- and post-dreissenid lake whitefish samples from Lake Huron to investigate the impacts of dreissenids of whitefish foraging behaviour, finding increased reliance on benthic resources by whitefish after dreissenid establishment.

In this study I used stable isotope ratios of carbon and nitrogen to investigate the effects of dreissenid invasion on the littoral benthic food web of Lake Simcoe, Ontario. Various components of the pre- and post-dreissenid food web were analysed to determine whether the establishment of dreissenids in Lake Simcoe had effects on the sources of energy and feeding relationships of the littoral benthos. I hypothesized that the pre-dreissenid food web was supported primarily by littoral benthic primary production, whereas the post-dreissenid food web was at least in part supported by redirected pelagic carbon, in the form of dreissenid biodeposits. The shift to greater reliance on pelagic primary production was expected to result in depleted ^{13}C values of members of the post-dreissenid food web compared with those of the pre-dreissenid food web (Hecky and Hesslein 1995, France 1995).

5.2 Materials and Methods

5.2.1 Study site

This study was carried out in Lake Simcoe, a large (722 km^2) oligo-mesotrophic lake located in southern Ontario, Canada. Lake Simcoe was invaded by dreissenid mussels in 1993, but they did not become abundant in the benthos until 1995 (Evans et al. in press). In 2006–2008 dreissenid biomass in Lake Simcoe reached an average of 27.2 g shell-free dry mass/m^2, with the majority of biomass concentrated in the nearshore areas of the lake (Chapter 2). Periphyton, biodeposit and most pre- and post- dreissenid invertebrate samples were collected from shallow depths (1–1.5 m) at McRae Point (44º33'49" N, 79º20'1" W). Seston samples were collected at nearshore stations throughout the lake.

5.2.2 Sample collection, processing and analysis

Sestonic material was collected in Late July and early August of 2008 at 8 stations throughout the littoral shallows of the lake. Seston samples were collected in a plastic bottle submerged to about 0.5 m, then filtered onto pre-ashed quartz filters, dried at 60^oC for ~ 24 hours and stored in a desiccator until analysis. Periphyton and mussel deposits were collected from shallow (~1.5 m) depths at McRae Point on September 21, 2008. Mussel-free, periphyton covered rocks were carefully brought to the surface, placed in plastic bags, and frozen until processing. In the lab, periphyton was scraped from the surface of rocks, dried at 60^oC for ~24 hours and stored in a desiccator until analysis. Two methods were used to collect mussel deposits *in situ*. A 60-mL syringe with an 18 gauge needle was used to collect mussel deposits and detritus beneath mussel colonies adhering to rocks. In addition I collected fresh mussel deposits from the surface of mussel colonies using a 60-mL syringe with a piece of 2 mm tygon tubing fitted to the syringe. I observed mussels expelling feces, which remained loosely deposited on the surface of colonies, and was able to carefully collect this material with the tube-fitted syringe without visibly disturbing the periphytic material covering the mussels. Mussel biodeposit samples were filtered onto pre-ashed quartz filters and treated the same way as seston samples.

Benthic invertebrates for isotope analysis were sampled in August of 1993 (pre-dreissenid period) and in September of 2008 (post-dreissenid period). Invertebrate sampling was conducted using the kick-and-sweep method in shallow (~1 m depth), rocky areas near McRae Point. Crayfish were collected from two adjacent sites. *Orconectes propinquus* in 1993 and 2007 were collected from

2–6 m-depths at Strawberry Island (44º33'3" N, 79º20'19" W). The rusty crayfish, *O. rusticus*, having invaded Lake Simcoe only recently, were only collected in 2007 from 2–6 m-depths at Grape Island (44º34'44" N, 79º23'7" W) where they were the dominant crayfish species at the time of sampling. I saw no evidence of variation of crayfish stable isotope values with depth, so isotopic ratios of crayfish from all depths were pooled for analysis. Macroinvertebrates collected in 1993 and 2008 were allowed to empty their guts for ~24 hours in refrigerated containers with lake water, separated into general taxonomic groups and stored frozen in de-ionized water. They were thawed in November 2008, where possible identified to genus or species, dried at 60^{o}C for 24-48 hours, and ground into a fine powder. Crayfish were stored frozen until processing, at which time pieces of tail muscle were removed, dried at 60^{o}C and ground to a fine powder. Nine littoral invertebrate taxa were collected in 1993, and fifteen in 2007–2008, of which five were collected in both years.

Macroinvertebrate samples were weighed to ~0.25 mg and packed in tin capsules for isotope analysis. I submitted acidified and unacidified sub-samples of periphyton, seston and biodeposits to eliminate the effect of carbonate material on the isotopic values of organic matter. Periphyton acidification was done using 10% HCl, which was slowly added to ground samples until bubbling stopped. The acidified samples were then dried again, reground and packed into tin capsules. Acidification of seston and biodeposit samples was achieved with acid fumigation, using concentrated HCl, for the duration of 8 hours (Lorrain et al. 2003). I used ~2 mg of material for unacidifed periphyton samples and ~4 mg for acidified periphyton. Samples were analysed on a Delta Plus continuous flow stable isotope ratio mass spectrometer (Thermo Finnigan / Bremen-Germany) coupled to a Carlo Erba elemental analyzer (CHNS-O EA1108 - Italy). Replicate sample analysis showed a standard deviation of 0.21 ‰ for ^{13}C and 0.28 ‰ for ^{15}N.

5.2.3 Mixing models and trophic position estimates

Stable isotope analysis results for ^{13}C and ^{15}N are expressed in δ (delta) notation which is a ratio of the ratios of the heavy and light isotope of the elements in the sample and a standard, expressed in per mil (‰), or parts per thousand:

(1) $\delta = (R_{sample}/R_{standard} - 1) \times 1000$, and R= (Heavy isotope/Light isotope)

Peedee belemnite and atmospheric air were used as the standards for carbon and nitrogen, respectively.

A simple two-source mixing model was applied to estimate the relative contributions (*f)* of different carbon sources to each invertebrate taxon:

(2) $f_{source\ 1}=(\delta_{sample}-\delta_{source\ 2})/(\delta_{source\ 1}-\delta_{source\ 2})$

Three different combinations of food sources were examined using the above mixing model for 2008 invertebrate samples. The first estimated the relative contributions of pelagic carbon and periphyton to different consumers based on isotope values of seston and periphyton. The second estimate compared the contributions of periphyton and dreissenid biodeposits to consumers. Finally, I used primary consumers to estimate the relative contributions of pelagic and periphytic carbon to the food web (Post 2002). In the third mixing model filter feeding dreissenids were used as a pelagic end member, and psephenid beetles, being the most enriched all post-dreissenid organisms, were used as the benthic end member. Because no samples of primary producers were available from 1993, I used the last, primary consumer-based approach for pre-dreissenid samples. Filter feeding hydropsychid caddisflies were the most depleted in $\delta^{13}C$ and were used as the pelagic end member. The snail *Physa* sp. was the most enriched taxon and was used as the benthic end member. I assumed no trophic fractionation of carbon (Post 2002).

Trophic position was estimated using the generalized equation given in Post (2002):

(3) Trophic position$=\lambda+(\delta^{15}N_{sample}-[\delta^{15}N_{source1}\times f_{source\ 1}+\delta^{15}N_{source2}\times(1-f_{source\ 1})]/\Delta_N$

Where λ is the trophic position of the sources on which the estimate is based (1 if using primary producers, 2 if using primary consumer) and Δ_N is the trophic fractionation of nitrogen. In order to examine the sensitivity of trophic position estimates to assumptions regarding nitrogen fractionation rates I used two different nitrogen fractionation schemes. The first fractionation scheme used 3.4 ‰ (± 0.98 SD) for all members of the benthos, as suggested by Post (2002). In the second I used 3.24 ‰ (± 0.41 SD) for carnivores, and 2.51 (± 2.50 SD) for herbivores and detritivores (Vander Zanden and Rasmussen 2001). The two fractionation schemes were used to make an estimate of trophic position based on all three combinations of carbon sources for 2008. Seston and periphyton, biodeposits and periphyton and finally the primary consumers dreissenids and psephenids were used as $\delta^{15}N$ baselines. No primary producers were collected in 1993, so I used *Gammarus fasciatus,* the primary consumer with the lowest $\delta^{15}N$ values as the nitrogen baseline for both pelagic and benthic nitrogen.

5.2.4 Statistical analyses

Comparisons of $\delta^{13}C$ and $\delta^{15}N$ stable isotope values for taxonomic groups that were sampled in both 1993 and 2008 were done using two-sample t-tests. One way ANOVA tests were applied to compare the proportion of periphytic carbon in the diets of different taxonomic groups as determined by the three approaches described earlier. Trophic level estimates based on different baselines and fractionation factors were also compared using one way ANOVA for each taxonomic group. Statistical significance was determined at $\alpha=0.05$. All statistical tests were done in SigmaPlot 11(Systat Software Inc., Chicago).

5.3 Results

The results of isotope analyses for the components of the littoral food web of Lake Simcoe are summarized in table 5.1. There was significant enrichment in $\delta^{13}C$ for all 93–08 pairs (Fig. 5.1, Table 5.2), with *Physa* sp. showing the smallest change (2.1 ‰) and *O. propinquus* showing the largest change (4.89 ‰). The average change in $\delta^{13}C$ for all groups was 3.94 (±0.51 SE) ‰. I also observed significant enrichment in $\delta^{15}N$ for most groups, although these were smaller than changes in $\delta^{13}C$ values. *Gammarus fasciatus* displayed the largest change in $\delta^{15}N$, while *O. propinquus* showed no significant change. The average change in $\delta^{15}N$ for all groups was 1.87 (±0.63 SE) ‰.

I noted good separation between potential food sources of the post-dreissenid food web: periphyton (-11.5 $\delta^{13}C$, 3.7 $\delta^{15}N$), biodeposits (-22.6 $\delta^{13}C$, 4.1 $\delta^{15}N$) and seston (-26.9 $\delta^{13}C$, 4.5 $\delta^{15}N$) (Fig. 5.2). Biodeposit material lies closer to sestonic material than to periphyton, so its $\delta^{13}C$ signature suggests that it is composed mostly of pelagic carbon. Organisms such as psephenids, dreissenid mussels, snails, amphipods and isopods appear to form the second trophic level, with predacious caddisflies and crayfish at the top of the littoral invertebrate food web. Most organisms have $\delta^{13}C$ values intermediate between sestonic and periphytic material, suggesting that pelagic material (in the form of dreissenid biodeposits) is an important energy source for the littoral food web.

Table 5.1: summary of the results of stable isotope analysis on various components of the littoral food web of Lake Simcoe prior to dreissenid establishment and following dreissenid establishment.

taxon	details	collection year	n	$\delta^{13}C$	$\delta^{15}N$	$\delta^{13}C$ SE	$\delta^{15}N$ SE
Ceraclea sp.	caddisfly	1993	2	-23.61	7.62	1.71	0.56
Gammarus fasciatus	amphipod	1993	5	-23.85	3.59	0.49	0.24
Hydropsychidae	caddisfly	1993	4	-28.16	8.64	0.27	0.33
O. propinquus large	crayfish	1993	18	-23.54	10.54	0.16	0.15
Oligochaetea		1993	2	-26.63	14.00	0.15	0.60
Physa sp.	snail	1993	5	-21.21	5.26	0.14	0.05
Stagnicola sp.	snail	1993	3	-21.64	5.49	0.41	0.38
Stenacron sp.	mayfly	1993	4	-25.19	5.26	0.10	0.57
Stenonema sp.	mayfly	1993	8	-24.91	4.58	0.23	0.31
Seston		2008	7	-27.26	5.90	0.15	0.10
Periphyton		2008	5	-11.49	3.73	0.70	0.12
Dreissenid biodeposits		2008	6	-22.56	4.15	0.32	0.10
Dreissena spp.		2008	7	-25.84	7.29	0.15	0.10
Echinogammarus ischnus	amphipod	2008	6	-18.60	6.05	0.18	0.20
Elmidae	beetle larvae	2008	4	-19.09	6.40	0.30	0.11
Gammarus fasciatus	amphipod	2008	6	-19.93	7.59	0.11	0.11
Goniobasis sp.	snail	2008	7	-17.89	8.18	0.30	0.21
Hydropsychidae	caddisfly	2008	2	-24.27	10.29	0.18	0.07
Isopoda	isopod	2008	6	-19.27	6.53	0.11	0.23
O. propinquus large	crayfish	2007	10	-18.75	10.52	0.09	0.08
O. propinquus small	crayfish	2007	7	-18.12	9.96	0.26	0.14
O. rusticus large	crayfish	2007	4	-20.25	10.78	0.15	0.02
O. rusticus medium	crayfish	2007	7	-17.78	9.30	0.57	0.12
O. rusticus small	crayfish	2007	7	-19.37	9.43	0.57	0.12
Physa sp.	snail	2008	6	-19.12	7.35	0.43	0.12
Polycentropus sp.	caddisfly	2008	4	-21.08	9.77	0.36	0.11
Psephenidae	beetle larvae	2008	5	-15.82	5.65	0.70	0.12
Stenacron sp.	mayfly	2008	2	-22.17	7.13	0.12	0.10
Stenonema sp.	mayfly	2008	6	-19.68	6.44	0.30	0.08
Tanypodinae	chironomid	2008	4	-19.61	8.29	0.15	0.10

Mixing models show that post-dreissenid organisms display a range of reliance on benthic carbon, with most organisms showing intermediate values and few feeding more exclusively on one or other source (Fig. 5.3, Table 5.3). The calculation based on primary consumers shows the highest degree of reliance on periphytic carbon for all taxa, while the calculation comparing periphyton and biodeposits shows the lowest. The three calculation methods offer a generally similar picture of relative reliance on benthic resources: all show Psephenidae to be the most reliant on benthic carbon, isopods, amphipods and snails to consume about equal amounts benthic and pelagic carbon; and

Dreissena spp., hydropsychids, *Stenacron* sp. and *Polycentropus* sp. were dependent mainly on pelagic carbon. Comparisons of benthic vs. pelagic carbon contributions based on primary producers and primary consumers show similar (not statistically different) results for all taxonomic groups. The comparison using biodeposits and periphyton as the two sources shows significantly lower use of benthic resources than the calculation based on primary consumers, and similar values in most cases to the calculation based on seston and periphyton. The results from the pre-dreissenid mixing model (Table 5.4) are not statistically different than post-dreissenid primary consumers-based results for most groups, with the exception of *Physa* sp. which shows higher reliance on periphytic carbon in the pre-dreissenid calculation, a consequence of using it as the benthic end-member in the mixing model.

Table 5.2: Average difference in $\delta^{13}C$ and $\delta^{15}N$ values of taxa collected in 1993 and 2008. Asterisks indicated significant difference. Positive numbers indicate enrichment, negative numbers indicate depletion.

Taxon	δ13C difference (1993–2008)	δ15N difference (1993–2008)
G. fasciatus	3.92*	4.0*
Heptageniidae	4.9*	1.59*
Hydropsychidae	3.88*	1.65*
O. propinquus	4.89*	-0.05
Physa sp.	2.10*	2.09*
Average difference	3.94	1.87

Trophic levels were calculated based on two $\delta^{15}N$ fractionation schemes (Table 5.5). The first was based on the results of Post (2002), who found average fractionation value of 3.4 (±0.98 SD) ‰ for carnivores and herbivores. The second was based on the results of Vander Zanden and Rassmussen (2001) whose data suggest fractionation of 2.52 (± 2.5 SD) ‰ for herbivorous consumers and 3.24 (±0.41 SD) ‰ for carnivores. Trophic levels were calculated within these two frameworks using seston and periphyton, biodeposits and periphyton and primary consumers as trophic baselines for 2008 data and using primary consumers for 1993 data. Calculations using fractionation factors suggested by Vander Zanden and Rasmussen (2001) resulted in higher trophic level values for all baseline comparisons than those based on Post (2002). Error values were also higher when using the fractionation factors suggested by Vander Zanden and Rasmussen (2001), because of the greater uncertainty associated with the fractionation factors they present.

Table 5.3: Fraction of periphyton carbon in post-dreissenid consumers, calculated using three different baselines.

Calculation method:	1º producer based	1º producer based	1º consumer based
Comparison:	seston-periphyton	biodeposits-periphyton	seston-periphyton
Taxon	*f* periphyton	*f* periphyton	*f* periphyton
Ceraclea sp.	--	--	--
Dreissena spp.	0.07 ±0.03^{A}	-0.3 ±-0.03^{B}	0 ±0.1^{A}
E. ischnus	0.54 ±0.04^{AB}	0.36 ±0.04^{A}	0.72 ±0. 09^{B}
Elmidae	0.51 ±0.04^{AB}	0.31 ±0.04^{A}	0.67 ±0.09^{B}
G. fasciatus	0.45 ±0.04^{AB}	0.24 ±0.03^{A}	0.59 ±0.08^{B}
Goniobasis sp.	0.58 ±0.04^{AB}	0.42 ±0.04^{A}	0.79 ±0.1^{B}
Hydropsychidae	0.17 ±0.04^{A}	-0.15 ±-0.03^{A}	0.16 ±0.07^{A}
Isopoda	0.50 ±0.04^{A}	0.3 ±0.03^{B}	0.66 ±0.09^{A}
Oligochaete	--	--	--
O. propinquus, large	0.53 ±0.04^{AB}	0.34 ±0.03^{A}	0.71 ±0.09^{B}
O. propinquus, small	0.57 ±0.04^{AB}	0.4 ±0.04^{B}	0.77 ±0.09^{A}
O. rusticus, large	0.43 ±0.04^{A}	0.21 ±0.03^{B}	0.56 ±0.08^{A}
O. rusticus, medium	0.59 ±0.06A^{B}	0.43 ±0.06^{B}	0.8 ±0.11^{A}
O. rusticus, small	0.49 ±0.05A^{B}	0.29 ±0.06^{B}	0.65 ±0.1^{A}
Physa sp.	0.51 ±0.05^{AB}	0.31 ±0.05^{A}	0.67 ±0.1^{B}
Polycentropus sp.	0.38 ±0.04^{A}	0.13 ±0.04^{B}	0.47 ±0.09^{A}
Psephenidae	0.72 ±0.06^{AB}	0.61 ±0.07^{B}	1 ±0.12^{A}
Stagnicola sp.	--	--	--
Stenacron sp.	0.31 ±0.04^{A}	0.04 ±0.03^{B}	0.37 ±0.08^{A}
Stenonema sp.	0.47 ±0.04^{A}	0.26 ±0.04^{B}	0.61 ±0.09^{A}
Tanypodinae	0.47 ±0.03^{AB}	0.27 ±0.03^{B}	0.62 ±0.08^{A}

Comparisons based on different baselines resulted in similar estimates of trophic position. The calculation based on primary producers consistently resulted in the lowest standard error, while the one based on primary consumers the highest. The calculation based on periphyton and biodeposits showed intermediate standard error values. Pre- dreissenid organisms for which a pair existed in the post-dreissenid dataset tended to be at a slightly higher trophic level than their post-dreissenid counterparts. Trophic level estimates were not statistically different for any of the calculations methods, regardless of fractionation values used, primarily owing to the large error values associated with the estimates. In 2008, psephenids and *E. ischnus* placed at the lowest trophic level for consumers, while large *O. rusticus* were placed at the highest trophic level, regardless of the approach used. In 1993, oligochaetes placed higher than any other group tested, pre- or post-dreissenid, at an average trophic level of 5.06 or 6.13, depending on which fractionation factor was used.

Table 5.4: Fraction of periphyton carbon in pre- and post-dreissenid consumers, calculated based on primary consumer baselines.

Period:	Post- dreissenid	Pre- dreissenid
Calculation method:	1º consumer based	1º consumer based
Comparison:	seston-periphyton	seston-periphyton
Taxon	*f* periphyton	*f* periphyton
Ceraclea sp.	--	0.66 ±0.25
G. fasciatus	0.59 ±0.08^{A}	0.62 ±0.07^{A}
Hydropsychidae	0.16 ±0.07^{A}	0 ±0.06^{A}
Oligochaete	--	0.22 ±0.05
O. propinquus, large	0.71 ±0.09^{A}	0.67 ±0.03^{A}
Physa sp.	0.67 ±0.1^{A}	1 ±0.05^{B}
Stagnicola sp.	--	0.94 ±0.06
Stenacron sp.	0.37 ±0.08^{A}	0.43 ±0.04^{A}
Stenonema sp.	0.61 ±0.09^{A}	0.47 ±0.05^{A}

5.4 Discussion:

The primary objective of this study was to determine the importance of dreissenid mussels in the littoral food web of Lake Simcoe, and to describe changes in energy flow associated with dreissenid establishment in the lake. I was interested in whether dreissenid establishment led to changes in the importance of different food sources in the littoral zone, and whether the use of different mixing models and trophic level estimates would result in consistent interpretations of trophic relationships. To this end, I used stable isotope analysis of potential food sources and of members of the benthic food web, and employed mixing models and trophic level estimates under different assumptions. I expected that carbon signatures of post-dreissenid benthos would become more depleted, signalling greater reliance on re-directed pelagic carbon (in the form of dreissenid biodeposits) than in pre-dreissenid years, when isotopically enriched benthic primary production would have been a relatively more important source of energy to consumers. The results surprised me on both counts. While a significant difference in carbon signatures between pre- and post-dreissenid members of the littoral benthos was found, the direction of the change was opposite to my expectations: post-

Table 5.5: trophic position of pre- and post- dreissenid invertebrates calculated based on different baselines and based on two different fractionation rates.

	Based on Post (2001)				Based on Vander Zanden 2001			
Baseline:	Seston-periphyton 08	Biodeposits-periphyton 08	Primary consumers 08	Primary consumers 93	Seston-periphyton 08	Biodeposits-periphyton 08	Primary consumers 08	Primary consumers 93
Taxon								
Ceraclea sp.	--	--	--	3.19 ±0.67	--	--		3.24 ±0.89
Dreissena spp.	1.73 ±0.56	1.89 ±0.27	2.00		1.98 ±0.89	2.2 ±0.49	2.00	--
E. ischnus	1.52 ±0.18	1.60 ±0.22	1.98 ±1.22		1.70 ±0.29	1.81 ±0.37	1.98 ±1.64	--
Elmidae	1.61 ±0.20	1.70 ±0.29	2.06 ±1.18		1.83 ±0.34	1.94 ±0.48	2.08 ±1.61	--
G. fasciatus	1.95 ±0.21	2.04 ±0.34	2.37 ±1.10	2.00	2.28 ±0.43	2.4 ±0.62	2.5 ±1.58	2.00
Goniobasis sp.	2.17 ±0.29	2.24 ±0.34	2.65 ±2.19		2.57 ±0.60	2.67 ±0.69	2.87 ±3.23	--
Hydropsychidae	2.64 ±0.47	2.79 ±0.70	2.96 ±2.41	3.49 ±0.44	2.73 ±0.50	2.88 ±0.75	3.01 ±2.57	3.56 ±0.41
Isopoda	1.65 ±0.18	1.74 ±0.25	2.09 ±1.08		1.88 ±0.31	2 ±0.43	2.13 ±1.15	--
Oligochaete	--	--	--	5.06 ±0.51	--	--	0.78 ±0.05	6.13 ±0.81
O. propinquus, large	2.84 ±0.32	2.92 ±0.39	3.29 ±1.90	4.04 ±0.33	2.93 ±0.34	3.01 ±0.42	3.36 ±2.03	4.15 ±0.29
O. propinquus, small	2.68 ±0.34	2.76 ±0.41	3.16 ±2.34		2.77 ±0.37	2.84 ±0.44	3.21 ±2.5	--
O. rusticus, large	2.88 ±0.33	2.98 ±0.57	3.29 ±1.49		2.97 ±0.35	3.07 ±0.61	3.36 ±1.59	--
O. rusticus, medium	2.50 ±0.46	2.57 ±0.54	2.98 ±3.06		2.57 ±0.50	2.64 ±0.58	3.03 ±3.26	--
O. rusticus, small	2.5 ±0.42	2.59 ±0.67	2.94 ±1.84		2.57 ±0.45	2.67 ±0.72	2.99 ±1.96	--
Physa sp.	1.90 ±0.27	1.98 ±0.40	2.34 ±1.41	2.49 ±0.35	2.21 ±0.50	2.32 ±0.7	2.46 ±2.02	2.67 ±0.45
Polycentropus sp.	2.56 ±0.35	2.67 ±0.99	2.96 ±1.38		2.64 ±0.38	2.75 ±1.07	3.01 ±1.47	--
Psephenidae	1.47 ±0.41	1.52 ±0.40	2.00		1.63 ±0.62	1.7 ±0.61	2.00	--
Stagnicola sp.	--	--	--	2.56 ±0.61	--	--		2.76 ±0.59
Stenacron sp.	1.76 ±0.21	1.88 ±1.82	2.13 ±0.95	2.49 ±0.86	2.03 ±0.38	2.19 ±2.87	2.18 ±1.32	2.66 ±0.7
Stenonema sp.	1.61 ±0.2	1.71 ±0.33	2.05 ±1.04	2.29 ±0.58	1.83 ±0.34	1.95 ±0.54	2.06 ±1.42	2.39 ±0.48
Tanypodinae	2.16 ±0.24	2.25 ±0.36	2.59 ±1.27		2.22 ±0.26	2.31 ±0.38	2.62 ±1.35	--

dreissenid benthic organisms were significantly more enriched in $\delta^{13}C$ and $\delta^{15}N$ than their pre-dreissenid counterparts. The results of mixing models were also surprising, showing relatively high levels of reliance on pelagic carbon by the pre-dreissenid food web. Despite not conforming to my pre-conceptions regarding the responses of the littoral food web of Lake Simcoe to the establishment of dreissenids, the results of this study shed considerable light on the role of dreissenid mussels in littoral food webs, and raise a number of interesting questions about the trophic resources available to littoral food webs.

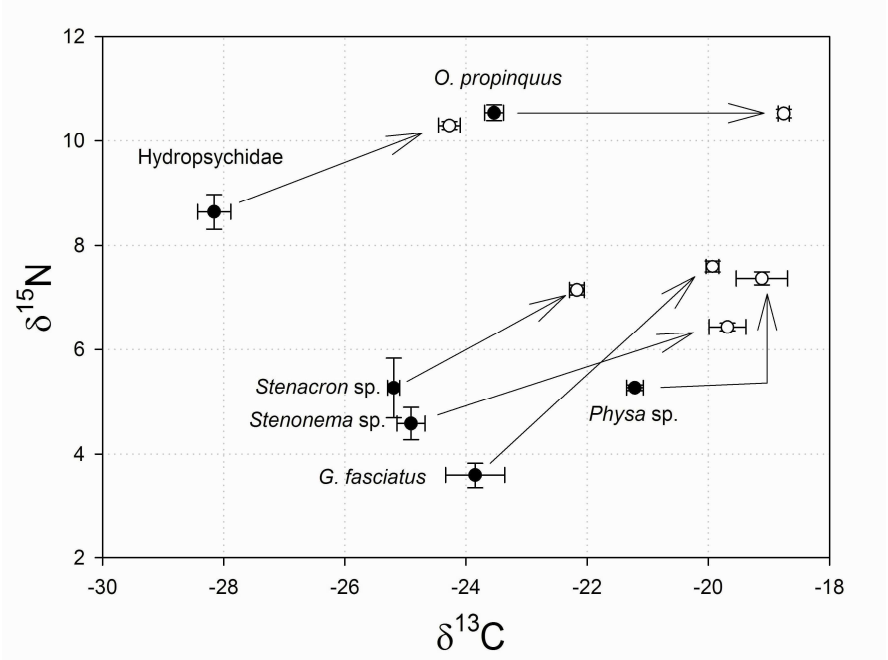

Figure 5.1: Changes to carbon and nitrogen isotopic values of pre-/ post- dreissenid taxa pairs. Filled circles: pre-dreissenid values, empty circles: post-dreissenid values.

I used mixing models to estimate the importance of different carbon sources to the post-dreissenid benthic food web, showing that different mixing models yielded generally similar estimates of the importance of potential food sources. Members of the littoral food web displayed an S-shaped distribution (Fig. 5.3) in their reliance on periphyton, with few exclusively pelagic or benthic-reliant organisms, and most groups relying on intermediate levels of benthic and pelagic production. As could be expected, known filter feeders such as dreissenids and hydropsychid caddisflies (Merritt and Cummins 1996) relied most on pelagic sources, while snails (*Physa* sp. and *Goniobasis* sp.), psephenid beetles and crayfish relied more on benthic carbon. Mixing models indicate that biodeposits could comprise a large part of the diet of many benthic invertebrates in the

post-dreissenid food web. Detritivores such as isopoda and gammarid amphipods appear to rely heavily on biodeposited material, and even grazers such as snails and heptageniid mayflies show a strong biodeposit signal. The isotope signal from biodeposits can be traced to higher trophic levels; predators such as crayfish also appear to rely in part on carbon from biodeposited material. This suggests that dreissenid biodeposits are an important element in the energy budget of the littoral food web, and energy from biodeposits is transferred up the food web to littoral predators, and potentially fish.

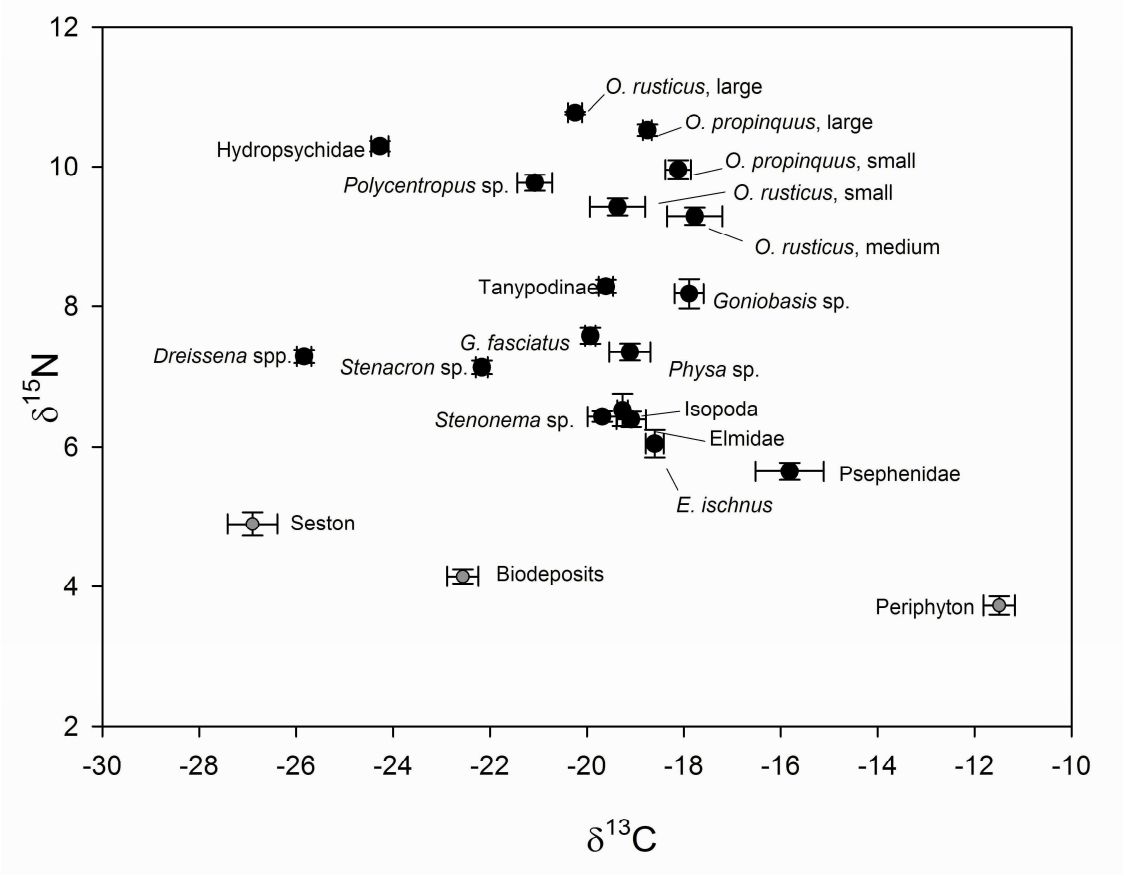

Figure 5.2: ^{13}C and ^{15}N biplot of post-dreissenid components of the littoral food web of Lake Simcoe.

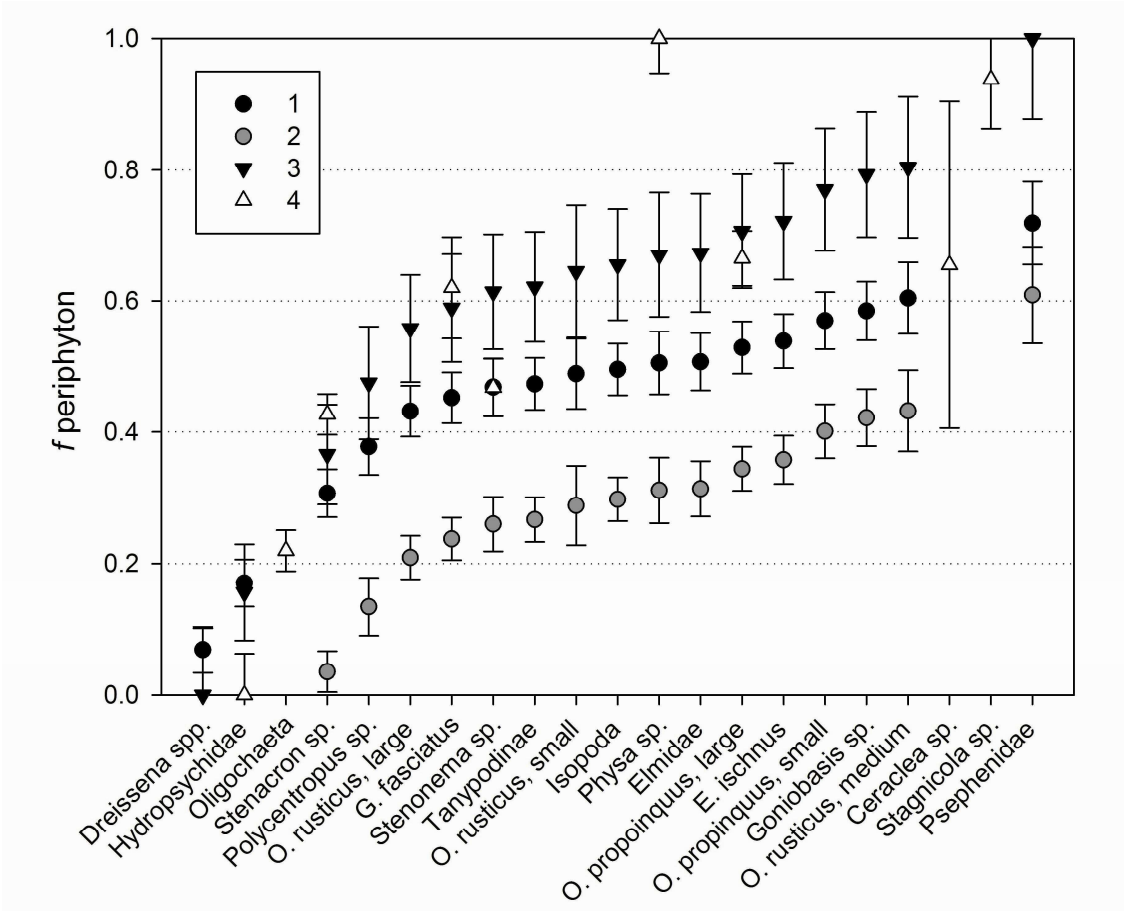

Figure 5.3: fraction of periphytic carbon in components of the littoral food web of Lake Simcoe based on different mixing models. 1: post-dreissenid f periphyton calculated based on seston and periphyton isotope values. 2: post-dreissenid f periphyton calculated based on biodeposit and periphyton isotope values. 3: post-dreissenid f periphyton calculated based on primary consumer isotope values, with psephenid beetles as the benthic end member, and dreissenids as the pelagic end member. 4: pre-dreissenid f periphyton calculated based on primary consumer isotope values, with the snails *Physa* sp. as the benthic end member, and hydropsychid caddisflies as the pelagic end member

Here I should address the enriched $\delta^{13}C$ signature of biodeposits compared to their putative source material, seston. If biodeposits were composed entirely of settled seston they would be expected to have the same carbon signature as the sestonic source material. However, biodeposits are enriched by almost 5 ‰ compared to seston. This result is similar to that found by Szabo (2004) who also observed dreissenid deposits to be enriched relative to seston in Lake Erie. A number of possible explanations can be invoked. One possibility is that in the shallow, relatively turbulent site where my samples were collected resuspended periphytic material periodically makes up a portion of the seston,

leading to a more enriched signal in the biodeposits. A contamination of my biodeposit samples by periphytic material is conceivable, but unlikely, since material from beneath mussel colonies as well as fresh material composed entirely of feces/pseudofeces collected from the surface of colonies exhibited the same carbon values. It is also possible that $\delta^{13}C$ enriched material such as detritus originating from aquatic macrophytes (Ozersky et al. unpublished data) is preferentially rejected in pseudofeces, or is assimilated to a lesser degree than isotopically lighter planktonic material, contributing to the enriched $\delta^{13}C$ values in biodeposits. Yet another possibility is that bacterial metabolism in the gut of dreissenids leads to an enrichment of the biodeposit material (McGoldrick et al. 2008). The similarity in $\delta^{13}C$ values between fresh feces/pseudofeces and aged material from underneath mussel colonies implies that bacterial carbon fractionation of biodeposits occurs mostly in dreissenid guts, and not after the material is expelled.

Comparison of $\delta^{13}C$ signatures of primary consumers between the pre- and post-dreissenid benthic littoral food web revealed the surprising finding that the pre-dreissenid benthic food web was about as reliant on sestonic primary production as the post-dreissenid food web. This raises the question what pelagic carbon source was available to non-filter feeding benthic organisms in the pre-dreissenid period. One possibility is that benthos utilized settled phytoplankton, although the likelihood of this is uncertain at the shallow and turbulent site where this study was carried out. Another possibility is that native filter feeders such as Unionidae and Sphaeridae acted to redirect pelagic material to the benthos in a manner similar to dreissenids. Unionidae and Sphaeridae constituted a large proportion of the littoral benthos in the pre-dreissenid period, and could have supplied a substantial amount of material to the much more numerically depauperate benthos of the time (Chapter 4). My use of *Physa* sp. and Hydropsychidae as end members for the pre-dreissenid food web may have skewed the results somewhat, since both were shown to rely on a mixture of benthic and pelagic material in the post-dreissenid period, which could possibly lead to an overestimate of the importance of pelagic material in the pre-dreissenid food web.

One of the most surprising findings of this study was the greater $\delta^{13}C$ and $\delta^{15}N$ enrichment of the post-dreissenid food web compared to the pre-dreissenid food web. This is in opposition to my expectation; I anticipated that the post-dreissenid food web would be depleted in $\delta^{13}C$ compared to the pre-dreissenid food web, as a consequence of greater reliance on pelagic carbon sources, which tend to have depleted $\delta^{13}C$ values compared to periphyton (eg. Hecky and Hesslein 1995). Since the mixing models indicate little change in the relative roles of benthic and pelagic carbon in driving the littoral food web another explanation for today's enriched food web is proposed. I suggest that the

carbon and nitrogen signatures of both pelagic and benthic primary production have become more enriched following dreissenid establishment. Dreissenid mussels increase water clarity and nutrient remineralization rates which could have contributed to increased rates of pelagic and benthic primary production. A number of studies have shown that as growth rates of periphyton increase their carbon and nitrogen fractionation rates decrease leading to more enriched $\delta^{13}C$ and $\delta^{15}N$ values (MacLeod and Barton 1998, Trudeau and Rasmussen 2003). If this is indeed the case here, an enrichment of about 8–10 ‰ should have occurred in the $\delta^{13}C$ values of periphyton to account for differences in $\delta^{13}C$ values of pre- and post-dreissenid consumers. Work in natural and artificial streams by Hill and Middleton (2006) and Hill et al. (2008) showed that changes in biomass and growth rates of periphyton had dramatic effects on $\delta^{13}C$ signatures of the periphyton, with enrichment levels comparable to the ones observed in this study with doubling of periphyton biomass. Like benthic grazers, filter-feeding hydropsychids also show enriched $\delta^{13}C$ and $\delta^{15}N$ values in the post-dreissenid food web. This implies that pelagic production rates may have increased, leading to more enriched carbon and nitrogen signatures of phytoplankton. A number of studies in marine systems have demonstrated that carbon fractionation by phytoplankton declines with growth rates (Laws et al. 1995; Burkhardt et al. 1999), and Higgins and Vander Zanden (2010) found that phytoplankton growth rates tend to increase in dreissenid invaded systems. Thus, dreissenid-mediated changes to the growth rates of periphyton and phytoplankton may have led to changes in the carbon and nitrogen baseline of the Lake Simcoe food web. The lack of change in $\delta^{15}N$ values in crayfish from pre- to post-dreissenid periods may be explained by two possible mechanisms. It is conceivable that post-dreissenid crayfish are less predacious than pre-dreissenid crayfish, utilizing more periphyton and detritus than their pre-dreissenid counterparts. Alternatively, or in addition, it is possible that post-dreissenid crayfish make greater use of primary consumers, which increased greatly in abundance following dreissenid establishment, whereas pre-dreissenid crayfish consumed more secondary consumers.

Estimates of trophic position were generally consistent with expectations. Organisms considered to be grazers or detritivores placed at lower trophic levels than ones known to be predacious regardless of the method used to estimate trophic level. Trophic level estimates based on seston and periphyton were lower than expected for some consumers, often being lower than 2, especially when using 3.4 ‰ as the fractionation factor. This suggests deviation in $\delta^{15}N$ fractionation from assumed rates. Trophic level estimates based on biodeposits and periphyton and on primary consumers generally yielded higher and more realistic trophic level estimates than those based on

seston and periphyton. Crayfish occupied the highest trophic level in the post-dreissenid food web, with their trophic position suggesting that they are entirely or nearly entirely predacious. This finding is consistent with work by Roth et al. (2006) and Whitledge and Rabeni (1997), who found that crayfish are primarily predators, assimilating mainly animal carbon, and are not indiscriminate omnivores as thought earlier (summarized in Momot, 1995). It appears that post-dreissenid crayfish do not rely on dreissenids as a direct food source, instead integrating a pelagic signature indirectly by feeding on primary consumers and detritivores which consume biodeposited material. Oligochaetes were the most $\delta^{15}N$ enriched organisms in the pre-dreissenid food web, placing them at the top of the pre-dreissenid food web. This finding is puzzling, considering that lumbriculid worms, like the ones analysed in this study are thought to feed primarily on algae, detritus and the associated bacteria (Moore 1978). It seems likely that oligochaetes may fractionate nitrogen to a much greater extent than many other aquatic organisms, which accounts for their unusually high $\delta^{15}N$ values.

The recent appearance of the rusty crayfish in Lake Simcoe has raised concerns regarding the role this invasive crayfish will play in the ecology of the Lake. My results suggest that the previously dominant *O. propinquus* and the newcomer *O. rusticus* occupy similar trophic niches, which may lead to competition. Both are predacious, with larger specimens significantly more enriched in $\delta^{15}N$ (and hence more predacious) than smaller conspecifics. The larger and more aggressive *O. rusticus* has almost completely displaced *O. propinquus* in some areas of the lake, and competition for shared food resources may be part of the reason, although competition for shelter and differences in susceptibility to predation likely also play an important role (Garvey et al. 1994)

The invasive amphipod *E. ischnus* was recently introduced to Lake Simcoe. My results show that *E. ischnus* and the native amphipod *G. fasciatus* share a similar carbon source, although *G. fasciatus* is more enriched in $\delta^{15}N$, suggesting it may be more predatory than the invasive *E. ischnus*. These results contrast with those of Limén et al. (2005) who studied food partitioning between these amphipod species in Lake Erie. They found that *E. ischnus* were more enriched in $\delta^{15}N$, indicating a greater level of carnivory but were depleted in $\delta^{13}C$ relative to *G. fasciatus* which displayed greater reliance on dreissenid biodeposits. Interpretation of their results and comparison with the results of this study is complicated because Limén et al. (2005) did not acidify dreissenid biodeposit material, a procedure that I found to be necessary to remove isotopically heavy carbonate from the samples.

The differences in the results of different mixing models and trophic level estimates highlight the sensitivity of these models to the assumptions made by investigators. I assumed no trophic fractionation of carbon, and applied two different $\delta^{15}N$ fractionation schemes, one using the oft-cited

3.4 ‰ tropic level^{-1} and another using 2.51 ‰ tropic level^{-1} for herbivores and 3.24 ‰ tropic level^{-1} for carnivores. My trophic level estimates suggest that the 2.51 ‰ tropic level^{-1} fractionation suggested by Vander Zanden and Rassmussen (2001) for herbivores may be more correct in the case of herbivores and detritivores in this study, while 3.4 ‰ tropic level^{-1} seems to be close to that observed here for predators such as crayfish and predacious caddisflies. Despite the general applicability of literature fractionation values the fractionation exhibited by many groups was quite variable. Psephenid beetles fractionated to a lesser degree (~2 ‰) than many other groups, and the snail *Goniobasis* sp. to a greater degree (~ 4 ‰) than expected. While it is well established that fractionation rates can vary widely among different taxonomic groups and locations, this is often not acknowledged by investigators attempting to use "standard" $\delta^{15}N$ fractionation rates to reconstruct trophic structure of food webs. In addition, some of the perceived variability in $\delta^{15}N$ fractionation in field studies may be due to greater levels of omnivory, even by "obligate" grazers or filter feeders than commonly assumed. The reality is that the diets of many aquatic invertebrates are poorly characterized, and are often based on fragmentary and incomplete information.

The assumptions I made in mixing models and trophic level estimates sometimes had noticeable effects on results. Use of primary producers and primary consumers as baselines for carbon and nitrogen values resulted in slightly different estimates of the importance of benthic and pelagic carbon to the littoral food web and to estimates of trophic level, although the differences were not very large. Differences in assumed fractionation of $\delta^{15}N$ also led to variation in trophic position estimates, although these tended to be no higher than ~0.4 trophic level for the groups most sensitive to changing assumptions regarding fractionation. The large error margins resulting from variability in isotope values of organisms, error associated with fractionation coefficients and error propagation in calculations made the results of different mixing models and trophic level estimates statistically similar. The large error associated with isotope-based food web reconstruction and the effects of assumptions on model results should remind ecologists that results of stable isotope studies should be interpreted with care and caution.

I have shown that dreissenid-redirected pelagic production in the form of biodeposits contributes significantly to the carbon budget of the post-dreissenid littoral benthos in Lake Simcoe, as does littoral benthic primary production. At the same time, the proportion of pelagic carbon in the diet of littoral benthos has changed little since the introduction of dreissenids, making up about half the carbon budget of the littoral food web. This should be viewed in light of the enormous increase (almost 50 times) in the standing stock of littoral benthos following dreissenid introduction (Chapter

4). Some of the largest increases in abundance following dreissenid introduction were among detritivores and omnivores such as amphipods and isopods which were shown to rely heavily on dreissenid biodeposits. Thus, while the relative importance of benthic and pelagic carbon to different taxonomic groups has changed little, the absolute importance of both carbon sources to the benthic food web increased by orders of magnitude. While few quantitative data exist, evidence from video recordings and the isotopic enrichment of benthic algae suggests that benthic algal production also increased considerably in the post-dreissenid period, likely driven by dreissenid-induced increases in water clarity and nutrient remineralization rates. Dreissenids appear to have increased food resource availability to benthic organisms in the littoral zone through two mechanisms. By increasing the rate of deposition of pelagic material to the benthos, dreissenids made large quantities of pelagic carbon available to benthic organisms able to utilize this resource. At the same time, dreissenids increased the productivity of benthic algae, further increasing food resource availability. These findings are consistent with the predictions of the nearshore shunt hypothesis, showing that redirection of pelagic carbon to the nearshore and stimulation of littoral benthic production by dreissenids contribute significantly to secondary production in the nearshore, which experienced considerable increases following dreissenid establishment.

The results of this study raise a number of questions regarding the effects of dreissenids on food webs and have an interesting implication for isotope-based studies of food web disruptions. I carried out this study in relatively shallow depths, where benthic primary production is expected to be high, finding it to be an important energy source to littoral benthos. I predict that at greater depths, where less benthic production occurs dreissenid biodeposits should be a more important energy source to the benthos. This prediction remains to be tested, and the importance of dreissenid biodeposits to the overall energy budget of invaded systems needs to be quantified. Another important question is how changes to energy flow in the littoral benthos affect higher vertebrate consumers. Preliminary evidence suggests that littoral fish have also undergone enrichment in $\delta^{13}C$ values following dreissenid establishment (D.O Evans, unpublished data), and integrate benthic primary production and redirected pelagic production. Future work needs to clarify energy flow pathways from the benthos to higher trophic levels in littoral zones in the wake of dreissenid establishment.

While I do not unequivocally show that dreissenids have changed the isotopic composition of benthic and pelagic primary producers, the results strongly suggest that this has occurred. This has an interesting implication for other food web studies comparing pre- and post-impact trophic relationships in lake food webs. If shifts in the isotopic composition of primary producers occur, but

are not quantified by the researchers, false conclusions may be reached. For example, if I analysed the isotopic composition of littoral fish before and after dreissenid invasion, finding more enriched carbon values in post-invasion fish I could have misinterpreted this result as increased reliance of the fish on benthic resources, while in reality their reliance on benthic and pelagic resources has not changed, but rather the isotopic composition of the food sources changed. Thus, researchers seeking to use isotopes to study the effects of food web disruptions would be wise to use other indicators of feeding relationships, such as gut content analysis (eg. Rennie et al. 2009), and exercise caution in interpreting the results of isotope based food web studies.

To summarize, dreissenid mussel invasion into Lake Simcoe has led to a number of changes to energy flow patterns in the littoral food web. Increased benthic primary production likely resulted in enriched carbon and nitrogen values of periphyton, leading to a shift in the overall isotopic composition of the food web. Many organisms seem to rely on redirected pelagic carbon, in the form of dreissenid biodeposits, although periphytic primary production also plays an important role in the energy balance of the post-dreissenid food web. While the relative importance of pelagic and benthic carbon for individual taxa appears to have changed little following dreissenid establishment, the overall importance of both carbon sources greatly increased due to the very large increases in the abundance of benthic invertebrates which followed dreissenid establishment. The results of this study show that dreissenids are shunting nutrients to the littoral zone directly, by making pelagic material available to the benthos, and indirectly, by stimulating benthic primary production. Future studies should expand on these results by investigating the importance of dreissenids to food webs of different lakes and different regions of lakes, as well as higher trophic levels.

Chapter 6
Discussion

6.1 General remarks

Dreissenid mussels have the potential to cause severe alterations to the ecological functioning of invaded ecosystems. The litany of their impacts covers almost all aspects of ecosystem function. From biogeochemical cycling, to physical characteristics of the water column and lake bottom, to biological production, community structure and species distributions, the tiny incriminating fingerprints of dreissenids are evident. I believe that our current understanding of the impacts of dreissenid on lake ecosystems can be summarized in one sentence: *dreissenids translocate biological productivity from the open water to the nearshore benthos* (Vanderploeg et al. 2002, Mills et al. 2003, Hecky et al. 2004, Gergs 2009, Higgins and Vander Zanden 2010). My thesis is set within this theoretical framework, and explores the interactions of dreissenids and their environment in the nearshore zone of large lakes, an area of dreissenology where considerable gaps in knowledge remain.

6.2 Chapter 2

The effects of any organism on its environment will depend, in large part, on its abundance and distribution in the ecosystem. Previous studies have identified a number of important parameters affecting dreissenid distribution in lakes, including substrate composition, salinity, calcium concentrations, productivity, and predator pressure. The effects of disturbance by surface waves on dreissenids have also been recognized, but few studies quantified the relationship between disturbance and dreissenids, and none has done so on a whole-lake scale. In chapter 2 I surveyed the distributions of dreissenid mussels in Lake Simcoe, Ontario and described the effects of a number of important parameters on dreissenid distribution in the lake.

I used video and ponar sampling to survey the distribution of dreissenids at close to 100 sites throughout Lake Simcoe. Using wind records I estimated the relative exposure of sampling sites to wave disturbance, and from video recording and ponar grabs determined the dominant type of substrate at each site. My results show that in shallow water dreissenid biomass is significantly and negatively associated with exposure to waves. This is the first demonstration of the importance of

disturbance in structuring dreissenid populations on a whole-ecosystem scale. I also found that dreissenids were more abundant on some macrophyte species than on others, suggesting that in macrophyte dominated areas the distribution of dreissenids may be related to the distribution of different macrophyte species.

The results of this chapter predict that dreissenid biomass peaks at intermediate depths of the littoral zone of large lakes. At shallow depth surface waves and ice scour can reduce dreissenid biomass through catastrophic disturbance. At intermediate depths, disturbance is not intense enough to cause destruction of mussels but is high enough to maintain an abundance of hard substrate which can support a high biomass of dreissenids. At greater depths soft substrates become more common, which can limit dreissenid biomass. Low levels of water movement at greater depths can also lead to lower food delivery rates to the mussels, possibly further limiting their growth and abundance. Using the results of my surveys and the relationships between dreissenid biomass and environmental parameters I made an estimate of the total biomass and distribution pattern of dreissenids in the lake. I found that the majority of dreissenid biomass (~80%) was concentrated in the littoral zone of the Lake Simcoe, where dreissenids presumably would have maximal impacts on benthic primary producers and littoral animals.

6.3 Chapter 3

The high abundance of dreissenids in the illuminated littoral zone of large lakes allows them to have considerable impacts on nearshore nutrient cycling and consequently on benthic primary producers. Past studies, based on laboratory experiments, demonstrated that large dreissenid populations can excrete considerable amounts of phosphorus, the nutrient most commonly limiting primary production in freshwater ecosystems. In chapter 3 I describe the results of an *in situ* study measuring dreissenid phosphorus excretion, and determine the importance of dreissenids to nearshore primary production. This study was conducted in the nearshore of Lake Ontario.

Dreissenid phosphorus excretion was measured in a series of *in situ* microcosm incubations, and dreissenid biomass along a portion of shoreline was measured using a video-based method. This allowed me to extrapolate dreissenid phosphorus excretion rates in the entire study area: a stretch of the littoral zone approximately 10 km^2 in area. To determine the relative importance of dreissenids to nearshore phosphorus cycling in the study area, the loading of phosphorus from the watershed was estimated, and phosphorus demand by primary producers in the study area was modeled with the help of Dr. S. Malkin.

The results of this chapter show that dreissenids can be a large and important source of dissolved phosphorus to nearshore areas. Dreissenids excreted more phosphorus in the study area than was contributed by watershed sources such as creeks, waste-water treatment plans and storm sewers. Dreissenids also contributed more phosphorus than needed to meet the demand by the large biomass of the benthic algae *Cladophora* which dominates benthic primary production in the study area. Dreissenid mussel excretion represents a novel source of nutrients in the nearshore of large invaded lakes, redirecting nutrients from the phytoplankton to benthic primary producers, and may be responsible for the nuisance growth of benthic algae which has occurred in the lower great lakes following dreissenid establishment. The results of this chapter suggest that controlling nuisance benthic algal growth in dreissenid-invaded large lakes may be difficult; local reductions in nutrient inputs may not appreciably reduce nuisance algal growth because dreissenids can draw on the large pool of nutrients contained in pelagic phytoplankton, translocating these nutrients to benthic algae.

6.4 Chapter 4

It has long been recognized that dreissenids can have large impacts on other benthic organisms. Generally, dreissenids are thought to enhance the production and standing stock of littoral benthos, while negatively impacting profundal benthic organisms. The positive impacts of dreissenids on nearshore benthos are likely due to increased food availability to the benthos (in the form of dreissenid biodeposits and enhanced benthic primary production), and due to increased habitat availability on and in between dreissenid shells. Because the benthos inhabiting rocky littoral substrates is difficult to sample, there have been few studies of impacts of dreissenids on such substrates. Most of these are short term studies using artificial substrates, conducted in a limited number of locations and depths. In chapter 4 I present the results of a long-term study of dreissenid impacts on the benthos inhabiting rocky littoral substrates, conducted at different depths and locations throughout the littoral zone of Lake Simcoe, Ontario.

In 2008 I used an airlift sampler to survey the benthic fauna of four sites in Lake Simcoe, sampling three different depths at each site. These sites were sampled using similar techniques in 1993, prior to dreissenid establishment in the lake by Dr. David Evans of the Ontario Ministry of Natural Resources. I identified and enumerated the benthic organisms present in the 1993 and 2008 samples, allowing me to compare the pre- and post-dreissenid benthic invertebrate communities in Lake Simcoe. I determined how the abundance, diversity, community composition, and spatial distribution of the benthos in Lake Simcoe changed fourteen years following dreissenid

establishment, making this one of the longest-term studies of dreissenid impacts on benthic communities.

The increase in the abundance of non-dreissenid benthos observed in this study is one of the largest reported in the literature. Detritivores and omnivores such as amphipods and isopods displayed some of the largest increases in abundance, but almost all taxa increased in abundance following dreissenid establishment. In addition to the increased abundance of benthos and changes in community composition, dreissenid establishment had significant effects on the spatial and depth distribution of the benthos. In 2008 the benthos was more evenly distributed among depths and sites than in 1993, both in terms of abundance and in terms of community composition. These changes are the result of a re-engineering of nearshore energy cycling and physical habitat by dreissenids. Dreissenids likely increased the availability of food resources to benthic organisms by stimulating benthic primary production and by biodepositing large quantities of edible material. Dreissenids also increased the amount of habitat available to invertebrates among living mussels and among discarded shells. Because dreissenid occur in large numbers throughout the littoral zone, and impact the benthic habitat in similar ways in different areas of the littoral zone, they have made the distribution of food and habitat more even, leading to a homogenization of littoral benthic communities.

6.5 Chapter 5

The impact of dreissenids on food webs remains an understudied aspect of dreissenid effects on ecosystems. It has been suggested that dreissenids could increase the reliance of the littoral food web on pelagic material by redirecting pelagic production to the littoral benthos. Stable isotopes of carbon and nitrogen offer a promising avenue for studying the impacts of invasive organism and other perturbations on food webs. In chapter 5 I used stable isotope analysis to describe the effects of dreissenid mussel establishment on energy sources and feeding relationships in the littoral food web of Lake Simcoe.

I analyzed pre- and post- dreissenid samples of benthic invertebrates and other components of the littoral food web, and used mixing models and trophic level analysis to compare the pre- and post-dreissenid littoral food web in Lake Simcoe. The results suggest that benthic primary production rates in Lake Simcoe increased following dreissenid establishment, consistent with expected effects of dreissenids on benthic primary producers. It appears that the post-dreissenid littoral food web is about equally dependant on two energy sources: dreissenid-biodeposited pelagic material and littoral primary production. Surprisingly, the pre-dreissenid benthic food web relied on pelagic and benthic

primary production to a similar extent to the post-dreissenid food web. This should be viewed in light of the enormous increase in the abundance of benthic organisms that occurred following dreissenid establishment (Chapter 4). While the relative contributions of benthic and pelagic primary production to the littoral food web did not change, the absolute amounts of both needed to sustain the post dreissenid benthos must have increased by orders of magnitude. Thus, dreissenids increased the efficiency with which pelagic material is directed to the littoral zone, while simultaneously increasing littoral primary production. This is the most extensive study of the effects of dreissenids on littoral food webs, and the first study to show that the stimulation of littoral primary production by dreissenids may be an important mechanism in fuelling the littoral food web in dreissenid invaded systems.

6.6 Conclusion

This thesis illustrated some of the mechanisms through which dreissenids translocate pelagic production to the nearshore benthos, and discussed some of processes controlling the movement of energy to the nearshore. Based on the results of this and other studies I believe it can be said that hydrodynamic forces are the most important controls on the strength of littoral-pelagic coupling by dreissenids. Because lake hydrodynamic regime is directly related to lake size, a relationship between lake size and dreissenid effects can be postulated. I suggest that dreissenid-mediated translocation of material and energy from the pelagic to the littoral peaks at intermediate lake size, and is closely related to hydrodynamic factors (Fig. 6.1).

Dreissenids will have only minor impacts on energy transport in very small bodies of water because water turbulence in these systems is low. While in theory dreissenids should have access to the entire water column in small and shallow lakes, removing a large amount of pelagic material, few dreissenids can establish in such systems. The soft bottom of such systems can support few dreissenids, and in lakes that freeze to the bottom (or nearly so) dreissenid populations would be extirpated every winter, reducing the impacts of dreissenids on energy translocation to the benthos.

In larger lakes that do not freeze to the bottom, and have a macrophyte community that can support high dreissenid abundance, the impacts of dreissenids may become more noticeable. Small to medium lakes should be well mixed, and the three-dimensional structure of the macrophyte-bound dreissenid community will maximize the ability of dreissenid mussels to access the water column. Many dreissenids however would be killed in the winter, when macrophytes senesce and dreissenid remains would become buried in the soft sediments, below layers of decomposing macrophytes.

Buried mussel shells and biodeposits would have minor direct impacts on benthic organisms, and their translocation of energy to the littoral zone would be expressed mainly in fertilizing macrophyte growth with their decomposing bodies and buried biodeposits, and in increasing the water clarity, enabling greater growth of macrophytes.

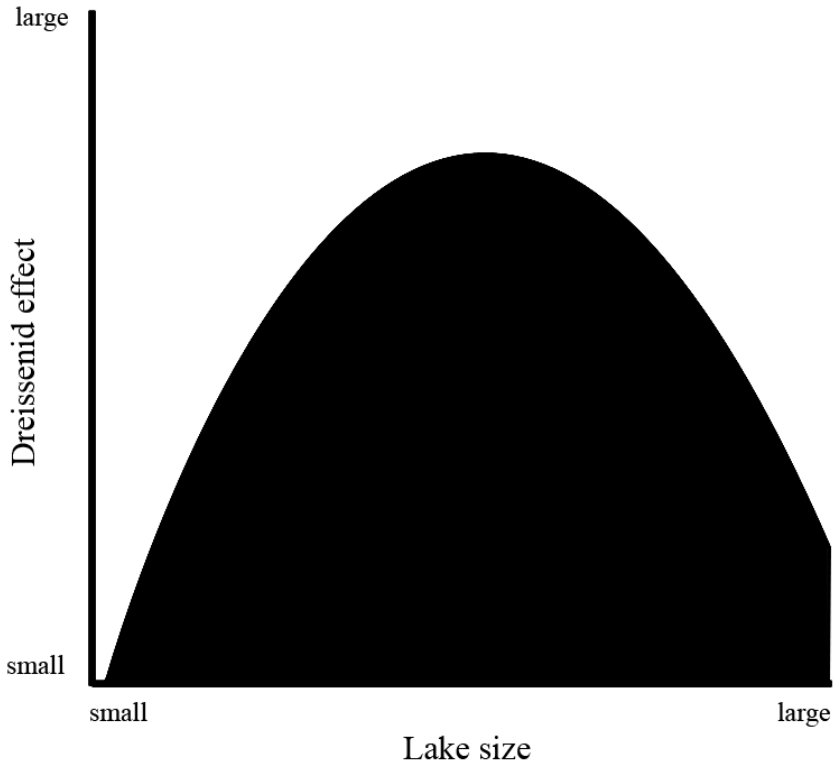

Figure 6.1: Conceptual representation of the ability of dreissenids to translocate pelagic production to the littoral zone, as a function on lake size.

In intermediate-sized lakes such as Lake Simcoe the impacts of dreissenids should be particularly high. Water movement in such systems should be high enough to maintain abundant hard substrate for dreissenid colonization of the littoral zone, while providing dreissenids with fresh supplies of phytoplankton through mixing of the water column. Additionally, water movement is not so intense as to remove discarded mussel shells and biodeposits trapped in the littoral zone to deeper portions of the lake. In such systems dreissenids can effectively translocate energy to the littoral, facilitating benthic primary producers through water clarity increases and nutrient excretion, while providing edible biodeposited pelagic material and shelter to the invertebrate community residing in the littoral zone. Because dreissenid mussels themselves, their shells and their biodeposits are retained

in the nearshore, they provide an abundant and stable supply of resources to the littoral benthos and to the fish community that depends on them.

In very large lakes hydrodynamic forces in the littoral zone are intense, and the efficiency with which biological production is shunted to the benthos by dreissenids decreases. While the water column in the littoral is well mixed, and ecosystem size ensures a large supply of suspended energy to dreissenids, the ratio between the size of the pelagic and littoral zones becomes very large, making the relative impact of littoral dreissenids on the entire system smaller than in intermediate sized lakes. The small size of the littoral zone relative to the pelagic zone also means that littoral production boosted by dreissenids is still a small portion of whole-lake productivity. In addition, intense water movement in the littoral zone would transport discarded dreissenid shells and biodeposits to greater depth, below the littoral zone. This means that dreissenid biodeposits and shells will have a lesser impact on the benthic invertebrate and littoral fish communities than in intermediate-sized lakes where dreissenid strongly benefit the benthos. Hydrodynamics may also be the reason that in large lakes such as Lake Ontario nutrients redirected to the nearshore by dreissenids fuel the production of inedible benthic algae like *Cladophora*, while in medium-sized lakes edible, diatom-dominated periphyton is favoured. Intense water movement in the nearshore of large lakes allows for effective diffusion of dreissenid excreted-nutrients into the string-like thalli of filamentous algae, which are not very edible, and hence do not appreciably increase the resource base of the benthic invertebrate community. In smaller lakes where wave action is less intense lower growing forms, which are less dependant on water movement for nutrient supply predominate, and being more edible than filamentous algae increase the resource base of the benthic invertebrate community.

To summarize, dreissenid mussels can be viewed as a biological entity that links the pelagic and littoral zones of lakes, translocating biological production from the open water to the illuminated nearshore zone of the lake. This shift in production occurs through a number of pathways including increases in water clarity, redirection of limiting nutrients, and direct transfer of energy in the form of biodeposits. I argue that hydrodynamics and consequently lake size are an important determinant of the strength of the connection between the pelagic and littoral zones, which peaks at intermediate lake size.

Appendix A

Appendix A: Average abundance of benthic invertebrates in samples from 1993 and 2008 from three depths and four sites. Number in brackets is one standard deviation of the mean.

Blackbird Point						
Year		1993			2008	
Depth (m)	2	4	6	2	4	6
n	4	4	3	3	4	4
Amphipoda						
H. azteca	44 (22.9)	28 (10.6)	10 (14.1)	2200 (1882.5)	1988 (1820.5)	212 (150.9)
Gammarus sp.	7 (6)	4 (6.9)	4 (5.7)	2372 (1716.8)	316 (200.9)	188 (83)
E. ischnus	0 (0)	0 (0)	0 (0)	740 (644.7)	32 (37)	0 (0)
Crangonyx sp.	0 (0)	4 (4)	0 (0)	696 (725.8)	128 (204.5)	876 (623.7)
Isopoda						
C. racovitzai	0 (0)	0 (0)	0 (0)	1380 (812)	712 (461.8)	3388 (1073.5)
Gastropoda						
Hydrobiidae	1 (2)	20 (17.4)	18 (25.5)	144 (124.6)	196 (212.8)	224 (242.7)
Physidae	1 (2)	1.3 (2.3)	2 (2.8)	12 (15.3)	4 (8)	0 (0)
Planorbidae	0 (0)	0 (0)	0 (0)	12 (8)	0 (0)	0 (0)
Pleuroceridae	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Viviparidae	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Lymnaeidae	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Valvatidae	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Ancylidae	0 (0)	0 (0)	0 (0)	0 (0)	24 (27.7)	1308 (680.4)
Bivalva						
Sphaeriidae	45 (22.9)	28 (35.6)	16 (0)	88 (102.4)	4 (8)	56 (91)
D. polymorpha	0 (0)	0 (0)	0 (0)	2512 (817)	1996 (334.4)	3848 (158.1)
D. bugensis	0 (0)	0 (0)	0 (0)	52 (44.1)	100 (99)	220 (76.6)
Unionidae	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Insecta						
Chironomidae	40 (11.8)	24 (6.9)	38 (2.8)	3612 (2341.9)	596 (292.2)	2224 (540.4)
Polycentropodidae	5 (2)	5.3 (6.1)	2 (2.8)	332 (224.5)	604 (433.7)	1048 (356)
Helicopsychidae	0 (0)	0 (0)	0 (0)	100 (129.6)	20 (24)	0 (0)
Leptoceridae	5 (5)	2.7 (4.6)	0 (0)	16 (18.5)	0 (0)	0 (0)
Hydroptilidae	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Hydropsychidae	4 (8)	0 (0)	0 (0)	4 (8)	0 (0)	0 (0)
Caenidae	1 (2)	0 (0)	0 (0)	44 (54.5)	0 (0)	0 (0)
Heptageniidae	31 (36.3)	21.3 (12.2)	2 (2.8)	108 (86)	12 (24)	8 (16)
Ephemeridae	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Sialidae	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	20 (30.3)
Elmidae	91 (52.6)	6.7 (4.6)	4 (0)	856 (679.9)	36 (33)	0 (0)
Psephenidae	8 (3.3)	0 (0)	2 (2.8)	0 (0)	0 (0)	0 (0)
Acari						
Oribatidae	0 (0)	0 (0)	0 (0)	736 (1397.5)	16 (18.5)	3424 (1108.2)
Other mites	16 (8)	40 (24.3)	10 (14.1)	136 (157)	68 (85)	496 (67.9)
Worms						
Planariidae	3 (3.8)	4 (4)	0 (0)	232 (266.6)	156 (159.1)	524 (213.6)
Oligochaeta	6 (6.9)	16 (27.7)	2 (2.8)	1804 (1588.2)	464 (236.2)	4880 (2234.5)
Hirudinea	2 (2.3)	0 (0)	0 (0)	0 (0)	28 (15.3)	8 (9.2)
Nematoda	0 (0)	0 (0)	0 (0)	108 (84)	44 (68.4)	728 (450.6)
Other	4 (3.3)	1.3 (2.3)	0 (0)	20 (30.3)	0 (0)	40 (69.7)
TOTAL	314 (108)	182 (68.6)	110 (65.1)	18316 (12216.9)	7544 (3895)	23720 (6565.1)

Grape Island						
Year		1993			2008	
Depth (m)	2	4	6	2	4	6
n	4	3	4	4	4	3
Amphipoda						
H. azteca	61 (41.4)	1.3 (2.3)	0 (0)	3524 (645.6)	1260 (423)	69.3 (66.6)
Gammarus sp.	2 (4)	0 (0)	0 (0)	3112 (2054.4)	1304 (877.8)	1253.3 (470.4)
E. ischnus	0 (0)	0 (0)	0 (0)	6240 (1013)	260 (355.5)	10.7 (9.2)
Crangonyx sp.	6 (5.2)	6.7 (8.3)	2 (2.3)	364 (82)	196 (157.5)	0 (0)
Isopoda						
C. racovitzai	0 (0)	0 (0)	0 (0)	512 (165.8)	592 (369.3)	154.7 (130.3)
Gastropoda						
Hydrobiidae	42 (12)	13.3 (16.7)	31 (20.8)	20 (20.1)	28 (35.5)	16 (0)
Physidae	4 (5.7)	0 (0)	2 (4)	4 (8)	0 (0)	5.3 (9.2)
Planorbidae	0 (0)	0 (0)	1 (2)	0 (0)	0 (0)	0 (0)
Pleuroceridae	41 (27.8)	2.7 (4.6)	0 (0)	0 (0)	0 (0)	0 (0)
Viviparidae	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	5.3 (9.2)
Lymnaeidae	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Valvatidae	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Ancylidae	0 (0)	1.3 (2.3)	0 (0)	188 (134.7)	196 (91.8)	704 (346.5)
Bivalva						
Sphaeriidae	23 (12.4)	10.7 (8.3)	16 (5.7)	4 (8)	20 (30.3)	133.3 (82.1)
D. polymorpha	0 (0)	0 (0)	0 (0)	2166 (991.5)	3632 (2664.1)	2650.7 (2296.6)
D. bugensis	0 (0)	0 (0)	0 (0)	20 (15.3)	0 (0)	181.3 (190.9)
Unionidae	0 (0)	1.3 (2.3)	0 (0)	0 (0)	0 (0)	0 (0)
Insecta						
Chironomidae	52 (39.1)	1.3 (2.3)	1 (2)	1456 (433.5)	840 (470.8)	6661.3 (2269.1)
Polycentropodidae	1 (2)	0 (0)	0 (0)	12 (8)	16 (22.6)	0 (0)
Helicopsychidae	0 (0)	0 (0)	0 (0)	0 (0)	4 (8)	0 (0)
Leptoceridae	0 (0)	2.7 (2.3)	1 (2)	0 (0)	0 (0)	10.7 (18.5)
Hydroptilidae	0 (0)	0 (0)	0 (0)	76 (73.2)	0 (0)	0 (0)
Hydropsychidae	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	5.3 (9.2)
Caenidae	0 (0)	0 (0)	0 (0)	12 (15.3)	32 (29.2)	16 (16)
Heptageniidae	17 (13.6)	2.7 (2.3)	1 (2)	20 (15.3)	20 (30.3)	0 (0)
Ephemeridae	0 (0)	0 (0)	0 (0)	0 (0)	4 (8)	96 (48)
Sialidae	0 (0)	0 (0)	0 (0)	12 (15.3)	16 (32)	0 (0)
Elmidae	6 (5.2)	0 (0)	0 (0)	48 (22.6)	16 (18.5)	5.3 (9.2)
Psephenidae	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Acari						
Oribatidae	0 (0)	0 (0)	0 (0)	20 (15.3)	28 (33)	26.7 (46.2)
Other mites	13 (15.8)	16 (16)	4 (5.7)	36 (24)	20 (20.1)	37.3 (24.4)
Worms						
Planariidae	2 (4)	0 (0)	0 (0)	48 (26.1)	16 (22.6)	37.3 (51.4)
Oligochaeta	6 (2.3)	2.7 (2.3)	4 (5.7)	5552 (2744)	1972 (673.7)	725.3 (106.5)
Hirudinea	1 (2)	5.3 (6.1)	0 (0)	52 (33)	12 (8)	5.3 (9.2)
Nematoda	0 (0)	0 (0)	0 (0)	248 (125.6)	260 (243.1)	314.7 (217.2)
Other	0 (0)	0 (0)	0 (0)	40 (27.7)	4 (8)	26.7 (9.2)
TOTAL	277 (102.9)	76.7 (33.4)	63 (34.2)	23786 (3385)	10748 (2912.2)	13152 (2179.1)

	Sibbald Point					
Year		1993			2008	
Depth (m)	2	4	6	2	4	6
n	4	4	3	3	4	4
Amphipoda						
H. azteca	105 (112.6)	14 (2.3)	2.7 (2.3)	6378.7 (6357.5)	1312 (986.7)	20 (24)
Gammarus sp.	5 (10)	0 (0)	1.3 (2.3)	3306.7 (3122.5)	916 (643.4)	2268 (1561)
E. ischnus	0 (0)	0 (0)	0 (0)	576 (372.2)	24 (27.7)	120 (91.9)
Crangonyx sp.	7 (6)	1 (2)	0 (0)	1141.3 (870)	612 (492.2)	4 (8)
Isopoda						
C. racovitzai	0 (0)	0 (0)	1.3 (2.3)	1056 (346.1)	4316 (1253.1)	456 (300.9)
Gastropoda						
Hydrobiidae	0 (0)	3 (3.8)	2.7 (2.3)	645.3 (431.2)	796 (197.4)	24 (20.7)
Physidae	19 (20.8)	14 (7.7)	4 (4)	133.3 (106.5)	116 (68.4)	76 (88)
Planorbidae	0 (0)	0 (0)	0 (0)	26.7 (33.3)	48 (41.3)	1368 (648.7)
Pleuroceridae	1 (2)	1 (2)	2.7 (4.6)	0 (0)	0 (0)	0 (0)
Viviparidae	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Lymnaeidae	0 (0)	0 (0)	0 (0)	5.3 (9.2)	12 (15.3)	12 (24)
Valvatidae	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Ancylidae	1 (2)	1 (2)	0 (0)	10.7 (18.5)	76 (84)	0 (0)
Bivalva						
Sphaeriidae	95 (38.1)	37 (24.3)	20 (14.4)	144 (127)	88 (71)	204 (52.9)
D. polymorpha	0 (0)	0 (0)	0 (0)	1562.7 (507.6)	3660 (1551.3)	5752 (4643.5)
D. bugensis	0 (0)	0 (0)	0 (0)	64 (27.7)	148 (60.4)	204 (229.8)
Unionidae	0 (0)	0 (0)	1.3 (2.3)	0 (0)	0 (0)	0 (0)
Insecta						
Chironomidae	115 (48.7)	92 (28.7)	0 (0)	3749.3 (3355.9)	4328 (1906.9)	9700 (3860.9)
Polycentropodidae	24 (13.5)	2 (2.3)	1.3 (2.3)	149.3 (88.1)	380 (179.8)	16 (32)
Helicopsychidae	0 (0)	0 (0)	0 (0)	901.3 (1281.2)	16 (22.6)	140 (139.7)
Leptoceridae	0 (0)	0 (0)	1.3 (2.3)	80 (97.3)	36 (33)	508 (210.4)
Hydroptilidae	1 (2)	1 (2)	1.3 (2.3)	0 (0)	4 (8)	0 (0)
Hydropsychidae	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Caenidae	0 (0)	0 (0)	0 (0)	128 (110.9)	12 (24)	4 (8)
Heptageniidae	41 (27.8)	17 (7.6)	2.7 (4.6)	5.3 (9.2)	40 (69.7)	0 (0)
Ephemeridae	0 (0)	2 (2.3)	1.3 (2.3)	0 (0)	8 (16)	144 (106.9)
Sialidae	0 (0)	0 (0)	1.3 (2.3)	5.3 (9.2)	76 (24)	8 (9.2)
Elmidae	22 (16.2)	0 (0)	0 (0)	90.7 (143.4)	4 (8)	12 (24)
Psephenidae	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Acari						
Oribatidae	0 (0)	0 (0)	0 (0)	858.7 (1473.4)	60 (120)	0 (0)
Other mites	19 (10)	12 (18.8)	6.7 (4.6)	906.7 (1434.1)	208 (353)	16 (13.1)
Worms						
Planariidae	0 (0)	0 (0)	0 (0)	544 (566.1)	580 (373)	1632 (1026.6)
Oligochaeta	73 (40.2)	43 (23.6)	36 (35.6)	2928 (2429)	1488 (644.9)	3128 (1170.8)
Hirudinea	1 (2)	2 (4)	0 (0)	5.3 (9.2)	4 (8)	4 (8)
Nematoda	0 (0)	0 (0)	0 (0)	853.3 (670.2)	152 (87.1)	0 (0)
Other	2 (4)	0 (0)	0 (0)	90.7 (96.4)	32 (26.1)	764 (820.9)
TOTAL	531 (293.1)	242 (73.1)	84.3 (33)	26346.7 (21162.4)	19552 (3586.2)	26584 (4410.3)

Strawberry Island						
Year		1993			2008	
Depth (m)	2	4	6	2	4	6
n	4	4	3	3	4	4
Amphipoda						
H. azteca	147 (215.4)	22 (7.7)	1.3 (2.3)	6592 (384)	6788 (3164.1)	3748 (2096.1)
Gammarus sp.	14 (14.8)	22 (17.7)	0 (0)	7210.7 (2781.9)	1388 (905.3)	708 (303.7)
E. ischnus	0 (0)	0 (0)	0 (0)	2496 (1275.2)	2504 (2375.9)	60 (40)
Crangonyx sp.	1 (2)	89 (38.4)	41.3 (20.1)	2794.7 (2816.2)	888 (627.7)	376 (434.6)
Isopoda						
C. racovitzai	1 (2)	0 (0)	0 (0)	3498.7 (1669.3)	2224 (2023.1)	1048 (435.3)
Gastropoda						
Hydrobiidae	11 (17.1)	27 (33.2)	0 (0)	437.3 (307.5)	544 (406.5)	68 (27.3)
Physidae	15 (12.4)	12 (13.5)	10.7 (4.6)	85.3 (37)	112 (75)	76 (60.4)
Planorbidae	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	68 (136)
Pleuroceridae	29 (15.4)	2 (4)	2.7 (4.6)	0 (0)	0 (0)	0 (0)
Viviparidae	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	4 (8)
Lymnaeidae	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Valvatidae	1 (2)	1 (2)	0 (0)	0 (0)	0 (0)	0 (0)
Ancylidae	0 (0)	0 (0)	1.3 (2.3)	682.7 (580.7)	1716 (990.1)	908 (407.2)
Bivalva						
Sphaeriidae	37 (20.5)	24 (26.9)	17.3 (10.1)	416 (32)	12 (15.3)	28 (15.3)
D. polymorpha	0 (0)	0 (0)	0 (0)	7661.3 (1770.7)	2832 (1614.1)	2074 (465.2)
D. bugensis	0 (0)	0 (0)	0 (0)	93.3 (81.7)	84 (46)	44 (15.3)
Unionidae	0 (0)	0 (0)	1.3 (2.3)	0 (0)	0 (0)	0 (0)
Insecta						
Chironomidae	521 (411.2)	189 (100.7)	86.7 (26.6)	6805.3 (258.7)	1016 (920.5)	872 (288.7)
Polycentropodidae	10 (9.5)	19 (17.4)	4 (4)	192 (110.9)	140 (131.5)	132 (63.2)
Helicopsychidae	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Leptoceridae	7 (6.8)	3 (2)	0 (0)	21.3 (37)	0 (0)	8 (9.2)
Hydroptilidae	0 (0)	0 (0)	0 (0)	85.3 (97.8)	88 (117.2)	4 (8)
Hydropsychidae	1 (2)	1 (2)	0 (0)	0 (0)	0 (0)	0 (0)
Caenidae	8 (8.6)	7 (6)	1.3 (2.3)	0 (0)	0 (0)	0 (0)
Heptageniidae	57 (45.3)	161 (110.2)	36 (10.6)	362.7 (266.5)	100 (109.6)	44 (33)
Ephemeridae	3 (6)	1 (2)	0 (0)	0 (0)	0 (0)	16 (13.1)
Sialidae	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	4 (8)
Elmidae	26 (32.2)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Psephenidae	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Acari						
Oribatidae	0 (0)	0 (0)	0 (0)	23506 (20253.3)	420 (292.2)	372 (310.4)
Other mites	150 (297.3)	7 (5)	5.3 (2.3)	942 (667.2)	572 (290.5)	680 (48)
Worms						
Planariidae	0 (0)	0 (0)	0 (0)	757.3 (610.8)	144 (143.7)	212 (99)
Oligochaeta	114 (164)	118 (90.8)	70.7 (53.7)	4992 (721.2)	1356 (200.4)	1456 (588.7)
Hirudinea	5 (3.8)	0 (0)	1.3 (2.3)	106.7 (133.2)	328 (53.1)	32 (13.1)
Nematoda	30 (27)	1 (2)	0 (0)	1450.7 (1040.5)	4 (8)	4 (8)
Other	2 (2.3)	0 (0)	0 (0)	21.3 (37)	48 (47.1)	28 (33)
TOTAL	1190 (1108.1)	706 (238)	270.5 (53.6)	71210.7 (26107.4)	23308 (8296.2)	13074 (1324.1)

Bibliography

Ackerman, J.D., M.R. Loewen, and P.F. Hamblin. 2001. Benthic-pelagic coupling over a zebra mussel reef in western Lake Erie. Limnology and Oceanography 46:892–904.

American Public Health Association (APHA). 1998. Standard methods for the examination of water and wastewater, 20th ed. United Book Press.

Aquafor Beech Limited. 2005. Final report: Conservation Halton LOSAAC water quality study. Aquafor Beech Limited. Brampton, Ontario.

Arnott, D.L., and M.J. Vanni. 1996. Nitrogen and phosphorus recycling by the zebra mussel (*Dreissena polymorpha*) in the western basin of Lake Erie. Canadian Journal of Fisheries and Aquatic Science 53:646–659.

Astanei, I., E. Gosling, J. Wilson, and E. Powell. 2005. Genetic variability and phylogeny of the invasive zebra mussel, *Dreissena polymorpha* (Pallas). Molecular Ecology 14:1655–1666

Auer, M.T., and R.P. Canale. 1982. Ecological studies and mathematical modeling of *Cladophora* in Lake Huron: 2. Phosphorus uptake kinetics. Journal of Great Lakes Research 8:84–92.

Baldwin, B.S., M.S. Mayer, J. Dayton, N. Pau, J. Mendilla, M. Sullivan, A. Moore, and E.L. Mills. 2002. Comparative growth and feeding in zebra and quagga mussels (*Dreissena polymorpha* and *Dreissena bugensis*): implications for North American lakes. Canadian Journal of Fisheries and Aquatic Science 59:680–694.

Barbiero, R.P., M.L. Tuchman, and S.E. Millard. 2006. Post-dreissenid increases in transparency during summer stratification in the offshore waters of Lake Ontario: Is a reduction in whiting events the cause? Journal of Great Lakes Research 32:131–141.

Barton, D.R., and H.B.N. Hynes. 1978. Wave-zone macrobenthos of the exposed Canadian shores of the St. Lawrence Great Lakes. Journal of Great Lakes Research 4:27–45.

Barton, D.R., and J.C.H. Carter. 1982. Shallow-water epibenthic communities of eastern Georgian Bay, Ontario, in relation to exposure to wave action. Canadian Journal of Zoology 60:984–993.

Barton, D.R., R.A. Johnson, L. Campbell, J. Petruniak, and M. Patterson. 2005. Effects of round gobies (*Neogobius melanostomus*) on dreissenid mussels and other invertebrates in Eastern Lake Erie, 2002–2004. Journal of Great Lakes Research 31:252–261.

Beekly, M.A., D.J. McCabe, and J.E. Marsden. 2004. Zebra mussel colonization of soft sediments facilitates invertebrate communities. Freshwater Biology 49:535–545.

Bentzen, E., and W.D. Taylor. 1991. Estimating Michaelis-Menten parameters and lake water phosphate by the Rigler bioassay: importance of fitting technique, plankton size and substrate range Canadian Journal of Fisheries and Aquatic Science 48:73–83.

Bially, A.B., and H.J. MacIsaac. 2000. Fouling mussels (*Dreissena* spp.) colonize soft sediments in Lake Erie and facilitate benthic invertebrates. Freshwater Biology 43:85–97.

Botts, P.S., B.A. Patterson, and D.W. Schloesser. 1996. Zebra mussel effects on benthic invertebrates: physical or biotic. Journal of the North American Benthological Society 15:179–184.

Brown, J.E., and C.A. Stepien. 2010. Population genetic history of the dreissenid mussel invasions: expansion patterns across North America. Biological Invasions. DOI 10.1007/s10530–010–9763–2

Budd, J.W., T.D. Drummer, T.F. Nalepa, and G.L. Fahenstiel. 2001. Remote sensing of biotic effects: zebra mussel (*Dreissena polymorpha*) influence on water clarity in Saginaw Bay, Lake Huron. Limnology and Oceanography 46:213–223.

Bunt, C.M., H.J. MacIsaac, and W.G. Sprules. 1993. Pumping rates and projected filtering impacts of juvenile zebra mussels *Dreissena polymorpha* in western Lake Erie. Canadian Journal of Fisheries and Aquatic Science 50:1017–1022.

Burkhardt, S., U. Riebesell, and I. Zondervan. 1999. Effects of growth rate, CO_2 concentration, and cell size on the stable carbon isotope fractionation in marine phytoplankton. Geochimica et Cosmochimica Acta 63:3729–3741.

Campbell, L.M., R. Thacker, D. Barton, D.C.G. Muir, D. Greenwood, and R.E. Hecky. 2009. Re-engineering of the eastern Lake Erie littoral food web: the trophic function of non-indigenous Ponto-Caspian species. Journal of Great Lakes Research 35:224–231.

Canale, R. P., and M. T. Auer. 1982. Ecological studies and mathematical modeling of *Cladophora* in Lake Huron: 5. Model development and calibration. Journal of Great Lakes Research 8:112–125.

Carlton, J.T. 1993. Dispersal mechanisms of the zebra mussel (*Dreissena polymorpha*). In Nalepa, T. F. and Schloesser, D.W., (Eds.) Zebra mussels: biology, impact and control. Lewis Publishers, Ann Arbour, pp. 677–697.

Clarke, K.R. and R.M. Warwick. 2001. Changes in marine communities: an approach to statistical analysis and interpretation. 2nd Edition. PRIMER-E: Plymouth, UK. 172 pp.

Coakley, T.P., G.L. Brown, S.E. Ioannou, and M.N. Charlton. 1997. Colonization patterns and densities of zebra mussel *Dreissena* in muddy offshore sediments of western Lake Erie, Canada. Water Air and Soil Pollution 99:623–632.

Conroy, J.D., W.J. Edwards, R.A. Pontius, D.D. Kane, H. Zhang, J.F. Shea, and D.A. Culver. 2005. Soluble nitrogen and phosphorus excretion of exotic freshwater mussels (*Dreissena* spp.): potential impacts for nutrient remineralization in western Lake Erie. Freshwater Biology 50:1146–1162.

Cotner, J.B., W.S. Gardner, J.R. Johnson, R.H. Sada, J.F. Cavaletto, and R.T. Heath. 1995. Effects of zebra mussels (*Dreissena polymorpha*) on bacterioplankton: evidence for both size-selective consumption and growth stimulation. Journal of Great Lakes Research 21:517–528.

Custer, C.M., and T.W. Custer. 1996. Food habits of diving ducks in the Great Lakes following the zebra mussel invasion. Journal of Field Ornithology 67:86–99.

Custer, C.M., and T.W. Custer. 1997. Occurrence of zebra mussels in near-shore areas of western Lake Erie. Journal of Great Lakes Research 23: 108–115.

Depew, D.C., A.J. Houben, T. Ozersky, R.E. Hecky, and Guildford S.J. 2010. Submerged aquatic vegetation in Cook's Bay, Lake Simcoe: Assessment of changes in response to increased water transparency. Journal of Great Lakes Research. doi:10.1016/j.jglr.2010.07.009.

Dermott, R., and D. Kerec. 1997. Changes to the deepwater benthos of eastern Lake Erie since the invasion of *Dreissena*: 1979–1993. Canadian Journal of Fisheries and Aquatic Science 54:922–930.

Dermott, R., Mitchell, J., Murray, I., and Fear, E. 1993. Biomass and production of zebra mussels (*Dreissena polymorha*) in shallow waters of northeastern Lake Erie. In Nalepa, T. F. and Schloesser, D.W., (Eds.) Zebra mussels: biology, impact and control. Lewis Publishers, Ann Arbour, pp. 399–413.

Diggins, T.P., M. Weimer, K.M. Stewart, R.E. Baier, A.E. Meyer, R.F. Forsberg, and M.A. Goehle. 2004. Epiphytic refugium: are two species of invading freshwater bivalves partitioning spatial resources? Biological Invasions 6:83–8.

Dodds, W.K., and D.A. Gudder. 1992. The ecology of *Cladophora*. Journal of Phycology 28:415–427.

Edwards, W.J., C.R. Rehmann, E. McDonald, and D.A. Culver. 2005. The impacts of a benthic filter feeder: limitations imposed by physical transport of algae to the benthos. Canadian Journal of Fisheries and Aquatic Science 62:205–214.

Effler, S.W., S.R. Boone, C.A. Siegfried, L. Walrath, and S.L. Ashby.1997. Mobilization of ammonia and phosphorus by zebra mussels (*Dreissena polymorpha*) in the Seneca River, New York. Chapter 12, in Diltri, F. (ed.), *Proceedings of the Sixth International Zebra Mussel and Other Aquatic Nuisance Species Conference*. Ann Arbor Press, MI.

Eimers M.C., J.G. Winter, W.A. Scheider, S.A. Watmough, and K.H. Nicholls. 2005. Recent changes and patterns in the water chemistry of Lake Simcoe. Journal of Great Lakes Research 31:322–332.

Evans D.O., A..J Skinner, R. Allen, and M.J. McMurtry. In press. Invasion of zebra mussel, *Dreissena polymorpha*, in Lake Simcoe. Journal of Great Lakes Research.

Evans D.O., K.H. Nicholls, Y.C. Allen, and M.J. McMurty. 1996. Historical land use, phosphorus loading, and loss of fish habitat in Lake Simcoe, Canada. Canadian Journal of Fisheries and Aquatic Science 53:194–218.

France, R.L. 1995. Differentiation between littoral and pelagic food webs in lakes using carbon isotopes. Limnology and Oceanography 40:1310–1313.

Frechette M., C.A. Butman, and W.G. Gayer. 1989. The importance of boundary-layer flows in supplying phytoplankton to the benthic suspension feeder, *Mytilus edulis*. Limnology and Oceanography 34:19–36.

French III, J.R.P. and M.T. Bur. 1992. Predation of the zebra mussel (*Dreissena polymorpha*) by freshwater drum in western Lake Erie. In Nalepa T. F., and. Schloesser, D.W. (Eds.) Zebra mussels: biology, impact and control. Ann Arbour, MI: Lewis Publishers, pp. 453–464.

Garton, D.W., C.D. Payne, and J.P. Montoya. 2005. Flexible diet and trophic position of dreissenid mussels as inferred from stable isotopes of carbon and nitrogen. Canadian Journal of Fisheries and Aquatic Science 62:1119–1129.

Garvey, J.E., R.A. Stein, and H.M. Thomas. 1994. Assessing how fish predation and interspecific prey competition influence a crayfish assemblage. Ecology 75:532–547.

Gergs, R., and K.O. Rothhaupt. 2008. Feeding rates, assimilation efficiencies and growth of two amphipod species on biodeposited material from zebra mussels. Freshwater Biology 53:2494–2503.

Gergs, R., K. Rinke, and K.O. Rothhaupt. 2009. Zebra mussels mediate benthic-pelagic coupling by biodeposition and changing detrital stoichiometry. Freshwater biology 54:1379–1391.

Gergs, R. 2009. *Dreissena polymorpha* in Lake Constance: an example of a keystone engineer? PhD thesis. University of Konstanz. 126 p.

Gergs, R., and K.O. Rothhaupt. 2008. Feeding rates, assimilation efficiencies and growth of two amphipod species on biodeposited material from zebra mussels. Freshwater Biology 53:2494–2503.

Glass, G. V, P. D. Peckham, and J. R. Sanders. 1972. Consequences of failure to meet assumptions underlying the fixed effects analysis of variance and covariance. Review of Educational Research 42:237–288.

Gonzalez, M.J., and A. Downing. 1999. Mechanisms underlying amphipod responses to zebra mussel (*Dreissena polymorpha*) invasion and implications for fish-amphipod interactions. Canadian Journal of Fisheries and Aquatic Science 56:679–685.

Gorokhova, E., S. Hansson, H. Hoglander, and C. M. Andersen. 2005. Stable isotopes show food web changes after invasion by the predatory cladoceran *Cercopagis pengoi* in a Baltic Sea bay. Oecologia 143: 251–259.

Griffiths, R.W. 1993. Effects of zebra mussels (*Dreissena polymorpha*) on the benthic fauna of Lake St. Clair. In Nalepa T. F., and. Schloesser, D.W. (Eds.) Zebra mussels: biology, impact and control. Ann Arbour, MI: Lewis Publishers, pp. 415–437.

Haynes, J.M., T.W. Stewart, and G.E. Cook. 1999. Benthic macroinvertebrate communities in southwestern Lake Ontario following invasion of *Dreissena*: Continuing change. Journal of Great Lakes Research 25: 828–838.

Haynes, J.M., N.A. Tisch, C.M. Mayer, and R.S. Rhyne. 2005. Benthic macroinvertebrate communities in southwestern Lake Ontario following invasion of *Dreissena* and *Echinogammarus*: 1983 to 2000. Journal of the North American Benthological Society 24:148–167.

Hebert, P.D., B.W. Muncaster, and G.L. Mackie. 1989. Ecological and genetic studies on *Dreissena polymorpha* (Pallas): a new mollusc in the Great Lakes. Canadian Journal of Fisheries and Aquatic Science 46:1589–1591.

Hecky, R. E., and R. H. Hesslein. 1995. Contributions of benthic algae to lake food webs as revealed by stable isotope analysis. Journal of the North American Benthological Society 14:631–653.

Hecky, R.E., R.E.H. Smith, D.R. Barton, S.J. Guildford, W.D. Taylor, M.N.Charlton, and T. Howell. 2004. The nearshore phosphorus shunt: a consequence of ecosystem engineering by dreissenids in the Laurentian Great Lakes. Canadian Journal of Fisheries and Aquatic Science 61:1285–1293.

Higgins, S.N., E.T. Howell, R.E. Hecky, S.J. Guildford, and R.E. Smith. 2005a. The wall of green: the status of *Cladophora glomerata* on the northern shores of Lake Erie's eastern basin, 1995–2002. Journal of Great Lakes Research 31:547–563.

Higgins, S.N., R.E. Hecky, and S.J. Guildford. 2005b. Modeling the growth, biomass, and tissue phosphorus concentration of *Cladophora glomerata* in eastern Lake Eire: model description and field-testing. Journal of Great Lakes Research 31:439– 455.

Higgins, S.N. R.E. Hecky, and S.J. Guildford. 2006. Environmental controls of *Cladophora* growth dynamics in eastern Lake Erie: Application of the *Cladophora* growth model (CGM). Journal of Great Lakes Research 32:629–644.

Higgins, S. N., S.Y. Malkin, T.E. Howell, S.J. Guildford, L. Campbell, and R.E. Hecky. 2008. An ecological review of *Cladophora glomerata* in the Laurentian Great Lakes. Journal of Phycology 44:839–853.

Higgins, S. N., and M. J. Vander Zanden. 2010. What a difference a species makes: a meta–analysis of dreissenid mussel impacts on freshwater ecosystems. Ecological Monographs 80:179–196.

Hill, W.R., and R.G. Middleton. 2006. Changes in carbon stable isotope ratios during periphyton development. Limnology and Oceanography 51:2360–2369.

Hill, W.R., S.E. Fanta, and B.J. Roberts. 2008. ^{13}C dynamics in benthic algae: effects of light, phosphorus, and biomass development. Limnology and Oceanography 53:1217–1226.

Horgan, M.J., and E.L. Mills. 1997. Clearance rates and filtering activity of zebra mussel (*Dreissena polymorpha*): implications for freshwater lakes. Canadian Journal of Fisheries and Aquatic Science 54:249–255.

Howell, E.T., C.H. Marvin, R.W. Bilyea, P.B. Krauss and, K. Somers. 1996. Changes in environmental conditions during *Dreissena* colonization of a monitoring station in eastern Lake Erie. Journal of Great Lakes Research 22:744–756.

Hunt, H.L., and R.E. Scheibling. 2001. Patch dynamics of mussels on rocky shores: integrating process and understanding pattern. Ecology 82: 3213–3231.

Izvekova, E.I., and A.A. Lvova-Katchanova. 1972. Sedimentation of suspended matter by *Dreissena polymorpha* Pallas and its subsequent utilization by Chironomidae larvae. Polskie Archiwum Hydrobiologii 19:203–210.

Izvekova, E.I., and A.A. Lvova-Katchanova. 1972. Sedimentation of suspended matter by *Dreissena polymorpha* Pallas and its subsequent utilization by Chironomidae larvae. Polskie Archiwum Hydrobiologii 19:203–210.

James, W.F., J.W. Barko, and H.L. Eakin. 2001. Phosphorus recycling by zebra mussels in relation to density and food resource availability. Hydrobiologia 455:55–60.

Jimenez, A., M.D. Rennie, W.G. Sprules, and J. La Rose. 2010. Temporal changes in the benthic invertebrate community of Lake Simcoe, 1983–2008. Journal of Great Lakes Research. DOI:10.1016/j.jglr.2010.07.002.

Johannsson, O.E., R. Dermott, D.M. Graham, J.A. Dahl, E.S. Millard, D.D. Myles, and J. LeBlanc. 2000. Benthic and pelagic secondary production in Lake Erie after the invasion of *Dreissena* spp. with implications for fish production. Journal of Great Lakes Research 26:31–54.

Jones, L.A., and A. Ricciardi. 2005. Influence of physiochemical factors on the distribution and biomass of invasive mussels (*Dreissena polymorpha* and *Dreissena bugensis*) in the St. Lawrence River. Canadian Journal of Fisheries and Aquatic Science 62:1953–1962.

Karatayev, A.Y., L.E. Burlakova, and D.K. Padilla. 1997. The effects of *Dreissena polymorpha* (Pallas) invasion on aquatic communities in Eastern Europe. Journal of Shellfish Research 16:187–203.

Kilgour, B., C. Clarkin, W. Morton, and R. Baldwin. 2008. Influence of nutrients in water and sediments on the spatial distribution of benthos in Lake Simcoe. Journal of Great Lakes Research 34:365–376.

Klerks, P.L., P.C. Fraleigh, and J.E. Lawniczak. 1996. Effects of zebra mussels (*Dreissena polymorpha*) on seston levels and sediment deposition in western Lake Erie. Canadian Journal of Fisheries and Aquatic Science 53:2284–2291.

Lavrentyev, P.J., W.S. Gardner, J.F. Cavaletto and J.R. Beaver. 1995. Effects of the zebra mussel (*Dreissena polymorpha* Pallas) on protozoa and phytoplankton from Saginaw Bay, Lake Huron. Journal of Great Lakes Research 21:545–557.

Laws, E.A., B.N. Popp, R.R. Bidigare, M.C. Kennicutt, and S.A. Macko. 1995. Dependence of phytoplankton carbon isotopic composition on growth rate and $[CO_2]_{aq}$: theoretical considerations and experimental results. Geochimica et Cosmochimica Acta 59:1131–1138.

Leach, J.H. 1993. Impacts of the zebra mussel (*Dreissena polymorpha*) on water quality and fish spawning reefs in western Lake Erie. In: Nalepa, T. F. and Schloesser, D.W., (Eds.) Zebra mussels: biology, impact and control. Lewis Publishers, Ann Arbour, pp. 381–397.

Lederer, A., J. Massart, and J. Janssen. 2006. Impact of Round Gobies (*Neogobius melanostomus*) on dreissenids (*Dreissena polymorpha* and *Dreissena bugensis*) and the associated

macroinvertebrate community across an invasion front. Journal of Great Lakes Research 32:1–10.

Lewandowski, K., and T. Ozimek. 1997. Relationship of *Dreissena polymorpha* (Pall.) to various species of submerged macrophytes. Polskie Archiwum Hydrobiologii 44:457–466.

Limén, H., C.D.A. van Overdijk, and H.J. MacIsaac. 2005. Food partitioning between the amphipods *Echinogammarus ischnus*, *Gammarus fasciatus*, and *Hyalella azteca* as revealed by stable isotopes. Journal of Great Lakes Research 31:97–104.

Litchman, E., C.A. Klausmeier, and P. Bossard. Phytoplankton nutrient competition under dynamic light regimes. Limnology and Oceanography 49:1457–1462

Lorrain, A., N. Savoye, L. Chauvaud, Y. Paulet, N. Naulet. 2003. Decarbonation and preservation methos for analysis of organic C and N contents and stable isotope ratios of low-carbonated suspended particulate material. Analytica Chimica Acta 491:125–133.

Love, J., and J.F. Savino. 1993. Crayfish (*Orconectes virilis*) predation on Zebra mussels (*Dreissena polymorpha*). Journal of Freshwater Ecology 8:253–259.

Lowe, R.L., and R.W. Pillsbury. 1995. Shifts in benthic algal community structure and function following the appearance of zebra mussels (*Dreissena polymorpha*) in Saginaw Bay, Lake Huron. Journal of Great Lakes Research 21:558–566.

Lozano, S.J., J.V. Scharold, and T.F. Nalepa. 2001. Recent declines in benthic macroinvertebrate densities in Lake Ontario. Canadian Journal of Fisheries and Aquatic Science 58:518–529.

MacIsaac, H.J., 1993. Population structure of an introduced species (*Dreissena polymorpha*) along a wave-swept disturbance gradient. Oecologia 105:484–492.

MacLeod, N.A., and D.R. Barton. 1998. Effects of light intensity, water velocity, and species composition on carbon and nitrogen stable isotope ratios in periphyton. Canadian Journal of Fisheries and Aquatic Science 55:1919–1925.

Malkin, S.Y., S.J. Guildford, and R.E. Hecky. 2008. Modeling the growth of *Cladophora* in a Laurentian Great Lake in response to changes due to the exotic invader *Dreissena* and to lake warming. Limnology and Oceanography 53:1111–1124.

Malkin, S.Y., A. Dove, D. Depew, R.E. Smith, S.J. Guildford, and R.E. Hecky. 2010. Spatiotemporal patterns of water quality in Lake Ontario and their implications for nuisance growth of *Cladophora*. Journal of Great Lakes Research. DOI:10.1016/j.jglr.2010.06.007.

May, G.E., G.W. Gelembiuk, V.E. Panov, M.I. Orlova and C.E. Lee. 2006. Molecular ecology of zebra mussel invasions. Molecular Ecology 15:1021–1031.

Mayer, C.M., L.G. Rudstam, E.L. Mills, S.G. Cardiff, and C.A. Bloom. 2001. Zebra mussels (*Dreissena polymorpha*), habitat alteration, and yellow perch (*Perca flavescens*) foraging: system-wide effects and behavioural mechanisms. Canadian Journal of Fisheries and Aquatic Science 56:2459–2467.

Mayer, C.M., R.A. Keats, L.G. Rudstam, and E.L. Mills. 2002. Scale-dependant effects of zebra mussels on benthic invertebrates in a large eutrophic lake. Journal of the North American Benthological Society 21:616–633.

McGoldrick, D.J., D.R. Barton, M. Power, R.W. Scott, and B.J. Butler. 2008. Dynamics of bacteria-substrate stable isotope separation: dependence on substrate availability and implications for aquatic food web studies. Canadian Journal of Fisheries and Aquatic Science 65:1983–1990.

Mellina, E., and J.B. Rasmussen. 1994. Patterns in the distribution and abundance of zebra mussel (*Dreissena polymorpha*) in rivers and lakes in relation to substrate and other physicochemical factors. Canadian Journal of Fisheries and Aquatic Science 51:1024–1036.

Merritt, R. W. and K. W. Cummins. 1996. An Introduction to the Aquatic Insects of North America, 3rd edition. Kendall/Hunt Publishing Company, Dubuque, IA.

Mills, E.L., G. Rosenberg, A.P. Spidle, M. Ludyanskiy, Y. Pilgin, and B. May. 1996. A review of the biology and ecology of the quagga mussel (*Dreissena bugensis*), a second species of freshwater dreissenid introduced to North America. American Zoologist 36:271–286.

Mills E.L., J.R. Chrisman, B.S. Baldwin, R.W. Owens, R. O'Gorman, T. Howell, E.F. Roseman, and M.K. Raths. 1999. Changes in the dreissenid community in the lower Great Lakes with emphasis on southern Lake Ontario. Journal of Great Lakes Research 25:187–197.

Mills, E.L., J.M. Casselman, R. Dermott, J.D. Fitzsimons, G. Gal, K.T. Holeck, J.A Hoyle, Johannsson O.E., B.F. Lantry, J.C. Makarewicz, E.S. Millard, I.F. Munawar, M. Munawar, R. O'Gorman, R.W. Owens, L.G. Rudstam, T. Schaner, and T.J. Stewart. 2003. Lake Ontario: food web dynamics in a changing ecosystem (1970–2000). Canadian Journal of Fisheries and Aquatic Science 60:471–490.

Minagawa M., and Wada E. 1984. Stepwise enrichment in 15N along food chains: further evidence and the relation between $\delta^{15}N$ and animal age. Geochemica et Cosmochemica Acta 48:1135–1140.

Ministry of Environment 2007*a*. The determination of ammonia nitrogen, nitrite nitrogen, nitrite plus nitrate nitrogen and reactive ortho-phosphate in surface waters, drinking waters and ground

waters by colorimetry. Laboratory Services Branch, Quality Management Unit. Catalogue Code: # RNDNP-E3364, Version 1.2.

Ministry of Environment 2007*b*. The determination of total Kjeldahl nitrogen and total phosphorus in water and precipitation by colourimetry. Laboratory Services Branch, Quality Management Unit. Catalogue Code # RTNP-E3367, Version 1.2.

Mitchell, J.S., R.C. Bailey, and R.W. Knapton. 1996. Abundance of *Dreissena polymorpha* and *Dreissena bugensis* in a warmwater plume: effects of depth and temperature. Canadian Journal of Fisheries and Aquatic Science 53:1705–1712.

Mitchell, M.J., E.L. Mills, N. Idrisi, and R. Michener. 1996. Stable isotopes of nitrogen and carbon in an aquatic food web recently invaded by *Dreissena polymorpha* (Pallas). Canadian Journal of Fisheries and Aquatic Science 53:1445–1450.

Momot, W.T. 1995. Redefining the role of crayfish in aquatic ecosystems. Reviews in Fisheries Science 3:33–63.

Moore, J.W. 1978. Importance of algae in the diet of the diet of the oligochaetes *Lumbriculus variegatus* (Müller) and *Rhyacodrilus sodalist* (Eisen). Oecologia 35:357–363.

Mörtl, M., and K.O. Rothhaupt. 2003. Effects of adult *Dreissena polymorpha* on settling juveniles and associated macroinvertebrates. International Review of Hydrobiology 88:561–569.

Morton, B. 1969. Studies on the biology of *Dreissena polymorpha* Pall. II: Correlation of the rhythms of adductor activity, feeding, digestion and excretion. Journal of Molluscan studies 38:401–413.

Müller, P., D.H. Geary, and I. Magyar. 1999. The endemic molluscs of the Late Miocene Lake Pannon: their origin, evolution, and family-level taxonomy. Lethaia 32:47–60.

Naddafi, R., K. Pettersson, and P. Eklöv. 2007. The effect of seasonal variation in selective feeding by zebra mussels (*Dreissena polymorpha*) on phytoplankton community composition. Freshwater Biology 52:823–842.

Naddafi, R., K. Pettersson, and P. Eklöv. 2008. Effects of the zebra mussel, an exotic freshwater species, on seston stoichiometry. Limnology and Oceanography 53: 1973–1987.

Nalepa, T.F., D.L. Fanslow, M.B. Lansing, and G.A. Lang. 2003. Trends in the benthic macroinvertebrate community of Saginaw Bay, Lake Huron, 1987 to 1996: Responses to phosphorus abatement and the zebra mussel, *Dreissena polymorpha*. Journal of Great Lakes Research 29:14–33.

Nalepa, T.F., D.L. Fanslow, S.A. Pothoven, A.J. Foley, and G.A. Lang. 2007. Long-term trends in benthic macroinvertebrate populations in Lake Huron over the past four decades. Journal of Great Lakes Research 33:421–436.

Ozersky, T., S.Y. Malkin, D.R. Barton, and R.E. Hecky. 2009. Dreissenid phosphorus excretion can sustain *C. glomerata* growth along a portion of Lake Ontario shoreline. Journal of Great Lakes Research 35:321–328.

Patterson, M.W.R., J.J.H. Ciborowski, and D.R. Barton. 2005. The distribution and abundance of *Dreissena* species (Dreissenidae) in Lake Erie, 2002. Journal of Great Lakes Research 31:223–237.

Peterson, B.J., and B. Fry. 1987. Stable isotopes in ecosystem studies. Annual review of ecology and systematics 18:293–320.

Peterson, B.J., and K.L. Heck Jr. 2001. Positive interactions between suspension-feeding bivalves and seagrass- a facultative mutualism. Marine Ecology Progress Series 213:143–155.

Pillsbury, R.W., R.L. Lowe, Y. D. Pan, and J.L. Greenwood. 2002. Changes in the benthic algal community and nutrient limitation in Saginaw Bay, Lake Huron, during the invasion of the zebra mussel (*Dreissena polymorpha*). Journal of the North American Benthological Society 21:238–252.

Post, D.M. 2002. Using stable isotopes to estimate trophic position: models, methods, and assumptions. Ecology 83:703–718.

Pothoven, S. A., T. F. Nalepa, P. J. Schneeberger, and S. B. Brandt. 2001. Changes in diet and body condition of lake whitefish in southern Lake Michigan associated with changes in benthos. North American Journal of Fisheries Management 21:876–883.

Pothoven, S.A. and C.P. Madenjian. 2008. Changes in consumption by alewives and lake whitefish after dreissenid mussel invasions in Lakes Michigan and Huron. North American Journal of Fisheries Management 28:308–320.

Prins, T.C. and A.C. Smaal. 1994. The role of the blue mussel *Mytilus edulis* in the cycling of nutrients in the Oosterschelde estuary (The Netherlands). Hydrobiologia 282:413–29.

Rawson, D.S., 1930. The bottom fauna of Lake Simcoe and its role in the ecology of the lake. Publication No. 40 of the Ontario Fisheries Research Laboratory. University of Toronto Press, Toronto.

Reeders, H.H., A., bij de Vaate, and R. Noordhuis. 1993. Potential of the zebra mussel (*Dreissena polymorpha*) for water quality management. In Nalepa, T. F. and Schloesser, D.W., (Eds.) Zebra mussels: biology, impact and control. Lewis Publishers, Ann Arbour, pp. 439–451.

Regional Municipality of Halton. 2008. Oakville Southeast wastewater treatment plant - Annual report 2007. Halton Regional Laboratory, Environmental Services Division, Oakville, ON.

Reigman, R., W. Stolte, A.A.M. Noordeloos, and D. Slezak. 2000. Nutrient uptake and alkaline phophatase (EC 3:1:3:1) activity of *Emiliania huxleyi* (prymnesiophyceae) during growth under N and P limitation in continuous cultures. Journal of Phycology 36:87–96

Rennie, M. D., W. G. Sprules, and T. B. Johnson. 2009. Resource switching in fish following a major food web disruption. Oecologia 159:789–802.

Reusch, T.B.H., A.R.O. Chapman, and J.P. Gröger. 1994. Blue mussels *Mytilus edulis* do not interfere with eelgrass *Zostera marina* but fertilize shoot growth through biodeposition. Marine Ecology Progress Series 108:265–282.

Ricciardi, A., F.G. Whoriskey, and J.B. Rasmussen. 1997. The role of the zebra mussel (*Dreissena polymorpha*) in structuring macroinvertebrate communities on hard substrata. Canadian Journal of Fisheries and Aquatic Science 54:2596–2608.

Ricciardi, A. and F. G. Whoriskey. 2004. Exotic species replacement: shifting dominance of dreissenid mussels in the Soulanges Canal, upper St. Lawrence River, Canada. Journal of the North American Benthological Society 23:507–514.

Roditi, H.A., D.L. Strayer, and S.E.G. Findlay. 1997. Characteristics of zebra mussel (*Dreissena polymorpha*) biodeposits in a tidal freshwater estuary. Archiv für Hydrobiologie 140:207–219.

Ross, S. J. 2006. Molecular phylogeography and species discrimination of freshwater *Cladophora* (Cladophorales, Chlorophyta) in North America. M.Sc. Thesis, University of Waterloo, Waterloo, Ontario.

Roth, B.M., C.L. Hein, and M.J. Vander Zanden. 2006. Using bioenergetics and stable isotopes to assess the trophic role of rusty crayfish (*Orconectes rusticus*) in lake littoral zones. Canadian Journal of Fisheries and Aquatic Science 63:335–344.

Sousa, R., J.L. Gutiérrez, and D.C. Aldridge. 2009. Non-indigenous invasive bivalves as ecosystem engineers. Biological Invasions 11:2367–2385.

Sousa, W.P., 1985. Disturbance and patch dynamics on rocky intertidal shores, in: Pickett, S.T.A., White, P.S. (Eds.), The ecology of disturbance and patch dynamics. Academic press, Orlando, pp. 101–124.

Sprung, M. 1993. The other life: an account of present knowledge of the larval phase of *Dreissena polymorpha*. In Nalepa, T. F. and Schloesser, D.W., (Eds.) Zebra mussels: biology, impact and control. Lewis Publishers, Ann Arbour, pp. 39–53.

Sprung, M., and U. Rose. 1988. Influence of food size and food quantity on the feeding of the mussel *Dreissena polymorpha*. Oecologia 77:526–532.

Stantec Consulting Ltd., 2007. Aquatic macrophyte survey of Cook's Bay, Lake Simcoe, August 2006. Stantec Consulting Ltd., Ottawa, File number: 160940049.

Stewart, T.W., and J.M. Haynes. 1994. Benthic macroinvertebrate communities of southwestern Lake Ontario following invasion of *Dreissena*. Journal of Great Lakes Research 20:479–493.

Stewart, T.W., and J.M. Haynes. 1994. Benthic macroinvertebrate communities of southwestern Lake Ontario following invasion of *Dreissena*. Journal of Great Lakes Research 20:479–493.

Stewart, T.W., J.G. Miner, and R.L. Lowe. 1998a. Quantifying mechanisms for zebra mussel effects on benthic macroinvertebrates: organic matter production and shell-generated habitat. Journal of the North American Benthological Society 17:81–94.

Stewart, T.W., J.G. Miner, and R.L. Lowe. 1998b. An experimental analysis of crayfish (*Orconectes rusticus*) effects on a *Dreissena*-dominated benthic macroinvertebrate community in western Lake Erie. Canadian Journal of Fisheries and Aquatic Science 55:1043–1050.

Stoeckmann, A. 2003. Physiological energetics of Lake Erie dreissenid mussels: a basis for the displacement of *Dreissena polymorpha* by *Dreissena bugensis*. Canadian Journal of Fisheries and Aquatic Science 60:126–134.

Stokstad, E. 2007. Feared quagga mussel turns up in western United States. Science 315:453.

Szabo, R. 2004. The benthic food web on nearshore hard substrates at Peacock Point, eastern Lake Erie. MSc thesis. University of Waterloo. 86 p.

Thayer, S.A., R.C. Haas, R.D. Hunter, and R.H. Kushler. 1997. Zebra mussel (*Dreissena polymorpha*) effects on sediment, other zoobenthos and the diet and growth of adult yellow perch (*Perca flavescens*) in pond enclosures. Canadian Journal of Fisheries and Aquatic Science 54:1903–1915.

Trudeau, V., and J.B. Rasmussen. 2003. The effect of water velocity on stable carbon and nitrogen signatures of periphyton. Limnology and Oceanography 48:2194-2199.

Vander Zanden, M. J., J. M. Casselman, and J. B. Rasmussen. 1999. Stable isotope evidence for the food web consequences of species invasions in lakes. Nature 401: 464–467.

Vander Zanden, M.J., and J.B. Rasmussen. 2001. Variation in $\delta^{15}N$ and $\delta^{13}C$ trophic fractionation: implications for aquatic food web studies. Limnology and Oceanography 46:2061–2066.

Vanderploeg, H.A., T.F.Nalepa, D.J. Jude, E.L. Mills, K.T. Holeck, J.R. Liebig, I.A. Grigorovich, and H. Ojaveer. 2002. Dispersal and emerging ecological impacts of Ponto-Caspian species in the Laurentian Great Lakes. Canadian Journal of Fisheries and Aquatic Science 59:1209–1228.

Virden, W.T., J.S. Warren, T.L. Holcombe, and D.F. Reid. 2000. Bathymetry of Lake Ontario CD-ROM, vol. G2, version 1, Data Announcement 2000-MGG-01. National Geophysical Data Center.

Ward, J.M., and A. Ricciardi 2007. Impacts of *Dreissena* invasions on benthic macroinvertebrate communities: a meta-analysis. Diversity and Distributions 13:155–165.

Westerbom, M., and S. Jattu. 2006. Effects of wave exposure on the sublittoral distribution of blue mussels *Mytilus edulis* in a heterogeneous archipelago. Marine Ecology Progress Series 306:191–200.

Wetzel, R.G., 2001. Limnology, 3rd ed. Elsevier Academic Press, San Diego.

Whitledge, G.W., and C.F. Rabnei. 1997. Energy sources and ecological role of crayfish in an Ozark stream: insights from stable isotopes and gut analysis. Canadian Journal of Fisheries and Aquatic Science 54:2555–2563.

Wilson, K.A., E.T. Howell, and D.A. Jackson. 2006. Replacement of zebra mussels by quagga mussels in the Canadian nearshore of Lake Ontario: the importance of substrate, round goby abundance, and upwelling frequency. Journal of Great Lakes Research 32:11–28.

Winter, J.G., J.D. Young, A. Landre, E. Stainsby, and H. Jarjanazi. In press. Changes in phytoplankton community composition of Lake Simcoe from 1980 to 2007 and relationships with multiple stressors. Journal of Great Lakes Research

Young, J.D., A.L. Landre, J.G. Winter, H. Jarjanazi, and J. Kingston. 2010. Lake Simcoe water quality update. Ontario Ministry of the Environment Report. Available at: http://www.ene.gov.on.ca/en/water/lakesimcoe/index.php

Zaiko A., D. Daunys, and S. Olenin. 2009. Habitat engineering by the invasive zebra mussel *Dreissena polymorpha* (Pallas) in a boreal coastal lagoon: impact on biodiversity. Helgoland Marine Research 63:85–94.

Zhu, B., D.G. Fitzgerald, C.M. Mayer, L.G. Rudstam, and E.L. Mills. 2006. Alteriatons of ecosystem function by zebra mussels in Oneida Lake: Impacts on submerged macrophytes. Ecosystems 9:1017–1028.

Zhu, B., C.M. Mayer, S.A. Heckathorn, and L.G. Rudstam. 2007. Can dreissenid attachment and biodeposition affect submerged macrophyte growth? Journal of Aquatic Plant Management 45:71–76.