Invasion dynamics of a nonindigenous zooplankton species, *Eubosmina coregoni*

(Cladocera, Bosminidae), in Central Canada.

By

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A Thesis submitted to the Faculty of Graduate Studies of the

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Abstract

Aquatic ecosystems around the world are threatened by invasions of non-indigenous species (NIS). This study examines the invasion dynamics of a European cladoceran, *Eubosmina coregoni*, into lakes in Central Canada. Well-preserved cladoceran remains in sediment cores from Lake of the Woods, Ontario, and Lake Winnipeg, Manitoba, provide a historical account of *E. coregoni* in these water bodies confirming this species is a recent invader. Lead-210 dating of the sediment cores indicates *E. coregoni* has been present in these water bodies since the late 1980s or early 1990s. Top/bottom sediments from Lake of the Woods show this species is most abundant in the northwest and eastern regions of the lake. Additionally, extant zooplankton samples from Lake Winnipeg reveal that *E. coregoni* is mostly restricted to the North Basin. Results from this study provide a basis for future investigations of the invasion of *E. coregoni* and other NIS into these water bodies.

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Chapter 1: Thesis Introduction

A Global Issue

Biological invasions of nonindigenous species (NIS) are not novel phenomena. Species range changes are a natural occurrence important in structuring communities (Lodge 1993, Davis and Thompson 2000, Mack et al. 2000). Aside from the natural background rate at which invasions occur, human activities are transporting species around the world at an accelerated rate (Lodge 1993, Lodge and Shrader-Frechette 2003). The extensive use of water bodies for aesthetic, recreation, and transportation purposes makes aquatic ecosystems particularly vulnerable to invasions (Lodge et al. 1998). Consequently, NIS have been introduced into aquatic ecosystems worldwide (Hall and Mills 2000) and provide one of the greatest threats to the integrity of lakes and rivers in Canada (Schindler 2001).

In general, a species is considered 'invasive' when it colonizes and persists in a new ecosystem (Mooney and Drake 1989). The terminology associated with the field of invasion ecology is inconsistent, however, and somewhat subjective (Davis and Thompson 2000, Colautti and MacIsaac 2004). For example, terms such as 'nonindigenous' may be misleading given that even native species likely originated in other locations (Lodge and Shrader-Frechette 2003). In an attempt to provide commonality to the field of invasion ecology, Davis and Thompson (2000) proposed a classification scheme for colonizers based on ecological and geographical concepts. This scheme was developed by focusing on characteristics of the colonization such as: whether the colonizer's dispersal distance is short or long, whether the colonizer is novel or common to the region, and whether the colonizer has a large or small impact on the invaded ecosystem (Davis and Thompson 2000). On the other hand, Colautti and

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MacIsaac (2004) argue that the aforementioned model does not recognize the differences between the colonization of NIS and the local spread of native colonizers. Therefore, based on previous invasion models, Colautti and MacIsaac (2004) proposed 'stage-based' terminology in an attempt to understand the invasion process more objectively. This proposed terminology recognizes that there are a number of stages NIS must transition through in order for a successful invasion to occur and that each stage acts as a 'filter' that may prevent transition to subsequent stages (Colautti and MacIsaac 2004).

Invasions of NIS are so widespread that they now contribute significantly to global environmental change (Vitousek et al. 1997). Other aspects of global change (e.g. climate change, change in atmospheric composition, increasing nitrogen deposition, and changing patterns of land use) will intensify the impacts of invasions (Dukes and Mooney 1999, Schindler 2001). Specifically, NIS may be more adaptable to the changing environmental conditions than native species which may, in turn, lead to further reductions in global diversity (Lodge 1993, Dukes and Mooney 1999). As a result, managing and controlling NIS will continue to be a serious challenge faced by biologists (Allendorf and Lundquist 2003).

Ecosystem Effects

Some NIS spread quickly and their impacts on the invaded ecosystem are large enough to be noticeable, whereas the effects of other species are unknown (Lodge and Shrader-Frechette 2003). In addition, some NIS can have both direct and indirect effects on an ecosystem, but the impacts of these species are poorly understood and remain speculative (Hall and Mills 2000). NIS may also extirpate native species by using up

resources (e.g. space or food), thereby disrupting the entire ecosystem (Mills et al. 1994, Lodge et al. 1998, Mack et al. 2000) and can destroy habitat or prey upon native species (Mack et al. 2000). Ultimately, the invasion of a NIS into a new location may alter the native community and potentially disrupt the entire ecosystem (Mack et al. 2000). As a result, ecosystems around the world have been impacted by NIS (Lodge et al. 1998) and NIS have even been suggested to contribute substantially to extinctions (Vitousek et al. 1997).

In aquatic ecosystems, an entire water body may quickly be subject to any major impacts that a NIS exerts upon the ecosystem (Lodge et al. 1998, Hall and Mills 2000). For example, the introduction of species that occupy lower trophic levels may create repercussions for higher trophic levels in a lake (Hall and Mills 2000). NIS have contributed significantly to biological artificiality within the Laurentian Great Lakes as almost 10% of established NIS in these ecosystems have had serious impacts on all niches found within these lakes (Mills et al. 1994). As these NIS continue to spread beyond the Laurentian Great Lakes, their effects will be observed in inland lakes and rivers in Central Canada.

Aside from ecosystem effects, NIS also have impacts on food supplies, human health, and the economy (Hall and Mills 2000). Biotic invasions impact the economy in two ways: the loss in potential economic output (i.e. crops, fisheries, forestry) and the direct cost of combating invasions (Mack et al. 2000). It is important to recognize, however, that not all NIS are harmful nor do they always affect ecosystems socially and economically (Mills et al. 1994).

Characteristics of Invasion

The successful invasion of a NIS requires that the NIS survives the initial dispersal stage, becomes established in a new habitat, and spreads to nearby habitats (Kolar and Lodge 2001). Several invader characteristics have been suggested to contribute to a successful invasion. First of all, due to the fact that all stages of invasion are based on the initial dispersal stage, potential invaders must possess effective dispersal mechanisms (Puth and Post 2005). In addition, propagule pressure, the number of individuals introduced and the number of release events, is a determining factor for successful establishment (Allendorf and Lundquist 2003). For example, the release of a large number of individuals may enable NIS to overcome environmental or behavioural limitations associated with small population sizes that may have otherwise resulted in an unsuccessful invasion (Lockwood et al. 2005). As well, a large inoculation increases the amount of genetic variation in the introduced population, thereby improving the chances that the population will be able to adapt in the new location (Lockwood et al. 2005).

Similarly, if a potential invader can tolerate a broad range of environmental conditions, has the capacity for rapid reproduction, and has a high reproductive potential (*r*-selected traits), it will have a greater chance of becoming established in a new location (Locke et al. 1993, Lodge 1993, Mills et al. 1994). There are many exceptions, however, to these characteristics and the evidence for such traits in successful NIS lacks statistical significance (Lodge 1993). Numerous combinations of invader characteristics unique to a specific situation most likely result in the persistence of an invader in a new habitat (Mack et al. 2000). Nevertheless, by compiling a broad list of traits that invaders share, it

may be possible to predict the outcome of an invasion or identify future invaders (Mack et al. 2000).

Characteristics of the invaded habitat are as important to the success of an invasion as the characteristics of the NIS itself (Lodge 1993). Mack et al. (2000) suggest that an invader may persist in a new ecosystem because the new location lacks competitors, grazers, predators, or parasites, and not because the invader possesses the right combination of characteristics. General characteristics of habitats that can make them prone to invasions include: climatic similarity with the native habitat of the NIS, disturbance to the ecosystem or early stages of succession, low diversity of native species, and absence of predators (Mooney and Drake 1989, Lodge 1993). The enemy release hypothesis (ERH), for example, states that NIS should experience a decrease in natural enemies when they are introduced into a new location, resulting in an increase in distribution and abundance (Keane and Crawley 2002). Predictions of this hypothesis are that specialist enemies of NIS will be absent in areas where the NIS has been introduced and that generalist enemies will have a greater impact on native competitors than on the invasive NIS (Keane and Crawley 2002). Colautti et al. (2004), however, caution against the acceptance of the ERH without more critical examination. They argue that all NIS lose some of their natural enemies during the initial stages of invasion and that there are many other hypotheses aside from ERH that can explain the abundance and/or impact of a given invader (Colautti et al. 2004). These characteristics suggested for the invaded community, like those suggested for the invaders themselves, also suffer from exceptions and lack statistical testing (Lodge 1993). Therefore, studies concerning the invasion of

NIS or the invasibility of a system should include an investigation of the characteristics of both the invader and the invaded community (Lodge 1993, Moyle and Light 1996).

Biotic Resistance

Biotic resistance, first proposed by Elton (1958), suggests that speciose communities are better able to resist invaders than communities with fewer species. This biotic resistance hinders the transition of propagules from the introduction stage of invasion to the establishment stage (Colautti and MacIsaac 2004). As community interactions increase with a greater number of species, an 'activation barrier' is created that repels potential invaders (Case 1991). Biotic resistance suggests that species-rich communities are less prone to invasion because the likelihood that an invader belongs to a new species or genus decreases as local diversity increases (Shurin 2000). Also, the number of potential interspecific interactions increases with species richness (Shurin 2000). Therefore, community-level rather than invader-level properties determine the differences in invasion success (Case 1990, 1991, Lodge 1993).

One major argument against this model is that most studies supporting biotic resistance are based on island systems where species arrivals are rare and generally in low numbers (Hewitt and Huxel 2002). Thus, this model cannot be generalized to mainland systems in which species arrive in greater frequencies and densities (Hewitt and Huxel 2002). Therefore, Hewitt and Huxel (2002) argue that successful species invasions do occur in species-rich communities, but that the rate of successful invasion decreases with increasing community size. Another argument against biotic resistance is that species richness in a particular community should be an indicator of conditions that

would also be favourable to invading NIS unless the invading species differ appreciably from native species (Levine and D'Antonio 1999). As a result, biotic resistance may be less important than other factors that influence invasions into these systems (i.e. predation, competition, and food availability) (Moyle and Light 1996, Levine and D'Antonio 1999).

Invasional Meltdown

Most invasion studies focus on the effects of introduced species on native species rather than on interactions among introduced species. The invasional meltdown model, or facilitated interaction, suggests that NIS facilitate the establishment of other NIS, instead of interfering with one another (Simberloff and Von Holle 1999). Once established, some invaders alter habitat conditions in favour of other invaders, thereby creating a positive feedback system that accelerates the accumulation of NIS (Simberloff and Von Holle 1999, Ricciardi 2001). Therefore, the invasion of NIS is enhanced by the presence of other NIS rather than being hindered by the composition of the native community as suggested by the biotic resistance model.

The invasional meltdown model may be better than the biotic resistance model in explaining the invasion history of the Laurentian Great Lakes as invasions have increased into these lakes over the last few centuries (Ricciardi 2001). Further, the success of some Ponto-Caspian invaders in the Laurentian Great Lakes appears to have been enhanced by previous invasions (Ricciardi and MacIsaac 2000). Because invasional meltdown may increase local diversity through the accumulation of introduced species, the continual

replacement of endemic species could reduce native diversity and accelerate the homogenization of biota observed in ecosystems worldwide (Ricciardi 2001).

Mechanisms of Invasion in Freshwater Ecosystems

The introduction of NIS can take place via both deliberate and accidental releases of individuals into new locations. Most invasive vertebrates such as fish, mammals, and birds have been deliberately introduced, whereas the majority of microorganism introductions have been accidental (Mack et al. 2000). A major vector of deliberate release is fish stocking (Hall and Mills 2000), and species such as common carp (*Cyprinus carpio*) and Pacific salmon (*Oncorhynchus* sp.) have been deliberately introduced in a variety of different regions (Mills et al. 1993). Accidental introductions, on the other hand, can occur when species imported for the aquaria trade are discarded into the environment, when unused bait by fishermen is released, and when fish are transported from one water body to another in fishing vessels (Carlton 1985, Mills et al. 1993, Hall and Mills 2000). Invaders may also enter a new location due to disturbances caused by the construction of railroads, highways, and canals an entry mechanism used by some of the invaders of the Laurentian Great Lakes (Hall and Mills 2000). Similarly, the construction of reservoirs may increase the number of NIS invasions by providing 'stepping-stones' into new landscapes where standing water is less abundant (Havel et al. 2005).

By far the most important form of accidental dispersal is the transoceanic and interoceanic movement of ballast water (Schormann et al. 1990). Ships take up ballast water in bays, estuaries, and inland waters that may contain various life stages of both

plants and animals (Ricciardi and MacIsaac 2000) and then release this water into similar environments around the world (Carlton and Geller 1993). The Laurentian Great Lakes, for example, have received an increasing amount of biological pollution during the past century due to the discharge of ballast water (Ricciardi and MacIsaac 2000). As a result, on May 1, 1989, guidelines were set into place by the Canadian Coast Guard (CCG) requesting voluntary exchange of ballast water of ocean-going vessels in the open sea prior to arrival at the St. Lawrence Seaway (Locke et al. 1991). Theoretically, freshwater or coastal organisms should be killed by the high salinity levels in the open sea whereas mid-ocean organisms imported from higher salinities should be unable to withstand the lower salinities found in the Laurentian Great Lakes (Locke et al. 1991).

In spite of this, the risk of ballast water invasions still exists because there has not been full compliance with these guidelines (Locke et al. 1991, Schindler 2001). In addition, the majority of ships entering the Laurentian Great Lakes claim "no ballast on board" (NOBOB) (Duggan et al. 2005), however, residual ballast water and sediments at the bottom of ballast tanks may still contain resting stages or cysts of plant and animal species that are capable of being resuspended in ballast water (Kelly 1993, Locke et al. 1993, Hall and Mills 2000, Bailey et al. 2005, Duggan et al. 2005). The ability of NOBOB ships entering the Laurentian Great Lakes to house potential NIS has been assessed by Duggan et al. (2005). Further, models have been constructed to predict the number of NIS entering the Laurentian Great Lakes via NOBOB ships (Bailey et al. 2005) and to evaluate the risk of invasions of vessels with NOBOB (MacIsaac et al. 2002, Wonham et al. 2005).

Although ballast water is the primary invasion route into the Laurentian Great Lakes, overland dispersal of invading aquatic species and dispersal via interconnecting river systems are more likely routes for species invading lakes and rivers in central Canada. The likelihood of invasion by these dispersal mechanisms has been modeled for the zebra mussel, *Dreissena polymorpha*, (Buchan and Padilla 1999, Allen and Ramcharan 2001) and for Eurasian watermilfoil (*Myriophyllum spicatum*) (Buchan and Padilla 2000). Similarly, MacIsaac et al. (2004) assessed local and long-distance dispersal of the spiny waterflea, *Bythotrephes longinmanus*, to inland lakes in Ontario, Canada, and Muirhead and MacIsaac (2005) investigated human movement as a vector for transporting NIS from invaded lakes to non-invaded lakes.

Cladoceran Biology and Invasion Potential

Cladocera, or water fleas, are a major component of the micro-crustacean fauna in freshwater lakes and ponds, occupying both offshore (pelagic) and shallow (littoral) zones (Hann 1989). The reproductive strategies employed by cladocerans enhance the invasion potential of this group. With respect to the initial stages of invasion, diapausing eggs may be instrumental in the dispersal of individuals to new water bodies (Frey 1982, De Melo and Hebert 1994). Many cladoceran species produce diapausing eggs (ephippia) via sexual reproduction during periods of environmental stress (Hann and Hebert 1982, Hairston et al. 1995, Reid et al. 2000). Ephippia either float to the water surface or sink into the sediments where they may accumulate and remain viable for decades (Hairston et al. 1995), centuries, or millennia (Limburg and Weider 2002). Diapausing stages of many species are transported by humans, animals, or surface water (Frey 1982, Shurin and

Havel 2002) and can emerge when suitable environment conditions are present (Frey 1982, Hairston 1996).

Cladocerans and other aquatic invaders may utilize many natural and anthropogenic methods of dispersal into new water bodies, making it virtually impossible to determine which vector(s) are responsible for each individual invasion. For instance, riverine connections provide one pathway for the dispersal of aquatic organisms. Shurin and Havel (2002) suggest that water bodies downstream of source populations are more likely to be invaded than water bodies that are not connected by surface waters. A number of zooplankton species, including the exotic cladoceran *Daphnia lumholtzi* (Stoeckel et al. 1996), have the ability to survive in large river systems, thereby providing a source population to downstream water bodies (Van den Brink et al. 1994). Further, the downstream movement of water is an important dispersal mechanism for planktonic larval stages of organisms such as *Dreissena* sp. (Vanderploeg et al. 2002).

In addition to providing a direct invasion pathway for aquatic organisms, riverine connections may indirectly act as a corridor when fish ingest resting eggs and subsequently move to new water bodies downstream. Due to the fact that the hatching success of resting eggs is not reduced when they pass through the gut of fish, this vector may assist in the initial introduction of exotic species to inland lakes (Jarnagin et al. 2000). For example, Jarnagin et al. (2000) suggest that a major factor in the persistence of the invasive zooplankter *Bythotrephes cederstroemi* is the survival of its resting eggs after consumption by fish.

Along with fish, dispersal by waterfowl has long been suggested as a mechanism for transport of species from one water body to another (Proctor 1964). Studies have

shown that animal propagules (typically resting eggs) can be transported when attached to the plumage or feet of waterfowl, or after being ingested by waterfowl (Figuerola et al. 2005). Figuerola et al. (2005) demonstrated that waterfowl movements explained invertebrate genetic population structure better than geographical distances between populations for the cladoceran species *Daphnia ambigua* and *D. laevis*. Further, birds that consume fish that have ingested resting eggs have the potential to transport those eggs great distances during seasonal migrations (Jarnagin et al. 2000).

Aside from the natural mechanisms that may transport organisms into new habitats, anthropogenic introductions have become a major concern over the last few decades. Anthropogenic introductions to inland lakes may occur when natural habitats are disturbed or altered. For example, some of the exotic species in the Laurentian Great Lakes entered the region due to the construction of railroads and highways (Hall and Mills 2000). Also, Hairston et al. (1999) documented that the appearance of *D. exilis* in Onondaga Lake, New York, a range extension of 1000 km from its otherwise exclusive location in southwestern United States, was likely the result of the transport of resting eggs in mud attached to industrial equipment. Additionally, species may be anthropogenically transported between water bodies in fishing vessels and fishing gear (Carlton 1985, Mills et al. 1993, Hall and Mills 2000). For example, the cladoceran invader *Cercopagis pengoi* has shown rapid, discontinuous dispersal patterns in the Laurentian Great Lakes region likely due to ship transport between these lakes (Vanderploeg et al. 2002). Therefore, survival of living individuals in boats could allow for long distance dispersal of zooplankton from water body to water body. The dispersal

of *B. longimanus* to inland lakes from the Laurentian Great Lakes has been assessed based upon these human-mediated vectors (MacIsaac et al. 2004).

Once dispersed into a new location, cladocerans may be more likely than other invaders to become established as a result of having the ability to occupy the full range of heterogeneity in a water body (Shurin 2000). Under favourable environmental conditions, most cladoceran species produce several generations of eggs via parthenogenesis, a process by which unfertilized eggs undergo immediate embryogenesis (Hann and Hebert 1982). Cladocerans also mature very rapidly and spend a large proportion of their lifetime as reproductive adults (Allan and Goulden 1980). These characteristics enhance the ability of cladocerans to colonize rapidly an aquatic ecosystem making it possible for a single asexual zooplankter potentially to colonize an entire water body (Shurin 2000).

Tracking Cladoceran Invasions

Paleolimnology provides an opportunity to understand the history of aquatic ecosystems that cannot be provided by extant sampling. Historical accounts of environmental changes within and surrounding lakes (Kerfoot 1974, Brugam and Speziale 1983) and the evolution of natural communities (Goulden 1969) can be examined using paleolimnological techniques. In addition, the impacts of present-day stressors on lake ecosystems can be predicted by studying a community's history in the lake sediments (Hann 1989).

Among aquatic invertebrates, Cladocera are one of the most abundant groups represented as fossils in lake sediments (Hann 1989). Their chitinous exoskeletons are resistant to microbial action and thus preserve well (Frey 1988). The preservation of a

complete exoskeleton is rare, however, as most will disarticulate into their component parts: head-shield, carapace, postabdomen, claws, antennules, mandibles, and ephippia, while still allowing for the identification of these skeletal fragments to species (Frey 1960, Hann 1989). Due to the accumulation of exoskeletal components in the sediments, the composition of the microfossil population can be interpreted to reflect the living population as to species present and the relative abundances of those species at the time of deposition (Frey 1960).

Cladoceran microfossil assemblages are best used to reconstruct past lacustrine environments, to investigate the effects of human disturbances such as eutrophication and acidification, and to assess long-term population and community changes (Hann 1989). Changes in the cladoceran fossil record are commonly regarded as being indicators of eutrophication over time (Hofmann 1978, Frey 1988). For instance, Hofmann (1978) investigated fossil *Eubosmina* remains in sediment cores from the Großer Segeberger See, Schöhsee, and Großer Plöner See and demonstrated the successive colonization of the lakes by three different *Eubosmina* species, which corresponded to levels of lake productivity. Similarly, Hann et al. (1994) used fossil cladocerans to assess the effects of whole-lake eutrophication by analyzing pre- and post-manipulation fossils. Despite the wide use of cladoceran microfossils, however, it has been argued that paleolimnological studies alone do not provide enough information necessary for understanding how present-day communities are assembled (Hebert and Cristescu 2002).

Objectives

As the rate of biological invasions continues to increase worldwide, the importance of investigating these invasions also increases. Aquatic invaders of the

Laurentian Great Lakes have drawn much attention over the years due to the comprehensive and intensive study of these lakes, resulting in detailed records of both native and nonindigenous species over many years. Studies of invasive species in the Laurentian Great Lakes region have included reports of initial introductions (Mills et al. 1993, MacIsaac et al. 1999, Mills et al. 1999), ecological effects of established exotics (Vanderploeg et al. 2002), and have even progressed to modeling the predicted spread of harmful aquatic invaders such as the zebra mussel, *Dreissena polymorpha* (Johnson and Padilla 1996, Allen and Ramcharan 2001, Bossenbroek et al. 2001) and the spiny water flea, *Bythotrephes longimanus* (MacIsaac et al. 2004, Muirhead and MacIsaac 2005). Species with high invasion and impact potential continue to invade the Laurentian Great Lakes (Ricciardi and Rasmussen 1998) and many of these invaders will likely continue to spread to inland lakes and rivers.

This study focuses on the initial invasion dynamics of a nonindigenous zooplankton species, *Eubosmina coregoni*, into lakes in Central Canada. *Eubosmina coregoni*, a European species native to the Ponto-Caspian region, invaded the Laurentian Great Lakes in the mid-1960s likely via ballast water (Deevey and Deevey 1971, Lieder 1991). Although *E. coregoni* dispersed to inland water bodies near the Laurentian Great Lakes within a few years of arriving in North America (Deevey and Deevey 1971), this species has not been reported in the literature west of this region despite comprehensive zooplankton sampling across Canada (Patalas and Salki 1992, Patalas et al. 1994).

The main objective of this study is to use a paleolimnological approach to determine when *E. coregoni* first appeared in two water bodies in Central Canada: Lake of the Woods, Ontario, and Lake Winnipeg, Manitoba. This approach provides historical

information that would otherwise be unknown due to a lack of continuous and comprehensive zooplankton sampling in these water bodies. Water from Lake of the Woods flows into Lake Winnipeg via the Winnipeg River as these systems are part of the larger Lake Winnipeg watershed. Because *E. coregoni* is the first known zooplankter to invade each of these systems, studying the dynamics of this early invader is an essential component to learning more about the invasion routes into these water bodies and the vulnerability of these ecosystems to future NIS that have already permanently changed the food web dynamics of the Laurentian Great Lakes. Although the invasion routes of NIS into water bodies may never be known for certain, comparing the timing of first appearance of *E. coregoni* in the Laurentian Great Lakes, Lake of the Woods, and Lake Winnipeg may lead to an understanding of potential invasion trajectories, thereby aiding in the prevention of future invasions. In addition, studying the initial stages of invasion of *E. coregoni* will lay the groundwork for understanding how this species and other NIS become established in these systems and how they may spread to nearby habitats. This research will provide the basis for future questions that may address factors that help facilitate the invasion of *E. coregoni* and other NIS, conditions that favour their establishment and spread, and the effects of *E. coregoni* and other NIS in Lake of the Woods and Lake Winnipeg.

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Chapter 2:

Using microfossil remains in lake sediments to examine the invasion of

Eubosmina coregoni **in Lake of the Woods, Ontario**

Introduction

Nonindigenous species (NIS) pose a major threat to water bodies around the world. In order for a successful invasion to occur, a NIS must survive three stages of the invasion process: initial dispersal into a new habitat, establishment in the new habitat, and spread to nearby habitats (Kolar and Lodge 2001). Studies of initial dispersal, establishment, and spread have been carried out on NIS in the Laurentian Great Lakes as species have been invading this region for decades (see Mills et al. 1993). However, as NIS spread beyond the Laurentian Great Lakes, more attention must be drawn to the invasion of these species into inland lakes and rivers (MacIsaac et al. 2004). Models have been developed to predict the spread of harmful NIS to inland lakes for the zebra mussel, *Dreissena polymorpha*, (Buchan and Padilla 1999, Allen and Ramcharan 2001, Bossenbroek et al. 2001) and the spiny waterflea, *Bythotrephes longimanus* (MacIsaac et al. 2004). Due to the cost and time commitment of comprehensive sampling, however, many inland lakes prone to invasions are overlooked until species with detrimental effects become established. By focusing on the early stages of invasion for NIS entering new water bodies, more can be learned about the invasion routes into those water bodies, potentially preventing the dispersal and establishment of future invaders (Puth and Post 2005).

Despite extensive use for cottage and recreational purposes, Lake of the Woods has not been well studied in the past. Recently, research in this region has focused on water quality monitoring (e.g. Anderson et al. 2000, Ontario Ministry of the Environment 2004, Pla et al. 2005) and fish studies (Rusak and Mosindy 1997). Comprehensive, multi-year studies of its zooplankton community are lacking. *Eubosmina coregoni*, a

cladoceran species common in water bodies of its native Eurasia (Lieder 1991), is one of the first zooplankters known to invade Lake of the Woods (Alex Salki, personal communication). This species initially appeared in North America in the mid-1960s when it colonized the Laurentian Great Lakes (Deevey and Deevey 1971, Lieder 1991). Although its North American range was thought to be restricted to the Great Lakes region (De Melo and Hebert 1994), Mabee (1988) documented a southern range extension in reservoirs located in Missouri, and Salki (1996) incorrectly reported *E. coregoni* as *E. longispina* in Lake Winnipeg in 1994 (Alex Salki, personal communication). Therefore, like many other aquatic invaders, *E. coregoni* has made its way from the Laurentian Great Lakes to inland water bodies.

In this study, paleolimnological techniques were used to examine the initial stages of *E. coregoni*'s invasion into Lake of the Woods to provide a historical account of this species that cannot be provided by extant sampling. Cladocera, or waterfleas, are one of the most abundant groups of aquatic invertebrates that leave fossils in lake sediments (Hann 1989). Their chitinous exoskeletons preserve well because they are resistant to microbial action (Frey 1988) and, therefore, the microfossil population can be interpreted to reflect the living population at the time of deposition (Frey 1960). Paleolimnological studies concerning cladocerans have generally been used to reconstruct historical lake environments, to investigate the effects of human disturbances such as eutrophication and acidification, and to assess long-term population and community changes (Hann 1989). More recently, cladoceran microfossils have specifically been used to assess the population growth of a known invader (Hall and Yan 1997) and to examine a failed invasion (Hairston et al. 1999).

Short sediment cores from various sites throughout Lake of the Woods provided samples for a 'top/bottom approach' commonly used in diatom studies (e.g. Wilkinson et al. 1999, Paterson et al. 2004). This approach involves the analysis of present-day (top) and pre-settlement (bottom) sediment samples from a variety of different sites within or between lakes (see Paterson et al. 2004 for rationale). The objectives of this study were to use the top/bottom sediment samples to confirm that *E. coregoni* is, in fact, a recent invader, and to obtain a spatial overview of *E. coregoni* in Lake of the Woods as determined by the presence/absence of this species in the sediments. Further, long sediment cores (time cores) provided a temporal account of *E. coregoni* in the lake and were used to determine when *E. coregoni* first appeared in this water body and its historical abundances since its arrival. The results from this study will shed light on the initial stages of *E. coregoni*'s invasion into Lake of the Woods, thereby laying the groundwork for the future understanding of why this (and other) species become established in this water body.

Materials and Methods

Study Site

Lake of the Woods, a complex water body with many different bays and islands, is the second largest inland lake in the province of Ontario, Canada (Pla et al. 2005) (Fig. 2.1). Situated on the Canada - U.S. border between northwestern Ontario, southeastern Manitoba, and northern Minnesota, Lake of the Woods has an average depth of 8 m, with some bays in the northern region having a maximum depth of over 45 m (Yang and Teller 2005). The Rainy River is the largest river to enter the lake, accounting for almost

70% of the region's inflow (Pla et al. 2005). In the northern region of the lake, the Winnipeg River near Kenora, Ontario, is the major outflow that eventually makes its way to Hudson Bay via Lake Winnipeg and the Nelson River (Anderson et al. 2000). Pla et al. (2005) delineate three geographic zones in this water body: eastern, northwestern, and central sites that are on a south-north axis, i.e. from the Rainy River inflow in the south to the outflow near Kenora, Ontario. Within the central zone, the large southern region is shallower and more turbid than other regions of the lake (Rusak and Mosindy 1997). As a result of the large volume of water in this area, coupled with a large fetch, this region is subject to constant mixing and does not thermally stratify (Anderson et al. 2000). The deeper sites in the northwest and eastern regions, on the other hand, are typically well-stratified in late summer and are more likely to be affected by local factors because they are isolated from the main flow of water (Pla et al. 2005).

Sediment Cores

Short cores used to obtain top-bottom sediment samples were collected at twenty sampling locations from different regions throughout Lake of the Woods in September 2003 (Fig. 2.2). The top (0-1 cm) and the bottom (>25 cm) layers of each sediment core were analyzed to represent present and past (pre-settlement) cladoceran populations, respectively (Cumming et al. 1991). Details of sampling collection and locations are given in Pla et al. (2005). The sampling sites were selected to represent a gradient of total phosphorus concentrations and were chosen based on lake-bed characteristics and their suitability for coring (Pla et al. 2005). Sediment samples were obtained using a modified Glew gravity corer (Glew 1989) fitted with 90 cm Lucite core tubes with an internal core

diameter of 7.62 cm. Samples were stored on ice and transported to Queen's University, Kingston, Ontario, where they were stored at 4 degrees C until subsamples were shipped to the University of Manitoba, Winnipeg, Manitoba. Of the 20 original sampling sites, sediment samples could not be obtained from three sites (PP8, PP14, and PP20). PP1 was also excluded from the study due to lab error leaving a total of 16 sites for analysis.

In addition to the top/bottom sediment samples, four cores collected in 2002 by a team led by Bob Danell, Department of Fisheries and Oceans, Freshwater Institute, Winnipeg, Manitoba, were analyzed (Fig. 2.3). The 2002 cores were collected through ice using a KB gravity corer with an internal diameter of 10 cm. Cores were sliced on site and slices were stored in individual Whirl Packs™ on ice until transport to the Freshwater Institute, Winnipeg, Manitoba, where they were stored at 4 degrees C. Samples were processed for wet/dry weight and freeze-dried for dating and elemental analysis. Sediment chronologies were determined by Paul Wilkinson and Mike Stainton at the Freshwater Institute by analysis of ^{210}Pb. These chronologies are based on the Constant Rate of Supply (CRS) model (Appleby and Oldfield 1983). All sedimentation rates were corrected for sediment focusing and ^{210}Pb dates are supported by the measurement of ^{137}Cs peaks.

Sediment Analysis

Sediment material was prepared for analysis following standard methods outlined in Frey (1960). Subsamples of a known weight were taken from each sediment layer, heated gently for approximately 30 minutes on a magnetic stirring plate in 10% KOH, and sieved using a 53 µm mesh screen in order to concentrate the number of microfossil

remains. Subsamples were made up to a known volume (10-20 ml) and a few drops of formalin were added as a preservative (Hann 1989). Quantitative slides were prepared by transferring 100 µL aliquots to a microscope slide using glycerin jelly as the mounting medium. Identification and counting was completed at 10X magnification using a Nikon Optiphot compound microscope. Entire coverslips were enumerated for carapaces because they were the most abundant type of exoskeletal fragment (Hann 1989). Three different groups were enumerated: *E. coregoni*, *Bosmina* sp., and "other" cladocerans (typically chydorids) (Fig. 2.4). Remains were identified following Deevey and Deevey (1971), De Melo and Hebert (1994), and Lieder (1983), and by using extant reference samples from the Lake of the Woods region.

A minimum of 100 intact carapaces was counted for each sediment layer for most samples. This ultra-conservative approach of counting only intact carapaces was taken to ensure correct identification of remains, as opposed to also counting fragments of carapaces and other exoskeletal remains, which can lead to incorrect or biased identifications (Hann 1989). Top and bottom samples from PP9, PP10, PP11, PP18, and PP19, in addition to the bottom sample from PP4, did not satisfy the required minimum count. Further, preliminary analyses of LW1, LW2, and LW7 showed a lack of remains and these cores were excluded from analysis. The locations of sites with few remains were consistent between the top/bottom samples and the long cores. The top twelve sediment layers (corresponding to 6 cm) of the LW6 core were analyzed, in addition to every fourth layer until the bottommost layer for which ^{210}Pb dates were available.

Data Analysis

Data from top/bottom samples are presented in terms of relative abundances, while data from the LW6 time core are presented as accumulation rates (number of remains/cm^2/year). Because the distribution of cladoceran remains in subsamples is assumed to follow a Poisson distribution (Goulden 1969), a series of slides were prepared from the top of the LW6 core in order to test the sediment samples for excess variance, which violates the assumption of the Poisson distribution (Davis 1965). Thirty slides were prepared in total, giving three series of 10 replicate slides (Table 2-I). For each series, Chi-square analysis comparing the variance of the counts to the mean resulted in low Chi-square values (p > 0.25) indicating that there was no significant departure from a Poisson distribution (Elliott 1977). Assuming a Poisson distribution, the standard error of the total number of remains in a sediment sample equals the square root of the number of remains counted (Megard 1967). The 0.95 confidence level can then be determined using the following formula, where T is the estimated number of remains per unit of sediment (Goulden 1969):

$$T +/- 1.96\sqrt{T}$$

Results

Short Cores

E. coregoni was absent from all bottom sediments from the top/bottom samples and, therefore, was not present in pre-settlement times in Lake of the Woods. In the top sediments, *E. coregoni* was found mainly in the northwest and eastern regions of Lake of the Woods, but was also present at a few locations in the south (Fig. 2.5). *Bosmina* sp.

had the highest relative abundance in the northwest region, whereas "other" cladoceran species had a higher relative abundance in the southern region of the lake. Nevertheless, absolute abundance, i.e. the actual number of remains that were counted, was extremely low (<20) in the south and west regions of the lake at five sampling sites (PP9, PP10, PP11, PP18, PP19) and results from these regions should be interpreted with caution (see Appendix for actual counts). Consequently, in terms of both absolute and relative abundance, the northwestern region of Lake of the Woods had the highest abundance of *E. coregoni*. In addition, sites where *E. coregoni* was detected had a greater mean depth than sites where *E. coregoni* was absent at 26.6 m and 12.0 m, respectively (t-test, p = 0.01, α = 0.05).

Long Core

Cladoceran remains were abundant at all sediment layers analyzed from the LW6 (Clearwater Bay) core. Prior to sediments dated to 1980, cladoceran dominance shifted between *Bosmina* sp. and "other" cladocerans, however neither group was clearly dominant at any given time (Fig. 2.6). After sediments dated to 1987, *Bosmina* sp. was clearly the dominant group of cladoceran remains with accumulation rates twice as high as "other" cladocerans. *E. coregoni* first appeared in the Clearwater Bay core in sediments dated to 1991 and has remained in this region to the most recent sediments. In spite of the persistent presence of *E. coregoni* in Lake of the Woods since the early 1990s, accumulation rates for *E. coregoni* in the Clearwater Bay region are very low, with the highest accumulation rate occurring in sediments dated to 1999 (14 remains/cm^2/yr) (Fig. 2.6).

Discussion

Lake of the Woods is a very complex basin with a highly convoluted shoreline. Thus, the presence of cladoceran remains in higher numbers in the northwest and eastern regions of the lake may be due to the relative isolation of these regions from the main body of water. The morphometric characteristics/features in the northwest and eastern regions of the lake may provide ideal conditions for *E. coregoni* populations to thrive as *E. coregoni* was present at all of the sites in these regions. Similarly, the relative abundances of *Bosmina* sp. were higher at sites in the northwest and eastern regions than they were in the southern region. The occurrence of *E. coregoni* and *Bosmina* sp. in these regions may be explained by the fact that both are pelagic species favouring deeper water rather than shallow littoral areas. Hofmann (1996) studied German lakes of differing depths and found that *E. coregoni* was most abundant in lakes with a mean depth greater than 10 m. Although *E. coregoni* was also present in some lakes with a mean depth between 3.5-9 m, this species was almost completely absent in shallow lakes (1.3-2.3 m) (Hofmann 1996). The results from the present study indicate that the mean depth of sites where *E. coregoni* occurred was greater than the mean depth of sites where *E. coregoni* was absent. Similarly, analyses of diatom community composition from the same sampling sites used in this study indicate planktonic diatom taxa also dominated (except at site PP16, which was the shallowest site at 4.1 m) (Pla et al. 2005).

Along with depth, the distribution of *Bosmina sp.* and *E. coregoni* in Lake of the Woods may be related to the productivity of different regions in the lake (Frey 1988). Numerous studies have examined the relationship between increasing nutrient enrichment and shifts in the zooplankton community (see Hann 1989). Changes in bosminid

community composition have long been associated with changes in trophic status in European systems. While some studies suggest that the predominance of *B. longirostris* indicates eutrophic conditions (Boucherle and Zullig 1983, Szeroczynska 2002, Gasiorowski and Szeroszynska 2004), others suggest a shift to *B. coregoni coregoni* is connected with an increased eutrophic state (Hofmann 1978). Although paleolimnological studies of cladocerans have frequently been used to assess the trophic status of lakes, the failure of many of these studies to incorporate water chemistry and algal data suggests that results must be interpreted with caution. Further, the taxonomic confusion notoriously associated with bosminids (Goulden and Frey 1963, Lieder 1983) makes it almost impossible to ensure species (or even genus) identifications are consistent across all studies.

Nevertheless, the results obtained in this study do not suggest the appearance of *E. coregoni*, or even the predominance of *Bosmina sp.*, is indicative of more eutrophic conditions. Nutrient levels were lower at sites with the highest relative abundances of both *Bosmina* sp. and *E. coregoni* in the northwest and eastern regions of the lake than they were at sites in the southern region, where *Bosmina* sp. and *E. coregoni* were rare (see Pla et al. 2005). Further, a comparison of total phosphorus concentration [TP] in different regions of Lake of the Woods in 2002 and 2003 showed a large increase in [TP] in the southern region, but a slight decrease in the [TP] in the eastern and northwestern regions (Ontario Ministry of the Environment 2004). As mentioned above, these findings are likely due to the isolation of the northwest and eastern regions of Lake of the Woods from the inflow of nutrients from the Rainy River and the internal loading of nutrients due to constant mixing of the sediments in the southern region of the lake (Anderson et

al. 2000). Although the northern region of Lake of the Woods near Kenora, Ontario, may experience a high input of nutrients due to extensive cottage development in this area, any effects of these nutrients may be minimized by the proximity of this region to the Winnipeg River outflow.

In addition to [TP], chlorophyll a concentrations are often used to indicate the trophic status of water bodies. Unlike [TP], chlorophyll a data obtained by Pla et al. (2005) from the same sampling sites used in the present study did not show any clear patterns. Therefore, a relationship could not be inferred between the higher relative abundances of *E. coregoni* and *Bosmina* sp. in the northwest and eastern regions and an increase in algal productivity as indicated by chlorophyll a concentrations. In this case, it may be more important to consider the types of phytoplankton present in a given area rather than attempting to relate the presence of *E. coregoni* and *Bosmina* sp. to inferred algal biomass data. For instance, severe cyanobacterial (blue-green algae) blooms have been occurring in Lake of the Woods for decades (Pla et al. 2005) and the presence of *E. coregoni* may be linked with these blooms. More specifically, areas dominated by blue-green algal blooms could show an increase in small-bodied cladoceran species such as *Bosmina* sp. and *E. coregoni*. Filter-feeding capabilities of smaller species are less likely to be inhibited by large filamentous cyanobacteria because they have a narrower carapace gap than larger-bodied species (Vijverberg and Boersma 1997).

The lack of remains in the southern region of Lake of the Woods as indicated by the short cores and the long cores that were excluded from analysis may also be explained, in part, by the differences in morphometric parameters in this region. For instance, the higher water turbidity in the southern region may result in decreased

abundances of zooplankton due to the negative effects of suspended clay particles on cladocerans (Dejen et al. 2004). Cladocerans are the dominant herbivores in lake ecosystems and suspended clay particles may interfere with the ingestion of algal cells causing a decrease in filtering and assimilation rates (McCabe and O'Brien 1983) or may produce conditions of light limitation that hinders algal growth (Hart 1992). In addition, sites that show a lack of cladoceran remains correspond to the main flow of water from Rainy River through to the north of Lake of the Woods. As a result, cladoceran populations in this water body may be more likely to thrive in isolated regions where they are not subject to changing conditions due to flow-through of water (Brook and Woodward 1956).

Although it appears that cladocerans are less abundant in the southern region of Lake of the Woods, the ability of the microfossil assemblage in the sediments to reflect accurately the composition of the living population in the southern region of the lake must be taken into consideration. For instance, all cladocerans do not preserve equally well in the sediments and in some species, e.g. *Sida crystallina*, *Leptodora kindti*, and *Daphnia* spp., only fragments such as mandibles, antennal segments, and postabdominal claws are preserved (Frey 1960). If species that do not preserve as well as bosminids and chydorids were more abundant in the southern region of Lake of the Woods, their presence may not be accurately represented because only intact carapaces were counted in this study. Therefore, whether the higher relative abundances of *E. coregoni* and *Bosmina sp.* in the northwest and eastern regions are due to conditions that favour establishment or whether these results are an artifact of an overall lack of remains in the southern region can not be determined at this time.

A closer look at the invasion dynamics of *E. coregoni* in Clearwater Bay in the northern region of Lake of the Woods indicates that *E. coregoni* first appeared in this region in sediments dated to the early 1990s, approximately 25 years after it was first reported in Lake Michigan in 1966 (Wells 1970). Once cladocerans have entered a new water body, populations may increase rapidly due to parthenogenetic (asexual) reproduction. However, established populations may be small and/or isolated thereby remaining undetected (MacIsaac et al. 2001, Havel and Medley 2006). The occurrence of *E. coregoni* in small numbers in the first few years following its arrival may explain why comprehensive zooplankton sampling of Canadian lakes failed to detect this species in Lake of the Woods in the early 1990s (Patalas et al. 1994). Further, because the accumulation rates of *E. coregoni* remain low in comparison with *Bosmina* sp. and other cladocerans, whether there will be any impacts or shifts in the cladoceran community as a result of this invasion are as of yet unknown.

Similarly, the exact means by which *E. coregoni* invaded Lake of the Woods may never be determined. Both living cladocerans and their resting eggs may be transported to new water bodies, resulting in a number of potential invasion vectors. In the case of cladoceran invasions, it is possible for populations to become established even if only a single asexual individual invades a new water body (Shurin 2000). Riverine connections between water bodies are one possible route for invading aquatic species. Shurin and Havel (2002) suggest that water bodies downstream of source populations are more likely to be invaded than water bodies not connected by surface waters. Moreover, downstream movement is thought to be an important dispersal mechanism for *Cercopagis pengoi* and the planktonic larvae of *Dreissena* spp. (Vanderploeg et al. 2002). It is possible that

extant *E. coregoni* entered Lake of the Woods via the Rainy River, originally from the Laurentian Great Lakes, and eventually established in the northwest and eastern regions of the lake where conditions are more favourable. In addition, resting eggs may have been transported by fish (Jarnagin et al. 2000), recreational boaters (Shurin and Havel 2002), or by waterfowl (Proctor 1964, Figuerola et al. 2005). Due to the proximity of the northwest region of Lake of the Woods to the Trans-Canada Highway, it is likely that human activities also played a role in the invasion of *E. coregoni* into this area.

In the last twenty years, the Laurentian Great Lakes region has experienced a surge of invasions. During the mid to late 1980s the spiny waterflea (*Bythotrephes cederstroemi*) (Bur et al. 1986), zebra mussels (*Dreissena polymorpha*) (Hebert et al. 1989), and quagga mussels (*Dreissena bugensis*) (Mills et al. 1999) were introduced into the Laurentian Great Lakes. In addition, another zooplankton species, *Cercopagis pengoi* was first reported in Lake Ontario in 1998 (Makarewicz et al. 2001). These aquatic invaders all have detrimental effects on the water bodies they invade. Both *Dreissena* species occur in very large densities and are responsible for biofouling and impacting the planktonic community by filter-feeding particles out of the water column (Johnson and Padilla 1996). Similarly, *Bythotrephes* sp. and *Cercopagis* sp. affect different trophic levels of the food web by feeding on small zooplankton species (Yan et al. 2002). The spread of these species beyond the Great Lakes into inland lakes has been modeled for both *D. polymorpha* (Johnson and Padilla 1996) and *B. longimanus* (MacIsaac et al. 2004). Judging by the constant influx of invaders into the Laurentian Great Lakes, invasions of harmful species into Lake of the Woods are probable in the near future.

Lake of the Woods is a water body of international importance used extensively for recreational purposes and by cottage owners. Recently, it has been suggested that the water quality in the northern region of the lake is deteriorating (Pla et al. 2005), making it even more critical to learn more about this complex system. This study has determined that *E. coregoni* first appeared in the northern region of Lake of the Woods in the early 1990s. Since then, this species has been found at sites throughout the lake, with the highest abundances in the northwest and eastern regions. In addition, because Lake of the Woods is part of the Winnipeg-Nelson river system and, ultimately, the Lake Winnipeg watershed (Rusak and Mosindy 1997), studying the introduction of aquatic invaders into these areas is crucial.

Knowledge of the initial stages of a species' invasion provides a basis for understanding why certain NIS become established. Future research should focus on developing a comprehensive zooplankton sampling regime in Lake of the Woods. Multi-year zooplankton data, which can then be compared to other biological and water chemistry data, is invaluable in tracking invasions and other community changes. This information could provide more insight regarding the factors that favour the establishment of *E. coregoni* in certain regions of Lake of the Woods. Also, analyses of sediment material from the Winnipeg River, which connects Lake of the Woods and Lake Winnipeg, in addition to the Rainy River, could indicate if riverine connections are a major vector for *E. coregoni* and other species. Another vector, the transport of *E. coregoni* in the digestive tract of rainbow smelt (*Osmerus mordax*), may be responsible for introducing this species into water bodies west of the Laurentian Great Lakes. Like *E. coregoni*, rainbow smelt first appeared in Lake of the Woods in the early 1990s (Franzin

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et al. 1994). Therefore, future studies could investigate the co-invasion of rainbow smelt and *E. coregoni* using gut content analyses and by comparing the current distributions of these two species. As Lake of the Woods is just one water body in the very large Lake Winnipeg watershed, modeling the dispersal of *E. coregoni* into Central Canadian water bodies may aid in the prevention of future invasions into this region.

Table 2-I: Statistical variables for cladoceran carapace counts from surface sediments of the LW6 (Clearwater Bay) core from Lake of the Woods, Ontario, to test for variance equal to the mean ($\alpha = 0.05$).

Sample	No. of Slides	No. of Remains	Range	Mean	Variance	X^2	P
1A	10	166	12-24	16.6	16.93	9.18	>0.25
1B	10	135	10-18	13.5	8.5	5.67	>0.25
1C	10	130	9-20	13	14.2	9.85	>0.25
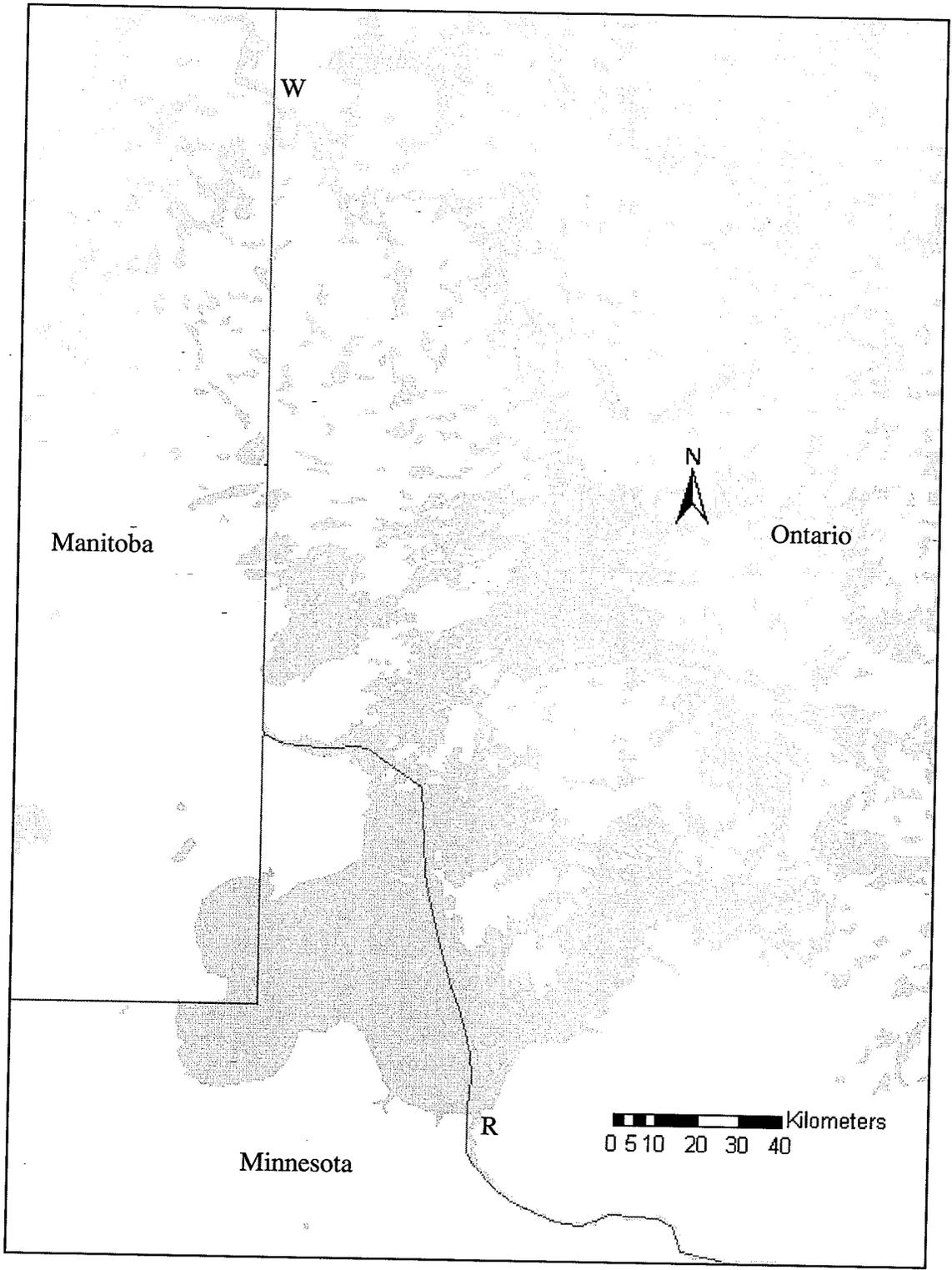
Figure 2.1. Map showing the geographic location of Lake of the Woods, Ontario, Canada.
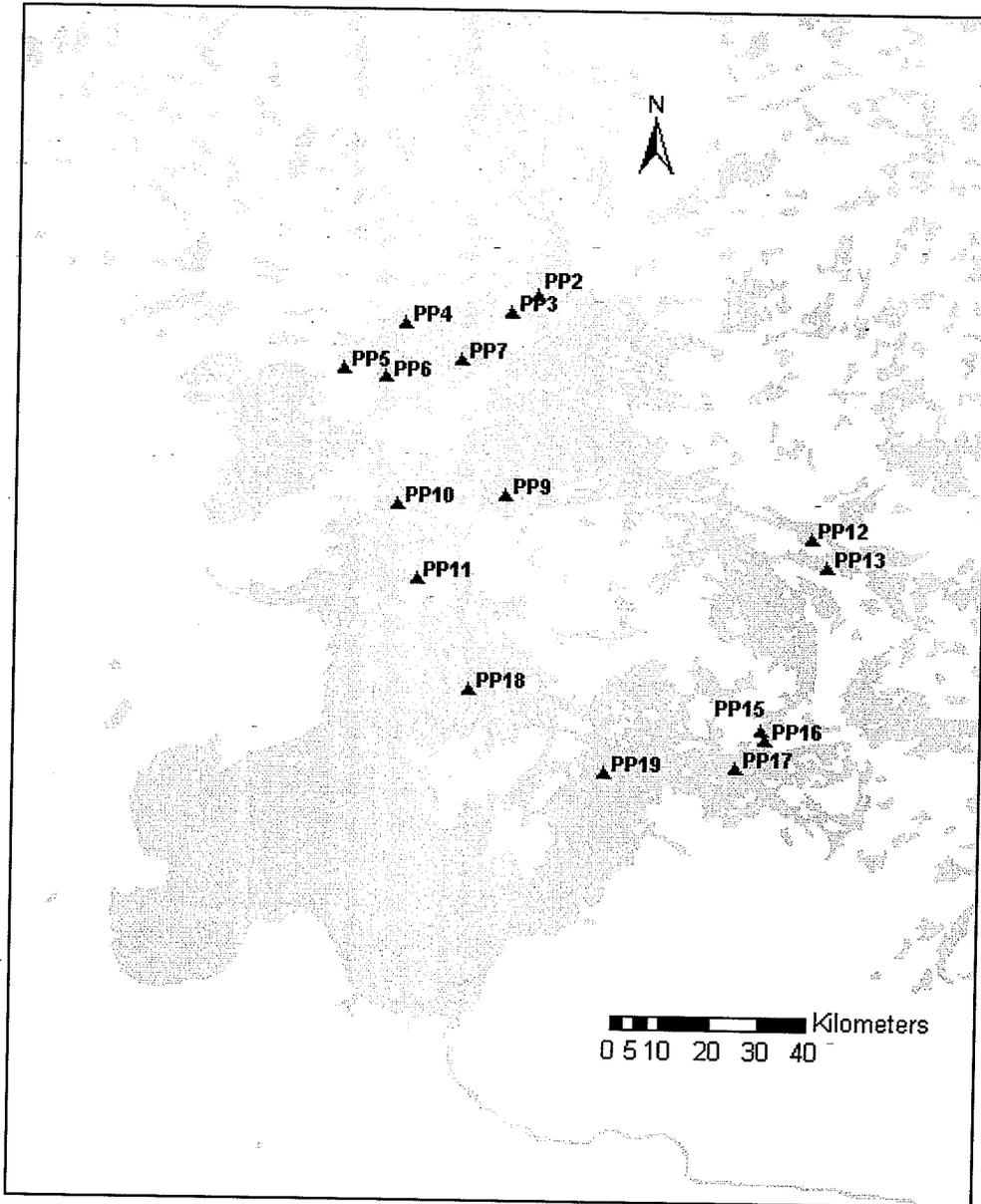
Figure 2.2. Sediment core locations used for top/bottom analysis collected in September 2003 in Lake of the Woods, Ontario, Canada.

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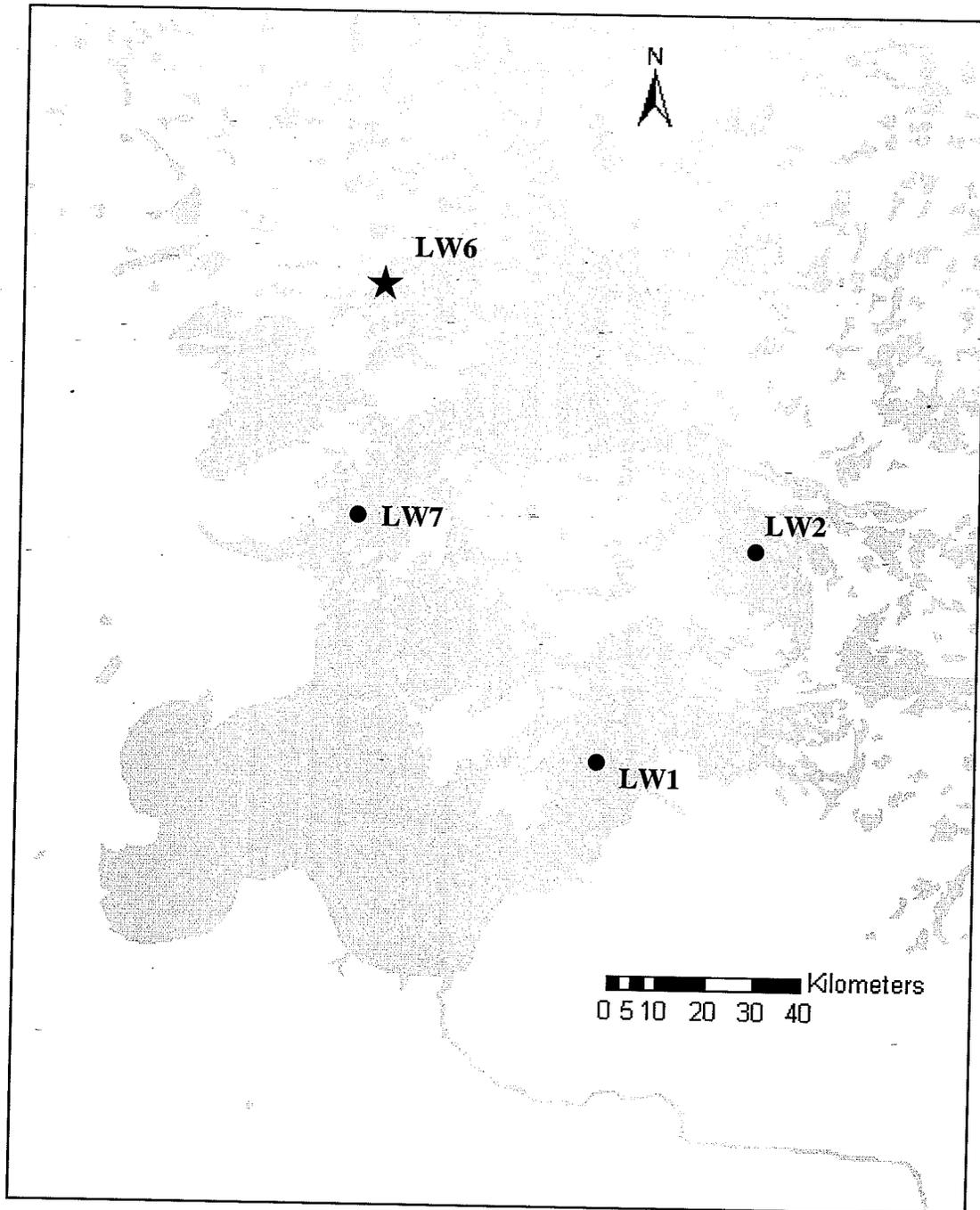
Figure 2.2. Locations of long cores (time cores) collected in 2002 in Lake of the Woods, Ontario, Canada. The Clearwater Bay core (LW6) analyzed in detail is highlighted with a star.
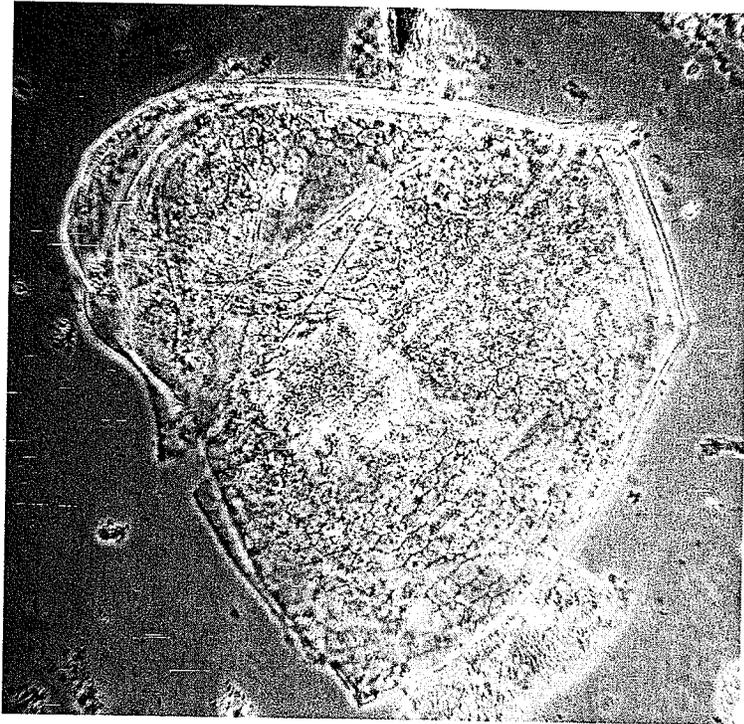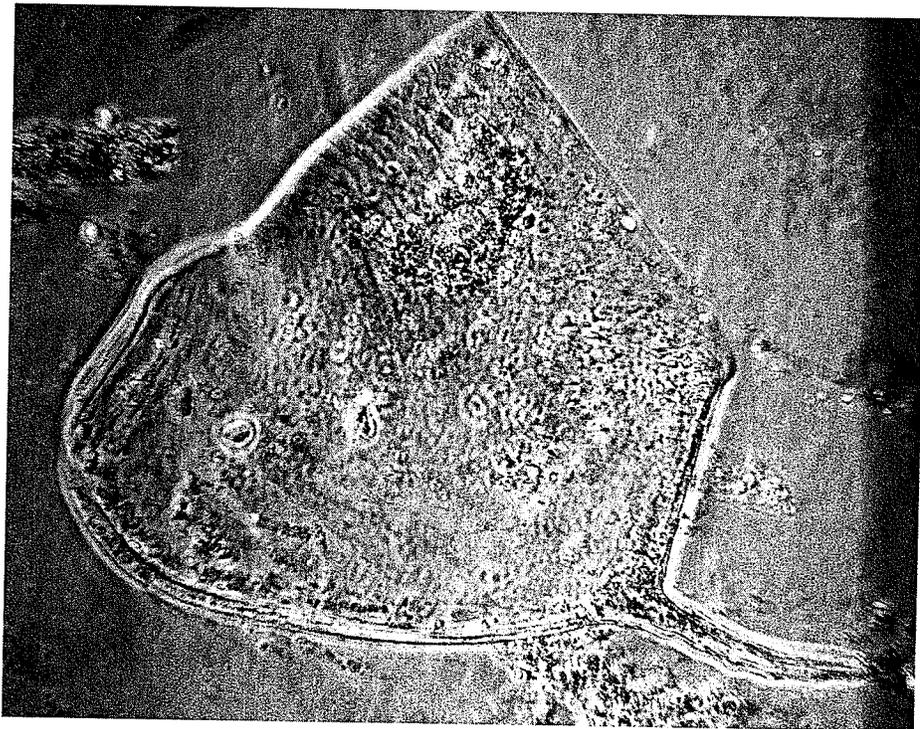
Figure 2.3. Photographs of intact *Eubosmina coregoni* (a) and *Bosmina longirostris* (b) carapaces in lateral view.
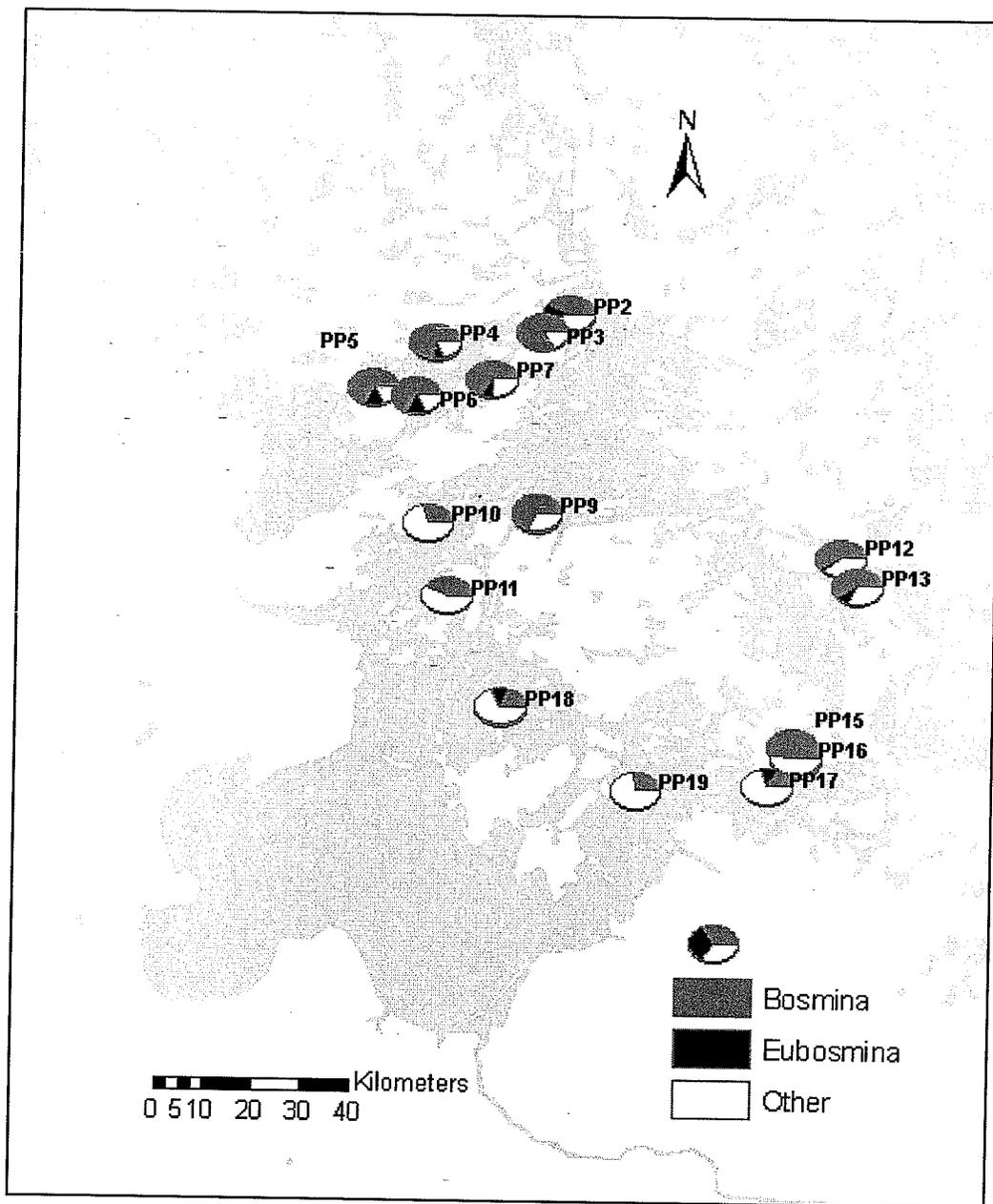
Figure 2.4. Relative abundances of *Bosmina* sp., *E. coregoni* and "other" cladocerans in the surface sediments collected in Clearwater Bay, Lake of the Woods, Ontario, Canada, in 2003.
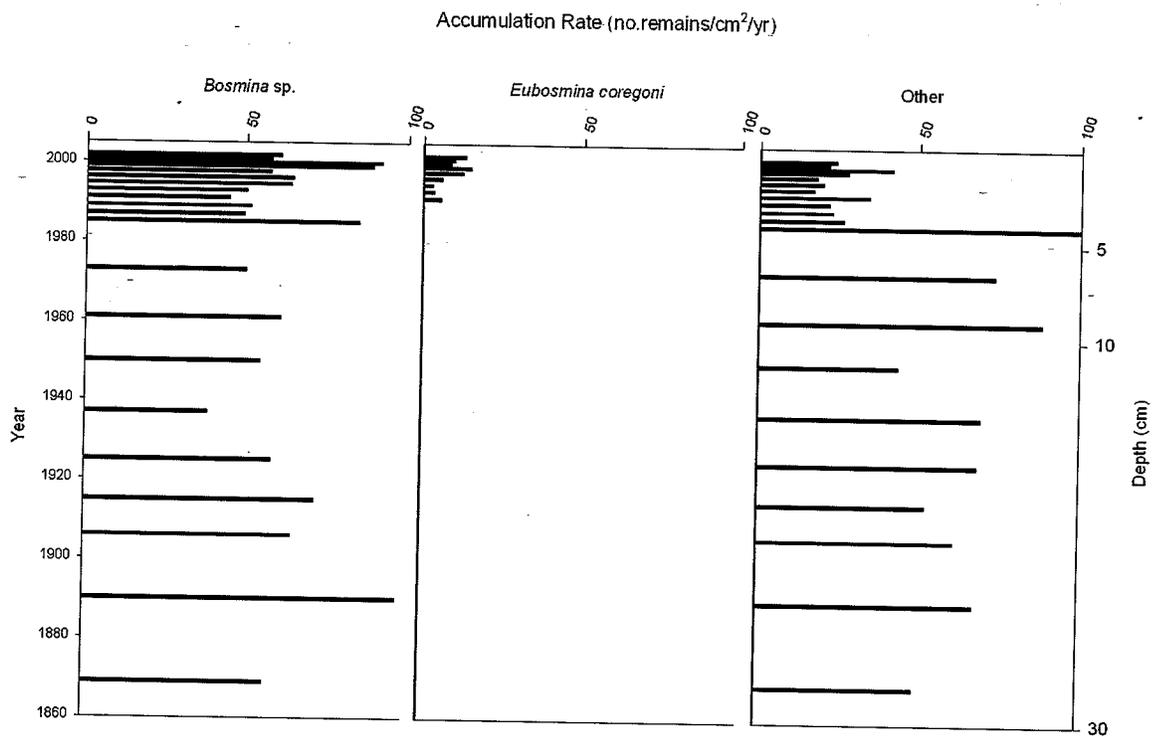
Figure 2.5. Accumulation rates (number of remains/cm²/yr) for *Bosmina* sp., *Eubosmina coregoni*, and "other" cladocerans in the 2002 core collected in Clearwater Bay (LW6), Lake of the Woods, Ontario, Canada.

Appendix

Table A. Actual counts for cladoceran remains in the top sediments collected from Lake of the Woods, Ontario, Canada, in September 2003.

Sample Site	Number of Cladoceran Remains Counted			
	Bosmina sp.	*E. coregoni*	Other	Total
PP2	45	9	49	103
PP3	123	1	19	143
PP4	75	8	18	101
PP5	95	20	24	139
PP6	82	19	20	121
PP7	71	9	26	106
PP9	10	0	5	15
PP10	5	0	12	17
PP11	6	0	8	14
PP12	61	4	39	104
PP13	76	13	40	129
PP15	68	0	34	102
PP16	55	0	58	113
PP17	18	16	81	115
PP18	3	2	10	15
PP19	3	0	8	11

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Chapter 3:

Investigating the early invasion stages of the cladoceran *Eubosmina coregoni* into Lake Winnipeg using sediment material and extant zooplankton samples

Introduction

The introduction of nonindigenous species (NIS) is an ongoing threat faced by aquatic ecosystems all over the world (Vitousek et al. 1997, Hall and Mills 2000, Schindler 2001). Although species invasions naturally occur, human activities are transporting species to new water bodies at an accelerated rate (Lodge and Shrader-Frechette 2003). Dispersal via ballast water is the most critical vector for the transport of aquatic species around the world (Schormann et al. 1990, Ricciardi 2001), and water bodies such as the Laurentian Great Lakes have received an increasing amount of biological pollution due to the discharge of ballast water over the last century (Ricciardi and MacIsaac 2000, Mills et al. 1993). With the implementation of legislation requiring ships to exchange ballast water before entering the Laurentian Great Lakes, the majority of vessels entering this region have no ballast on board (NOBOB) but, nevertheless, still act as vectors for NIS that are present in ballast residuals (Bailey et al. 2005, Duggan et al. 2005). For lakes in central Canada, however, invading species are more likely to disperse over land and via interconnecting river systems. The likelihood of invasion by these mechanisms of dispersal has been modeled for Eurasian watermilfoil (*Myriophyllum spicatum*) (Buchan and Padilla 2000), the zebra mussel (*Dreissena polymorpha*) (Buchan and Padilla 1999, Allen and Ramcharan 2001), and for the spiny waterflea (*Bythotrephes longimanus*) (MacIsaac et al. 2004).

In order for a species to successfully invade new ecosystems, three stages of the invasion process must be overcome: initial dispersal, establishment, and spread to nearby habitats (Kolar and Lodge 2001). Cladocera (water fleas), a major component of the micro-crustacean fauna in freshwater lakes and ponds (Hann 1989), possess a number of

characteristics that enable them to be successful invaders. Living individuals and diapausing, or resting, eggs may be dispersed to new water bodies via transport by humans, animals, or surface water (Frey 1982, Shurin and Havel 2002). Upon arrival into a new location, the reproductive strategies employed by cladocerans enhance their ability to rapidly establish in aquatic ecosystems. For instance, cladocerans mature very rapidly and spend a large proportion of their lifetime as reproductive adults (Allan and Goulden 1980). Further, most cladoceran species produce several generations of unfertilized eggs via parthenogenesis (Hann and Hebert 1982) and produce diapausing eggs via sexual reproduction during periods of environmental stress (Hann and Hebert 1982, Hairston et al. 1995, Reid et al. 2000). Diapausing eggs produced by cladocerans accumulate in the sediments and potentially can remain viable for decades (Hairston et al. 1995). Due to these reproductive characteristics, even a small cladoceran inoculation has the potential to colonize an entire water body (Shurin 2000).

Cladocerans such as *Bythotrephes longimanus* and *Cercopagis pengoi* are among the many successful zooplankton invaders that have established in the Laurentian Great Lakes. *B. longimanus* was first reported in the Laurentian Great Lakes region in the mid to late 1980s (Bur et al. 1986), whereas the first record of *C. pengoi* was in Lake Ontario in 1998 (Makarewicz et al. 2001). Both of these species continue to spread to water bodies beyond the Laurentian Great Lakes (MacIsaac et al. 1999, Makarewicz et al. 2001, MacIsaac et al. 2004). Since many of the present invaders of the Laurentian Great Lakes region are potential invaders of Lake Winnipeg, it is essential to learn more about the invasion routes to Lake Winnipeg and the vulnerability of this ecosystem to future

invaders that have had major economic impacts and have already permanently changed the food web dynamics of the Laurentian Great Lakes.

Eubosmina coregoni is the first known zooplankter to invade Lake Winnipeg (Alex Salki, unpublished data). This species was first described by Baird 1857 from individuals found in the stomachs of whitefish (*Coregonus* sp.) collected in Great Britain (De Melo and Hebert 1994a). Like the majority of cladoceran groups, the systematics of *Eubosmina* and other bosminids remains problematic, as *Eubosmina* has been recognized as both a genus (Deevey and Deevey 1971) and a subgenus (Lieder 1983). Most recently, Taylor et al. (2002) provided the first robust molecular phylogeny for bosminid crustaceans and proposed a revision for the group that recognizes three genera and five subgenera, wherein *Eubosmina* is considered a genus.

Common in water bodies of its native Eurasia (Lieder 1991), *E. coregoni* first colonized North America in the mid-1960s, likely in the ballast water of transoceanic vessels (Deevey and Deevey 1971, Lieder 1991). By the late 1960s, *E. coregoni* had dispersed to inland lakes within 100 km of the Laurentian Great Lakes (Deevey and Deevey 1971) and was thought to be restricted to this region (De Melo and Hebert 1994a). However, Mabee (1988) reported a southern range extension in Missouri for *E. coregoni* and Salki (1996) reported this species (incorrectly as *E. longispina*) in Lake Winnipeg in the early 1990s (Alex Salki, personal communication). In 1994, *E. coregoni* was found in low abundance at two main sites: the Traverse Bay region (Winnipeg River inflow) in the South Basin and at the Nelson River outflow in the North Basin (Salki 1996).

This study combines the analysis of microfossil remains from a sediment core with extant zooplankton samples to examine the temporal and spatial pattern of *E. coregoni*'s invasion into Lake Winnipeg. A paleolimnological approach provides information regarding the initial stages of *E. coregoni*'s dispersal into Lake Winnipeg by giving a historical account of when *E. coregoni* first appeared in the lake and how abundant this species has been since its arrival. With an understanding of the initial stages of *E. coregoni*'s invasion, the extant samples provide a spatial overview of this species, which can be used to address the establishment of *E. coregoni* in Lake Winnipeg. More specifically, limnological conditions and other factors that may favour the establishment of *E. coregoni* in this lake can be examined. Ultimately, results from this study will provide a framework for future studies concerning the invasion of *E. coregoni* and other potential invaders that are dispersing to lakes in Central Canada.

Materials and Methods

Study Site

Lake Winnipeg (50°0' - 53°50' N, 96°15' - 99°15' W), located in Manitoba, Canada, is the 11th largest freshwater lake in the world in terms of its 23,750 km² surface area (Patalas and Salki 1992). Lake Winnipeg has a large watershed of 953,250 km² spanning three provinces and four U.S. states (Fig. 3.1) (Brunskill et al. 1994). The lake is divided into distinct South and North basins that are separated by a region only a few kilometers wide called 'The Narrows' (Todd et al. 1997). The geology of Lake Winnipeg is unique in that the eastern region is underlain by Precambrian rock whereas the west is underlain by Palaeozoic limestone (Brunskill et al. 1994, Todd et al. 1997). As a result,

water received in the south and western regions of the lake has a higher alkalinity, mineral and nutrient content than the Canadian Shield waters received in the north and eastern regions of the lake (Kling 1998). The mean depth of the North Basin is 13.3 m, whereas the South Basin has a mean depth of 9.7 m (Patalas and Salki 1992). Lake Winnipeg receives water from the south and west via the Red and Saskatchewan rivers, respectively, and from the east mainly by the Winnipeg, Pigeon, Berens, and Poplar rivers (Patalas and Salki 1992). The only outflow of Lake Winnipeg, the Nelson River, flows northward from the North Basin to Hudson Bay (Brunskill et al. 1994). Residence time of the water in Lake Winnipeg is 2.9 – 4.3 years (Brunskill et al. 1994).

Sediment Analysis

See Chapter 2 for details on sediment and data analyses.

Extant Zooplankton

Zooplankton sampling was carried out in July and August of 2002-2004 as part of a more comprehensive sampling of Lake Winnipeg onboard the MV NAMAO (347524), formerly the CCGS (Canadian Coast Guard Ship) NAMAO. Approximately 65 stations throughout the lake were sampled in 2002-2004, however, due to adverse weather conditions not all stations were sampled each year (Fig. 3.2). At each sampling station, a Wisconsin net with a 25 cm mouth diameter, 72 μm mesh size, and a filtering cone length of 1 m was hauled vertically from just above (0.25 m) the lake bottom to the surface. Stations were sampled during daytime hours. Zooplankton samples were preserved in 8% formalin. A 10 ml subsample was examined and *Bosmina* sp., *E. coregoni*, and "other"

cladocerans were identified and counted. Relative abundances of zooplankton were calculated for each station for the three years and mapped using ArcGIS 9.0 (ESRI, Redlands, California, USA) with base maps provided by Hearn et al. (2003) to illustrate the distribution of cladocerans throughout the different regions of the lake. Other limnological data for each site, e.g. chlorophyll a, settled volume (total phyto- and zooplankton, see Patalas and Salki 1992) were provided by Alex Salki and Mike Stainton. Mantel's tests based on Pearson's product-moment correlations were performed using R: A Language and Environment for Statistical Computing (R Foundation for Statistical Computing, Vienna, Austria) in order to measure the association between the relative abundance of $E.$ $coregoni$ and these limnological data (Manly 1997).

Results

Sediment Cores

In general, cladoceran remains were abundant and well preserved. Few, if any, remains were present between sediments dated to 1860 and 1924, however (Fig. 3.4). Therefore, analysis of sediment layers between ^{210}Pb dates 1860 and 1924 did not satisfy the minimum count of 100 individuals due to the lack of remains. The cladoceran species assemblage was dominated by the planktonic genus $Bosmina$ throughout all sediment layers analyzed (Fig. 3.4). $E.$ $coregoni$ first appeared in sediments dated to 1988. Between ^{210}Pb dates 1988 and 1995 the accumulation rate of $E.$ $coregoni$ was very low, i.e. fewer than 15 individuals/cm^2/year (Fig. 3.4). After sediments dated to 1997, the $E.$ $coregoni$ accumulation rate increased substantially with a peak of approximately 480 individuals/cm^2/year in sediments dated to 2003. Although $E.$ $coregoni$ continues to be

present in sediments deposited recently, the accumulation rates of this species are lower in comparison to *Bosmina* sp. accumulation rates. Accumulation rates of *Bosmina* sp. peaked from ^{210}Pb dates 1986 to 1988 and from 1993 to 1999, with the highest accumulation rate of approximately 1700 individuals/cm^2/year in sediments dated to 1993. Phosphorus and nitrogen levels in the sediments remained relatively constant throughout all sediment layers while carbon levels showed a general increase, reaching levels over 30 µg/mg after ^{210}Pb date 1980 (Fig. 3.5). Chlorophyll *a* concentrations, on the other hand, dramatically decreased between the late 1870s and 1890s and were highest in the most recent sediments with values over 100 ng/mg (Fig. 3.6).

Extant Zooplankton

In summer 2002, *E. coregoni* was present at most stations in the North Basin and at three stations in the South Basin near the Winnipeg River (Fig. 3.7). During the following summer, the highest relative abundance of *E. coregoni* occurred in the North Basin, wherein this species was restricted (Fig. 3.8) (see Appendix for actual counts). Similarly, in 2004, *E. coregoni* was predominantly present in the North Basin of Lake Winnipeg, though the relative abundance of this species was much lower than in 2003 (Fig. 3.9). In all three years, *Bosmina* sp. was most abundant in the North Basin, however, this species was also present in low abundance at various stations throughout the South Basin (Figs. 3.7-3.9). The relative abundance of *Bosmina* sp. in the North Basin during the summer of 2003 was lower than in 2002, while the relative abundances of *Bosmina* sp. in 2002 and 2003 in the South Basin were comparable. "Other" cladocerans (e.g. daphniids, chydorids) typically larger than the smaller-bodied *E. coregoni* and

Bosmina sp., predominated at stations in the South Basin in all three years, but were also present throughout the North Basin and the Narrows.

Sampling stations where *E. coregoni* was present were, on average, significantly deeper than stations where *E. coregoni* was absent for all three years (Table 3-II). Further, stations where *E. coregoni* was present showed positive spatial autocorrelation in all three years, i.e. there was a significant correlation between the relative abundance of *E. coregoni* in reference to its spatial location in the lake (Table 3-III). Therefore, *E. coregoni* was more likely to be present at stations that were adjacent to other stations where this species was present. In contrast, there were no significant correlations between the relative abundance of *E. coregoni* and chlorophyll *a*, while a significant correlation between *E. coregoni* and settled volume was found only in summer 2002 (Table 3-III).

Discussion

Analysis of sediments from Lake Winnipeg indicates that *E. coregoni* first appeared in the North Basin in the late 1980s, providing the only historical information available regarding the early stages of *E. coregoni*'s introduction. Once cladocerans and other zooplankters disperse into new habitats, established populations may be small and/or isolated thereby remaining undetected (MacIsaac et al. 2001, Havel and Medley 2006). It is possible that *E. coregoni* was present in Lake Winnipeg prior to the timing indicated by the sediments analyzed in this study. Further, it is important to recognize that some introductions are unsuccessful and do not lead to establishment or spread of the invading species (Hairston et al. 1999, Puth and Post 2005). Thus, *E. coregoni* may have

been introduced into Lake Winnipeg multiple times before it successfully established in this system.

The majority of invasion research focuses on the establishment of invasive species, however, Puth and Post (2005) argue there should be more of a focus on the initial dispersal of organisms because all other stages are dependent on this stage. One of the first questions to arise when a NIS enters a new water body addresses how that particular NIS entered the new habitat. With the many different vectors available to aquatic invaders such as *E. coregoni*, the exact mechanism by which this species entered Lake Winnipeg may never be known. Further, it is possible that more than one vector facilitated the invasion of this species. For example, *E. coregoni* may have entered Lake Winnipeg via the Winnipeg River from Lake of the Woods, Ontario, where it is known to occur (Salki 1996). Riverine connections provide a pathway for the dispersal of NIS because water bodies downstream of source populations are more likely to be invaded than water bodies not connected by surface waters (Shurin and Haven 2002). Because *E. coregoni* was found in both the South and North Basin of Lake Winnipeg in extant samples from 1994 (Salki 1996), it is not known whether an inoculation from the Winnipeg River could have resulted in the establishment of *E. coregoni* in the North Basin, or whether this species entered the North Basin from rivers on the east side of the lake (Salki 1996).

Another likely vector for the introduction of *E. coregoni* into Lake Winnipeg is transport in the gut of fish. Riverine connections, therefore, act as indirect corridors when fish that have ingested resting eggs move to water bodies downstream. The appearance of *E. coregoni* in Lake Winnipeg in sediments dated to the late 1980s coincides with the

appearance of rainbow smelt (*Osmerus mordax*). The first report of rainbow smelt in Lake Winnipeg was in 1990, although it is possible that smelt appeared as early as 1975 (Campbell et al. 1991). Populations of *E. coregoni* may have established in the Traverse Bay region if smelt transporting *E. coregoni* resting eggs entered Lake Winnipeg via the Winnipeg River and subsequently migrated into the North Basin. Further investigation of the invasion history of these two species is essential to document this instance of co-invasion of two NIS. Although these mechanisms of invasion are the most likely vectors for the introduction of *E. coregoni* into Lake Winnipeg, other vectors such as transport by waterfowl (Proctor 1964) or by humans in association with fishing vessel/gear (Mills et al. 1993), may have also played a role.

Despite the fact that *E. coregoni* first appeared in the North Basin of Lake Winnipeg in sediments dated to the late 1980s, the accumulation rates of this species remained relatively low for a few years following its arrival. It was not until sediments dated to the late 1990s that *E. coregoni* began to represent a substantial proportion of the cladoceran remains in this lake. As with all NIS, establishment in a new location cannot take place unless conditions are suitable for that particular species (Kolar and Lodge 2001). Even though the reproductive strategies employed by Cladocera, in general, allow for very rapid establishment in new water bodies, low abundances following *E. coregoni*'s arrival could indicate that conditions were not ideal for this particular species in the North Basin of Lake Winnipeg at the time of its arrival. Further, the extant samples showed that *E. coregoni* was almost completely restricted to the North Basin in 2002, 2003, and 2004, aside from its presence at a few sites near the mouth of the Winnipeg R. in the South Basin. The positive spatial autocorrelation shown by the relative abundance

of *E. coregoni* during these three years may explained by the fact that stations that are closer together are more likely to have similar limnological conditions, thereby facilitating or hindering the establishment of a NIS.

There are many reasons to suggest why *E. coregoni* has become established in Lake Winnipeg and, more specifically, in the North Basin. One of the most obvious explanations is that *E. coregoni* has flourished in the North Basin because it is a pelagic species. It is not surprising that sites with *E. coregoni* present were, on average, deeper than sites where this species was absent, corresponding to the deeper waters of the North Basin rather than the shallower South Basin. Similarly, in a study of sediments from 13 German lakes, Hofmann (1996) found that the abundance of *Eubosmina* spp. (including *E. coregoni*) was highest in deep lakes (mean depth >10 m), while being almost completely absent in the shallowest lakes (1.3-2.3 m) (Hofmann 1996).

On the other hand, the variation in *E. coregoni* abundance between 2002, 2003, and 2004 could be attributed to the different weather patterns observed during each of these three years. Parameters such as temperature, rainfall, and amount of available sunlight all have an effect on the primary producers of the lake and thus indirectly affect the zooplankton community. For example, August 2002 had a mean temperature of 17°C and a total rainfall of 84.0 mm (Environment Canada) representing a fairly average summer. During this year, *E. coregoni* was abundant at the majority of sites in the North Basin, in addition to a few sites near the mouth of the Winnipeg River. The following year, 2003, was an extremely warm, dry summer with a mean August temperature of 21.3°C and total August rainfall of 17.0 mm. Lastly, the low abundance of *E. coregoni* at all sites in the North Basin during summer 2004 could be explained by the fact that it was

a very cold and wet year with a mean August temperature of 13.6°C and a total August rainfall of 95.4 mm.

The success of invading zooplankters such as *E. coregoni* may also be influenced by the trophic status of a lake (Lennon et al. 2003). Cladocerans are the dominant herbivores in a lake ecosystem and will be affected by changes in primary production due to differing nutrient concentrations (Hofmann 1996). As a result, biological invasions may be facilitated in eutrophic lakes where excess nutrients are likely to modify the structure of the existing community (Lennon et al. 2003). Studies concerning changes in zooplankton communities in response to trophic state are numerous. For example, another small cladoceran species, *Chydorus sphaericus*, has been found to dominate the zooplankton community when nutrient enrichment increased zooplankton biomass (Szeroczynska 2002, Lennon et al. 2003).

Additionally, shifts in bosminid species have long been associated with changing trophic levels in studies of lake sediments. More specifically, changes in the dominant *Bosmina* species as a result of large increases in algae are thought to be indicative of eutrophication (Boucherle and Zullig 1983). While some studies suggest that a shift to *B. longirostris* in European lakes indicates eutrophic conditions (Boucherle and Zullig 1983, Szeroczynska 2002, Gasiorowski and Szeroczynska 2004), others suggest a shift to the dominance of *B. longispina* is indicative of oligotrophic conditions (Boucherle and Zullig 1983, Szeroczynska 2002). Hofmann (1978), on the other hand, linked the successive colonizations by *B. longispina*, *B. coregoni kessleri*, and *B. coregoni coregoni* (*E. coregoni*) with increasing eutrophication. Due to the taxonomic inconsistency associated

with bosminids, the literature concerning this link between shifts in bosminid species and changes in the trophic state of a lake must be interpreted with caution.

Regardless, inferring a relationship between the cladoceran community and the trophic status of lakes is insufficient without considering other abiotic or biotic indicators. For instance, the phytoplankton in a system is undoubtedly a major factor affecting any shifts observed in zooplankton communities. As such, algal biomass, as inferred by chlorophyll *a* concentration, is commonly used as an indicator of the trophic status of a lake. Although there were no significant correlations between chlorophyll *a* and the relative abundance of *E. coregoni* within each year, future analyses of the relationship between chlorophyll *a* and *E. coregoni* densities (individuals/L) may provide a more accurate assessment of the correlation between these two variables.

Aside from using chlorophyll *a* as an indicator of algal biomass, it may be just as important to assess the types of phytoplankton present in a lake. For example, Vijverberg and Boersma (1997) found that *C. sphaericus* and other small-bodied species actually decreased in biomass with increasing chlorophyll *a* concentration. Small cladoceran species such as *E. coregoni* have a narrow carapace gap and are less likely to be inhibited by the presence of large filamentous algae (Vijverberg and Boersma 1997). Therefore, species with high grazing rates and species that are tolerant of filamentous algae are more likely to succeed in eutrophic conditions where intense cyanobacterial (blue-green algal) blooms may occur. The warmer than average temperatures in summer 2003 resulted in intense blue-green algal blooms in the North Basin when the highest relative abundances of *E. coregoni* occurred. Although large settled volumes typically result from the

presence of filamentous cyanobacteria, a significant correlation between settled volume and relative abundance of *E. coregoni* was only found in 2002.

Summary

Research on Lake Winnipeg, as a system, is at its very earliest stages and studies concerning the introduction of species into Lake Winnipeg are virtually non-existent. The invading zooplankter *E. coregoni* is now a substantial component of the zooplankton community in the North Basin of Lake Winnipeg. Due to the large number of vectors that could be utilized by aquatic invaders, it is unlikely that the exact mechanism(s) by which *E. coregoni* entered Lake Winnipeg will ever be determined. Similarly, the parameters that govern the success of *E. coregoni*, and other aquatic invaders, once they have entered new water bodies may never be deciphered. In all likelihood, *E. coregoni* will persist in Lake Winnipeg and this species' abundance will continue to fluctuate based on yearly limnological conditions. The establishment of *E. coregoni* has likely been facilitated by both a variable climate and human activities. In the near future, other aquatic invaders will undoubtedly enter the Lake Winnipeg ecosystem, some of which will have enormous ecological and economic impacts.

Future studies concerning *E. coregoni* in Lake Winnipeg should examine the relationship between *E. coregoni* and parameters associated with eutrophication (e.g. chlorophyll *a*, algal community composition, etc.). For example, analysis of algal microfossils in 1994 from sediments in the North Basin of Lake Winnipeg showed that species changes occured at the top of the core, thereby indicating an increase in anthropogenic eutrophication in this region (Kling 1998). Analyses of the algal

microfossils from the 2003 core used in the present study have yet to be completed. Further, the association between *E. coregoni* and other small- and large-bodied cladocerans should be explored because the effect of this species on other zooplankters is unknown. The extant samples in this study did indicate that *E. coregoni* tends to be present at sites where "other" (typically larger-bodied) cladocerans are lower in abundance. A number of studies have examined the relationship between large-bodied and small-bodied species in response to predation (Kerfoot 1981, Sanford 1993, Sarmaja-Korjonen 2002) and in response to habitat changes (Kerfoot 1974, Grigorovich et al. 1998). Therefore, future studies looking at effects that this species might have on other trophic levels, i.e. fish populations, could be investigated, as well as the competitive interaction between *E. coregoni* and other small-bodied cladocerans in the North Basin versus the larger species common in the South Basin.

Although this is the first study of zooplankton invaders in Lake Winnipeg, another aquatic invader, rainbow smelt, continues to expand its distribution in the Lake Winnipeg watershed (Franzin et al. 1994). An examination of smelt gut contents could indicate whether or not this species is a vector for transporting *E. coregoni* into Lake Winnipeg, thereby providing insight regarding the co-invasion of species into this lake. Moreover, the exploration and documentation of food web structure and dynamics of this lake are in very preliminary stages and more attention must be given to understanding the ecosystem as a whole. For a lake with such enormous economic outputs due to its recreational and commercial (fishing, boating, and angling) uses, the consequences of a deteriorating system due to the invasion of aquatic species, in addition to other anthropogenic and climatic factors will be numerous. More effort and time must be

dedicated in order to protect Lake Winnipeg before the conditions of this valuable

ecosystem degenerate.

Table 3-I. Statistical variables for cladoceran carapace counts from surface sediments of the 2003 North Basin core from Lake Winnipeg, Manitoba, to test for variance equal to the mean ($\alpha = 0.05$).

Sample	No. of Slides	No. of Remains	Range	Mean	St. Dev.	Variance	X^2	P
1A	10	125	7-19	12.5	3.89	15.17	10.92	>0.25
1B	10	62	3-10	6.2	2.39	5.73	8.32	>0.5
1C	10	63	3-9	6.3	2.31	5.34	7.63	>0.5

Table 3-II. Statistical variables for sampling station depth at sites with *E. coregoni* was absent versus sites with *E. coregoni* was present in Lake Winnipeg, Manitoba (t-test, α = 0.05).

Year	n	*E. coregoni* Absent			n	*E. coregoni* Present			P-Value
		Range (m)	Mean (m)	St Dev		Range (m)	Mean (m)	St Dev	
2002	30	5.18-19.51	9.98	3.41	31	6.40-17.38	12.80	3.31	<0.001
2003	24	3.20-20.43	9.46	3.42	29	6.71-17.07	13.57	2.92	<0.0005
2004	23	3.29-16.46	9.23	3.33	21	8.75-16.77	14.88	2.53	<0.0005

Table 3-III. Mantel statistic (r) and significance results for Mantel's tests performed on the relative abundance of *Eubosmina coregoni* with other limnological variables based on Pearson's product-moment correlation, 1000 permutations ($\alpha = 0.05$).

	2002			2003			2004		
	n	r	p-value	n	r	p-value	n	r	p-value
% E. coregoni and UTM coordinates	59	0.10	0.01*	58	0.32	<0.001*	45	0.22	0.001*
% E. coregoni and chlorophyll *a*	57	0.14	0.11	55	0.04	0.28	5	0.58	0.16
% E. coregoni and settled volume	53	0.28	0.02*	55	-0.07	0.81	43	-0.02	0.37

* indicates significant results

Note: Chlorophyll *a* data provided by Mike Stainton are still preliminary and 2004 data are lacking for most stations.
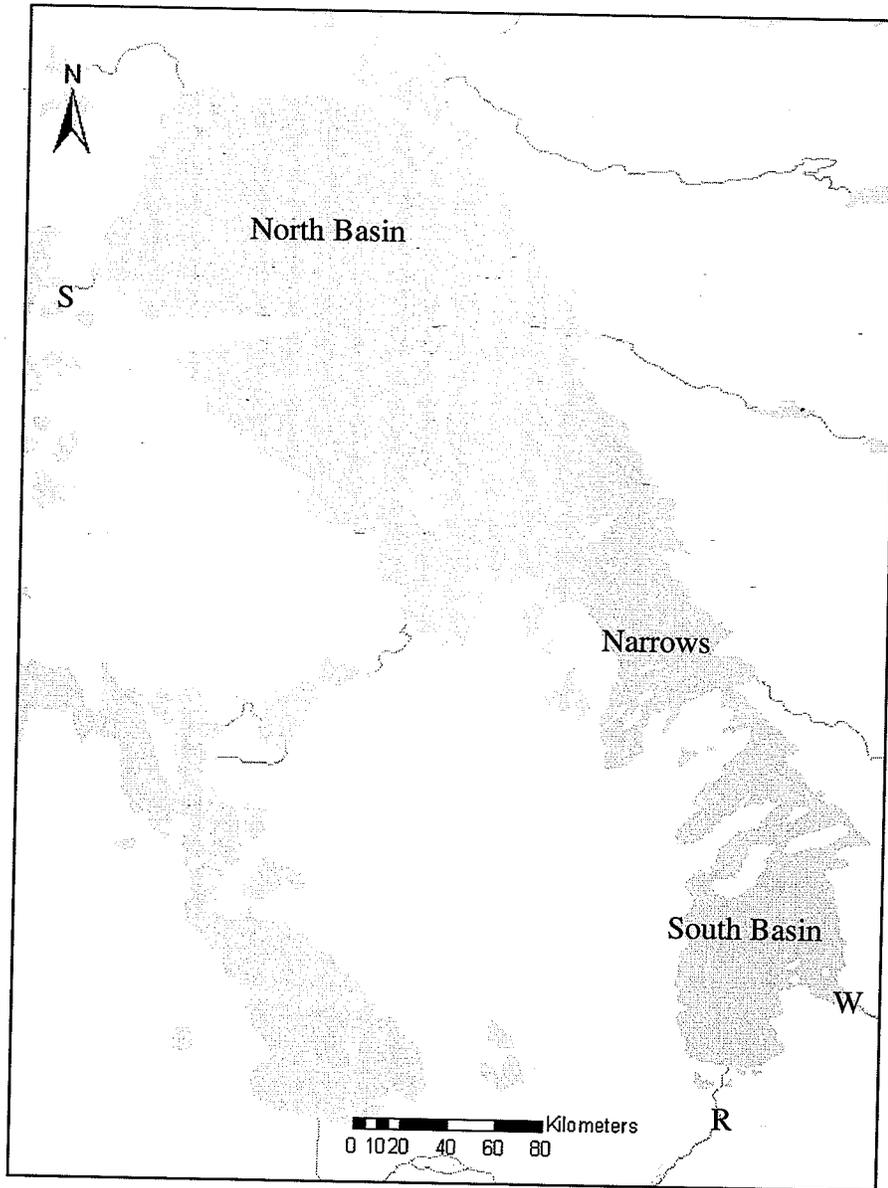
Figure 3.1. Map of Lake Winnipeg showing the North and South basins and the Narrows (S, Saskatchewan River; R, Red River; W, Winnipeg River).
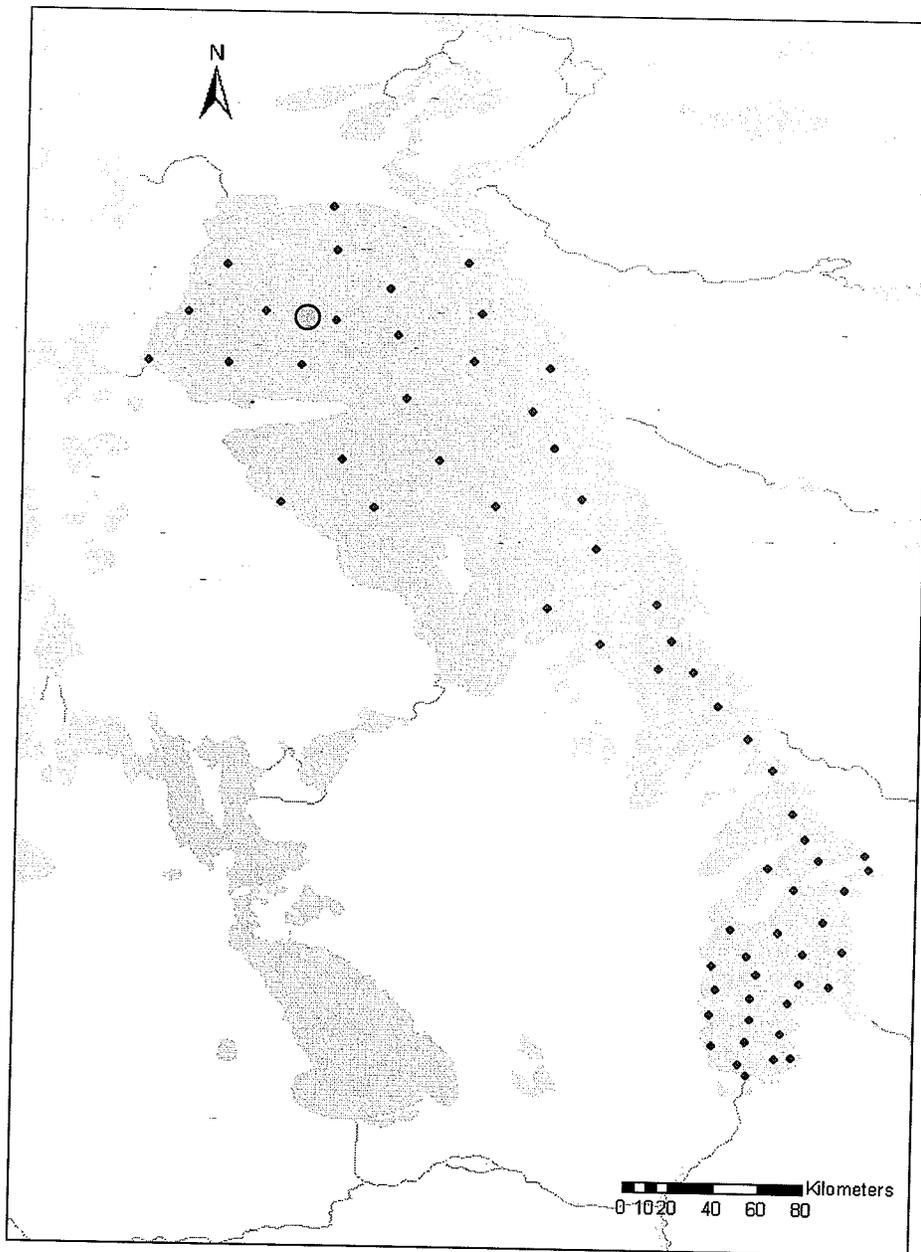
Figure 3.2. Sampling stations for Lake Winnipeg 2002 to 2004. Diamonds indicate extant zooplankton sampling stations, circle indicates the location of the sediment core collected in 2003.

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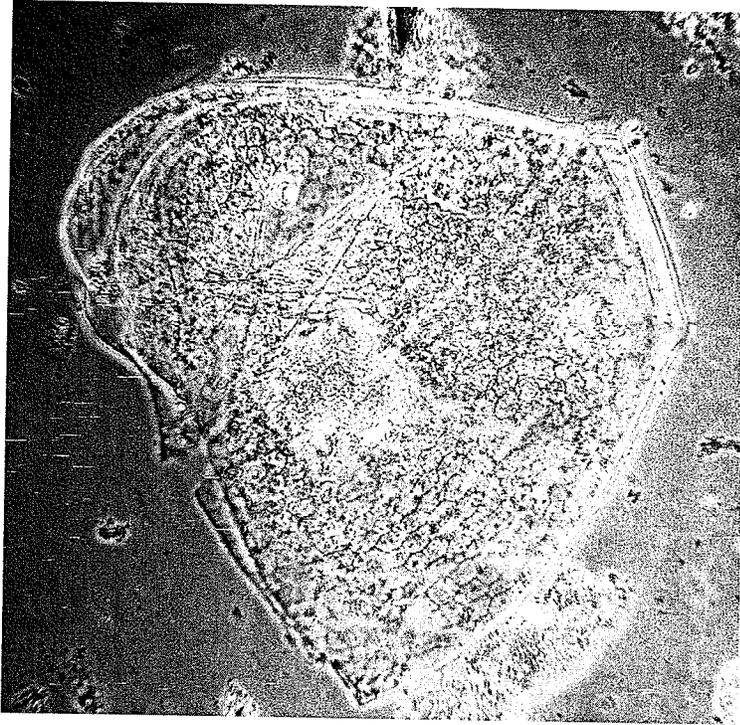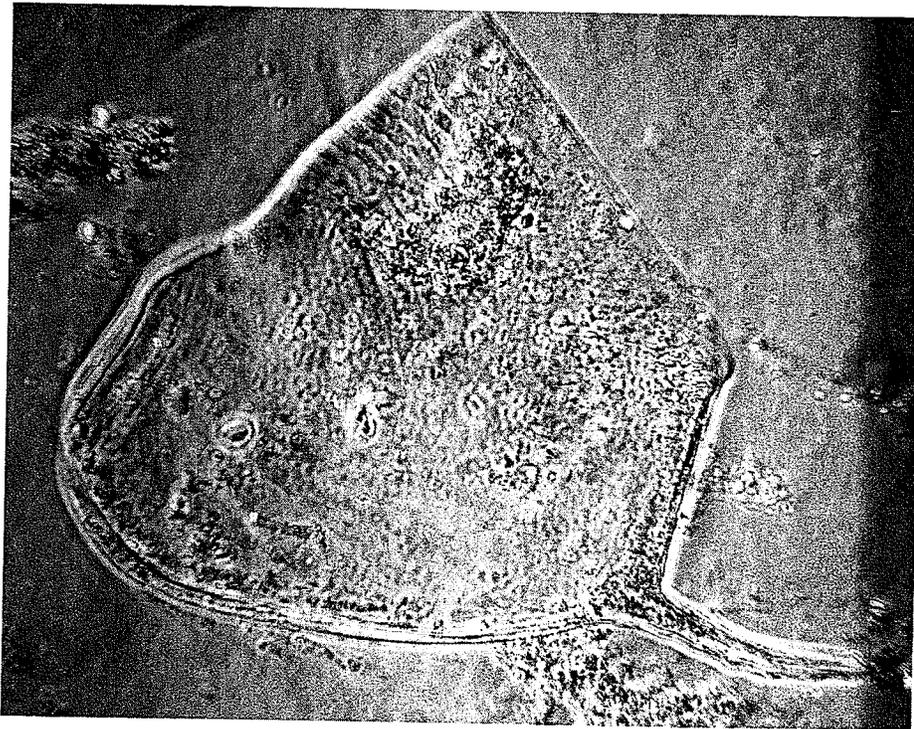
Figure 3.3. Photographs of Lake Winnipeg specimens of *Eubosmina coregoni* (a) and *Bosmina longirostris* (b) carapaces in lateral view.
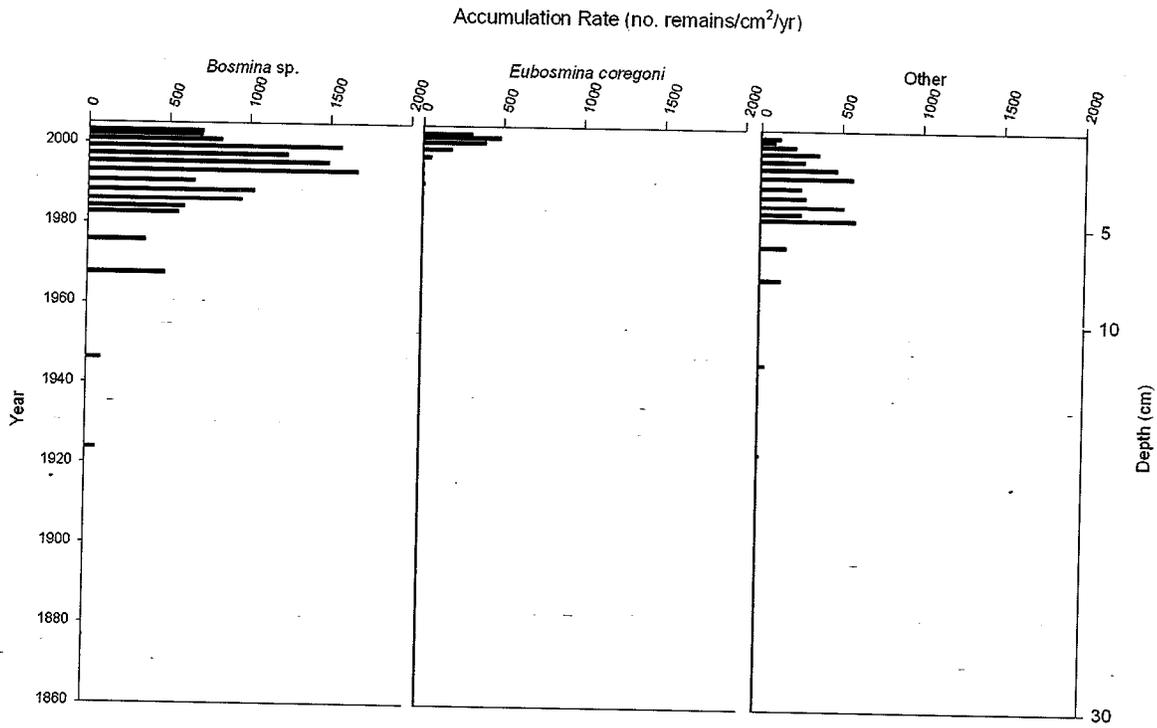
Figure 3.4. Accumulation rates (number of remains/cm^2/yr) for *Bosmina* sp., *Eubosmina coregoni*, and "other" cladocerans in the 2003 core from the North Basin of Lake Winnipeg, Manitoba.
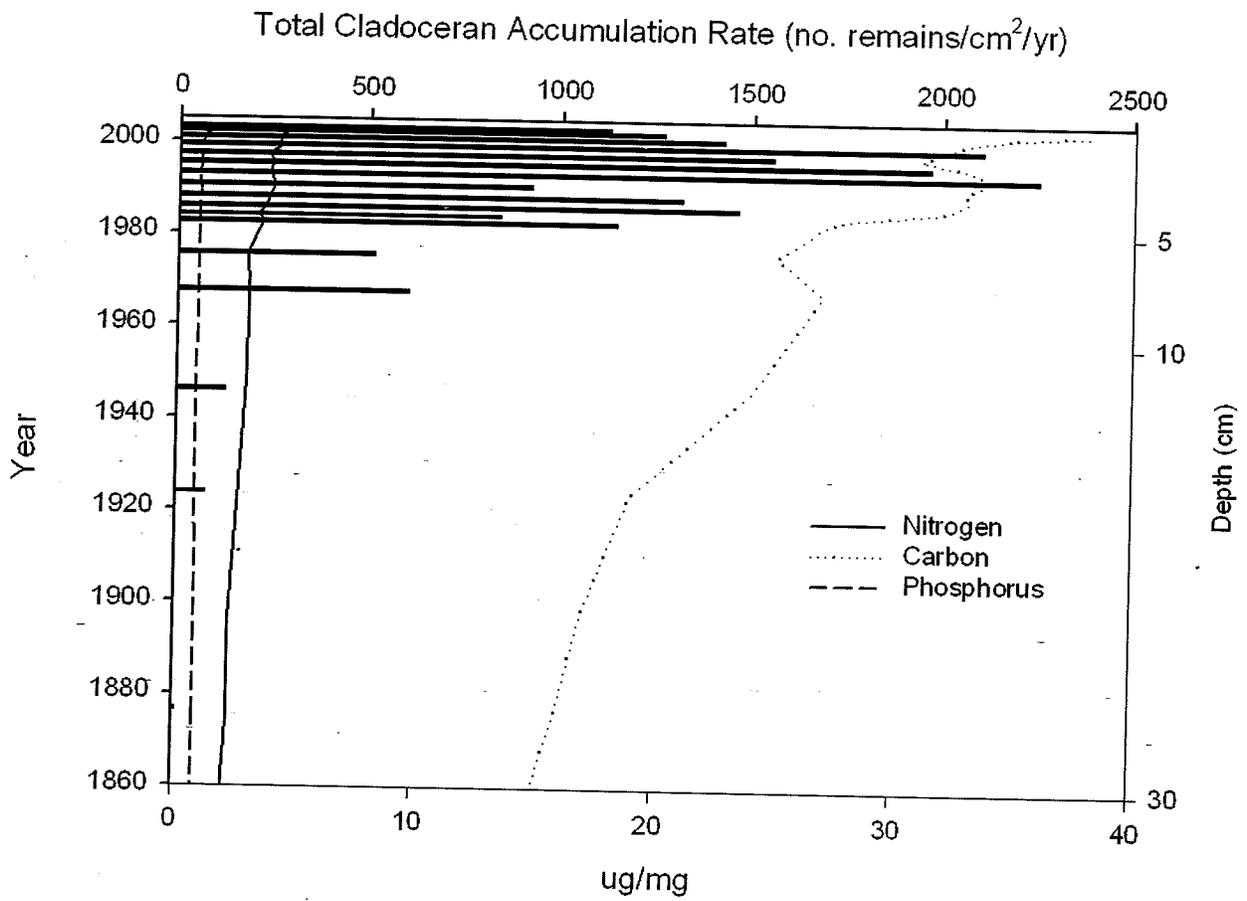
Figure 3.5. Total cladoceran accumulation rates and sediment core chemistry (N, C, and P) in the 2003 core from the North Basin of Lake Winnipeg, Manitoba.
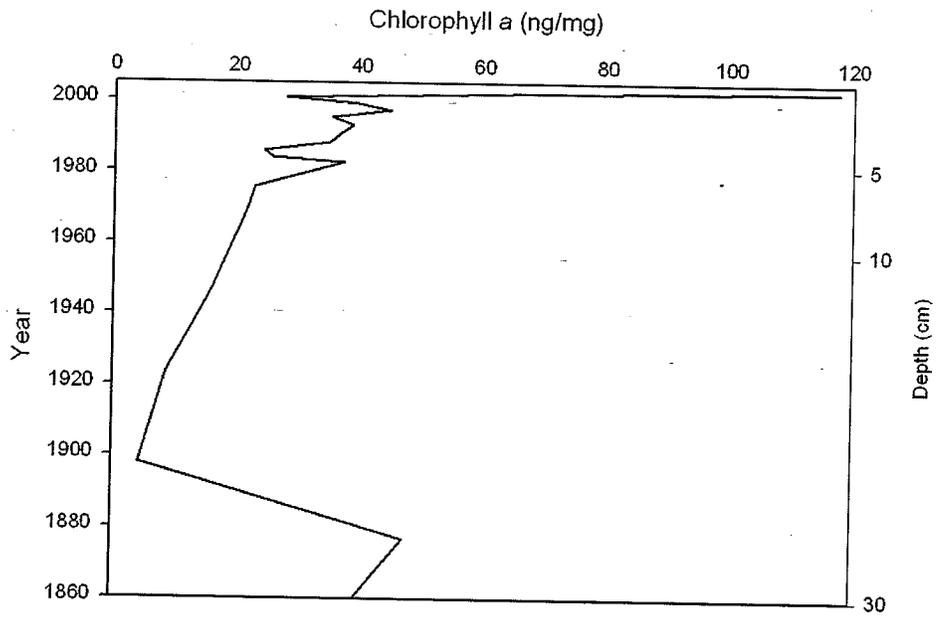
Figure 3.6. Chlorophyll *a* values from the 2003 core from the North Basin of Lake Winnipeg, Manitoba.
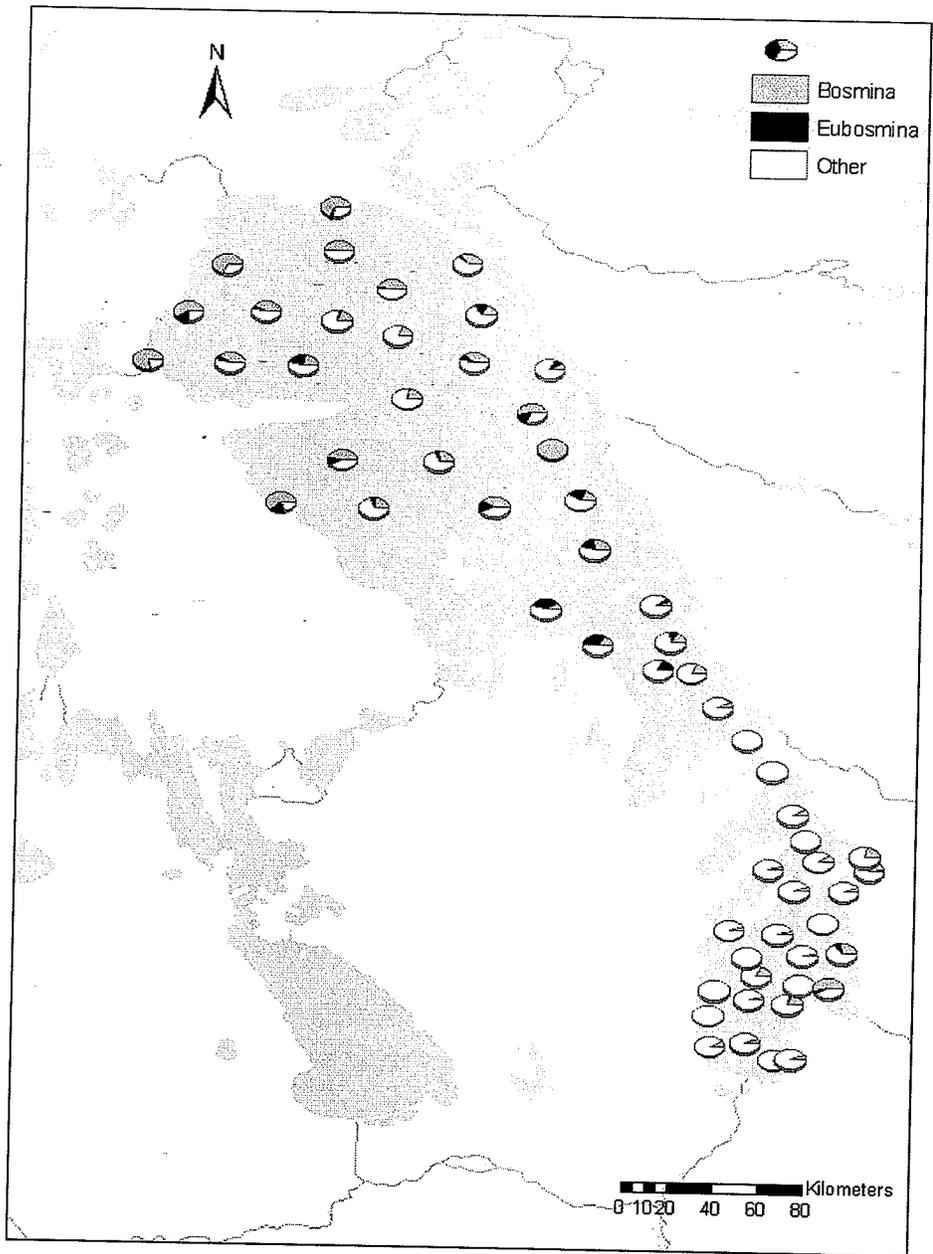
Figure 3.7. Relative abundances of *Bosmina* sp., *Eubosmina coregoni*, and "other" cladocerans from extant samples collected in summer 2002 from Lake Winnipeg, Manitoba.
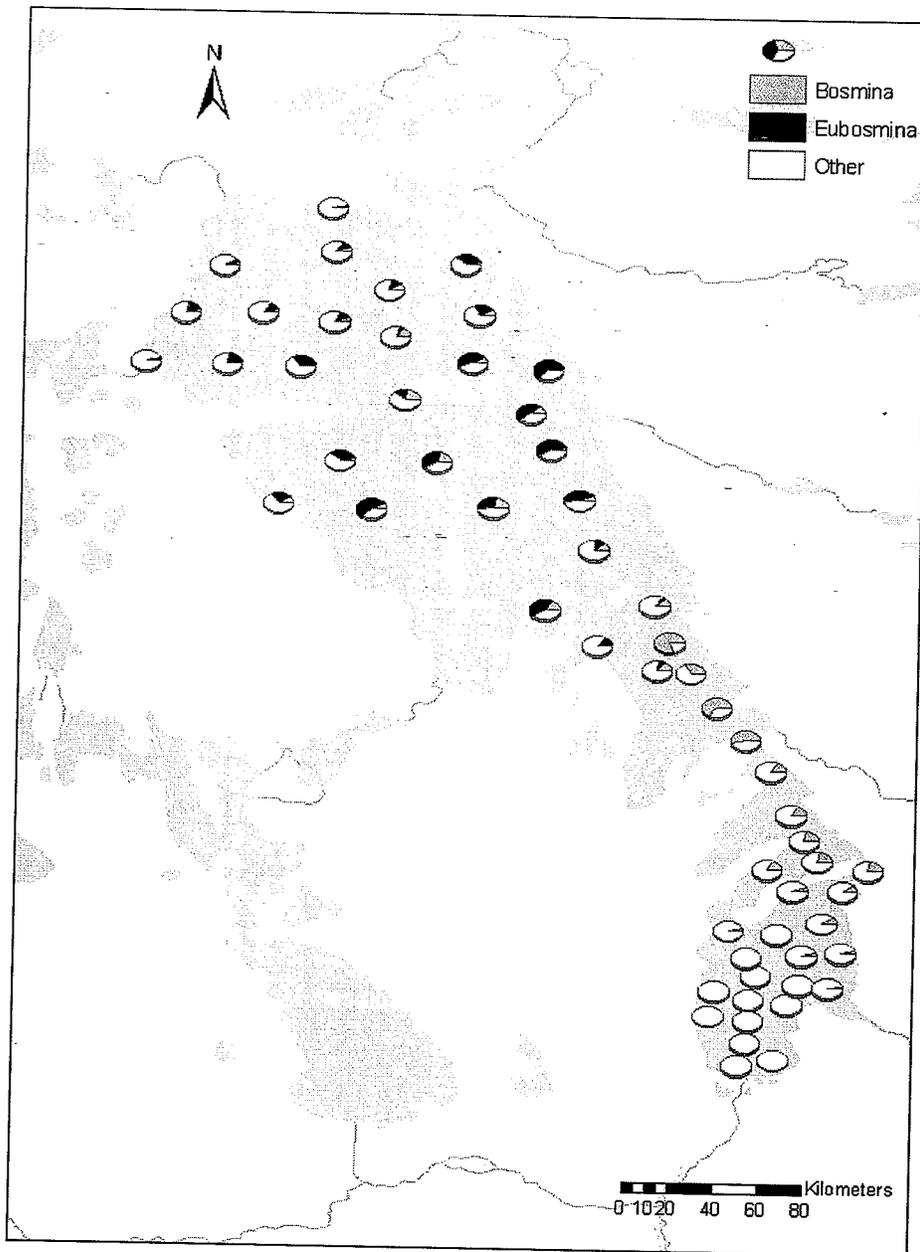
Figure 3.8. Relative abundances of *Bosmina* sp., *Eubosmina coregoni*, and "other" cladocerans from extant samples collected in summer 2003 from Lake Winnipeg, Manitoba.
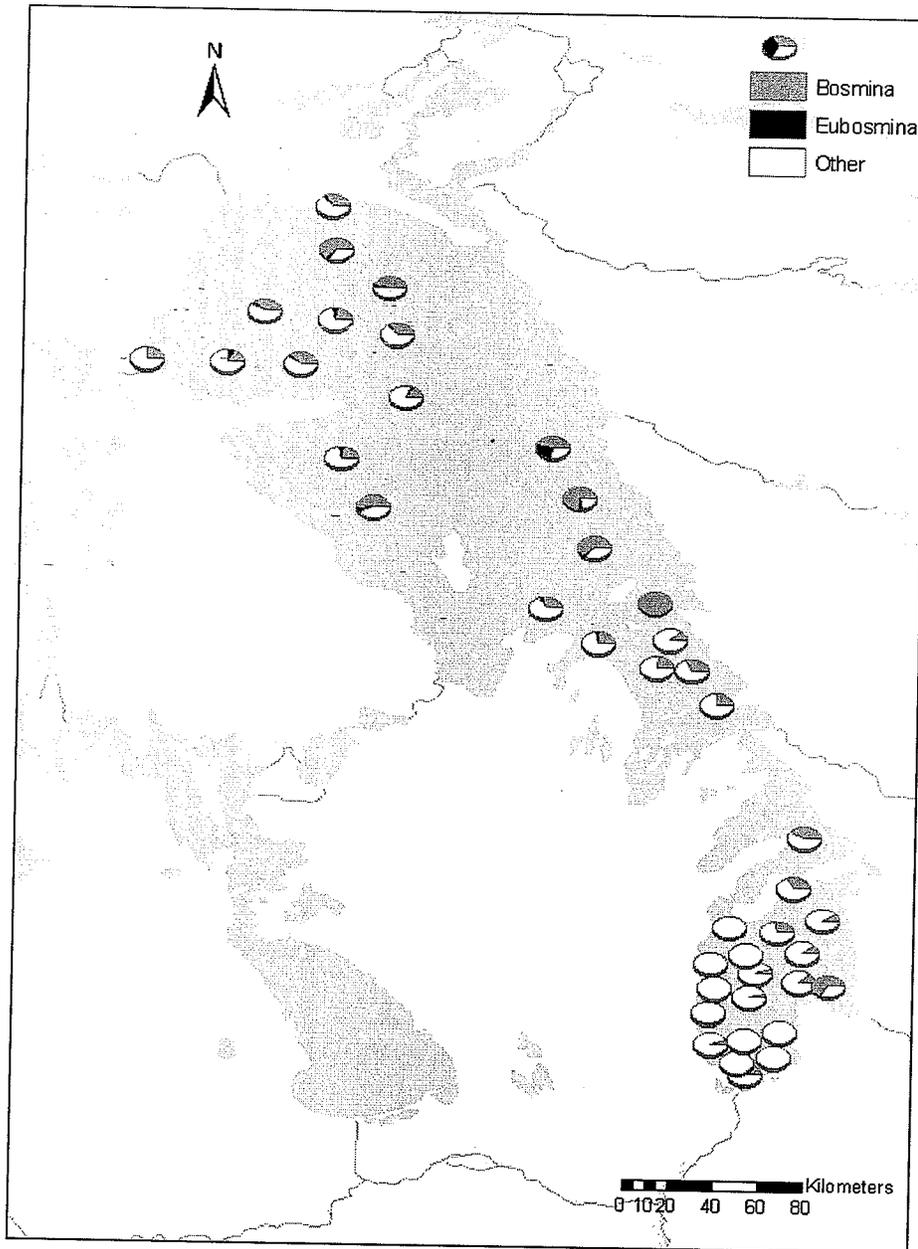
Figure 3.9. Relative abundances of *Bosmina* sp., *Eubosmina coregoni*, and "other" cladocerans from extant samples collected in summer 2004 from Lake Winnipeg, Manitoba.

Appendix

Table A. Cladoceran counts from extant samples collected throughout Lake Winnipeg, Manitoba, Canada, in summer 2002.

Station	Bosmina sp.	Number of Cladocera Counted E. coregoni	Other	Total
10A	0	0	8	8
10S	0	0	17	17
11	4	0	100	104
12B	6	0	93	99
13B	0	0	3	3
14	0	0	2	2
15	0	0	59	59
16S	0	0	8	9
17	4	0	0	4
18	24	36	82	142
19	47	14	27	88
20	12	15	127	154
20S	60	12	77	149
21	23	21	82	126
22	104	16	174	294
23B	45	2	45	92
23ES	5	0	21	27
23S	67	74	157	298
25S	77	10	98	185
26S	14	2	17	33
27S	180	56	76	312
28	176	7	47	230
31	219	3	98	320
33	49	5	21	75
34S	160	4	163	327
35S	4	1	17	22
36S	0	0	25	25
37S	0	0	6	6
37S (B?)	4	0	18	22
39	14	1	50	66
3B	4	0	125	129
3C	7	0	106	113
41	152	27	127	306
42S	8	2	22	32
43S	36	10	12	58
44S	0	0	7	8
45	77	23	203	303
46S	3	0	58	61
47S	2	0	67	69
48	21	7	22	49
49S	0	0	5	5
5	1	0	155	156
5	6	1	24	31
50S	5	3	9	17
53	1	1	5	7
54	1	0	3	4

Table A (cont'd)			
	Number of Cladocera Counted		
Station	Bosmina sp.	E. coregoni	Other	Total
55	1	0	8	9
56	0	0	37	37
57	0	0	61	61
57BS	4	0	72	76
59	1	0	22	23
6	2	0	236	238
60B	0	0	29	29
60B	0	0	25	25
61	1	0	19	20
62	1	0	14	15
64	8	29	46	83
68	12	26	38	76
69	0	4	16	20
7	1	0	2	3
8	12	1	· 10	23
9	11	3	26	40
BI4	9	0	33	42

Table B. Cladoceran counts from extant samples collected throughout Lake Winnipeg, Manitoba, Canada, in summer 2003.

Station	Bosmina sp.	Number of Cladocera Counted E. coregoni	Other	Total
10A	0	0	5	5
10S	0	0	10	10
11	0	0	27	27
12B	2	0	42	44
13B	2	0	8	10
14	3	0	14	16
15	8	0	7	14
16S	1	0	10	12
17	13	224	174	412
18	17	135	139	291
19	62	224	192	479
2	1	0	111	112
20	5	136	87	228
20S	12	72	67	151
21	6	18	49	73
22	11	160	261	391
23B	1	2	8	11
23ES	3	2	20	25
23S	2	36	63	101
25S	1	19	63	83
26S	1	3	22	26
27S	6	29	132	165
28	2	7	160	169
31	1	1	18	19
33	1	1	62	65
34S	2	3	21	26
35S	1	2	17	20
36S	0	0	115	115
37S	0	0	8	8
39	5	3	13	21
3B	1	0	357	358
41	9	122	202	333
42S	10	16	18	44
43S	11	30	74	115
44S	15	0	86	101
45	14	118	77	209
46S	6	0	56	62
47S	19	0	64	83
48	4	5	8	17
49S	4	0	14	18
5	1	0	243	244
50S	4	4	24	33
53	15	0	3	18
54	5	0	10	15
55	24	0	13	37
56	13	0	70	83
57	1	0	69	70
57B	1	0	28	29
59	0	0	1	1

Table B (cont'd)

Station	Bosmina sp.	Number of Cladocera Counted E. coregoni	Other	Total
59	0	0	2	2
6	1	0	102	103
60	0	0	1	1
61	0	0	40	40
64	39	105	101	242
68	1	6	41	48
69	14	9	72	85
7	1	0	56	57
8	1	0	49	50
9	4	0	72	76
RR81	2	0	316	318

Table C. Cladoceran counts from extant samples collected throughout Lake Winnipeg, Manitoba, Canada, in summer 2004.

Station	Number of Cladocera Counted			
	Bosmina sp.	*E. coregoni*	Other	Total
1	11	0	47	58
10A	18	0	249	267
10s	13	0	101	114
11	28	0	73	101
12B	40	0	77	117
13B	74	0	95	169
16S	1	0	0	1
17	95	53	53	201
18	381	28	109	518
2	1	0	137	138
23B	62	3	64	129
23ES	160	10	284	454
23S	217	11	334	562
25s	17	9	77	103
26s	245	18	368	631
28	54	2	171	227
33	173	19	319	511
34s	458	19	262	739
35s	192	55	644	891
36S	0	0	313	313
37S	24	0	485	509
39	31	10	188	229
3B	0	0	313	313
41	68	23	230	321
45	176	22	146	344
50s	249	12	152	413
53	42	4	351	397
54	77	2	163	242
55	50	0	151	201
57BS	2	0	410	412
57S	2	0	474	476
58S	2	0	489	491
59	16	0	527	543
6	12	0	99	111
60B	2	0	415	417
60C	0	0	292	292
61	0	0	182	182
62	4	0	101	105
64	91	21	214	326
68	54	8	162	224
69	86	2	292	380
7	50	0	16	66
8	101	1	57	159
DV13	8	0	333	341
W1	168	28	291	487
W442s	150	20	309	479

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Chapter 4: General Discussion

Comprehensive, multi-year studies of Lake of the Woods and Lake Winnipeg have only recently commenced. The basic ecological data that is being gathered for these systems is comparable to studies that were conducted on the Laurentian Great Lakes over thirty years ago. As the rate of biological invasions continues to increase worldwide, the importance of investigating these invasions also increases. Although little is known regarding the aquatic communities within Lake of the Woods and Lake Winnipeg, the number of invading aquatic species in these water bodies is relatively low compared with the current number of invaders present in the Laurentian Great Lakes. As a result, information surrounding the invasion dynamics of *E. coregoni* in the Lake Winnipeg watershed will lay the foundation for future studies concerning aquatic invasions in inland lakes and rivers in Central Canada.

E. coregoni has been in North American waters for nearly four decades. Despite relatively rapid dispersal within the Laurentian Great Lakes (Mills et al. 1993), the range of *E. coregoni* is still reported to be restricted to this region (DeMelo and Hebert 1994a). This study provides the first documentation of *E. coregoni*'s presence in Lake of the Woods and Lake Winnipeg, including historical information regarding the initial introduction of this species that is only available from the sediment record. The dates provided by sediment analyses for both of these water bodies indicate *E. coregoni* likely appeared in the Lake Winnipeg watershed in the late 1980s or early 1990s. Because the estimated dates of *E. coregoni*'s first appearance obtained for Lake of the Woods and Lake Winnipeg are within a few years of each other, it may never be known which of these water bodies was invaded first.

Due to the many different vectors of dispersal available to *E. coregoni* and other aquatic invaders, the mechanism(s) by which this species has moved beyond the Laurentian Great Lakes region may never be determined. It is likely that *E. coregoni* entered Lake of the Woods via Rainy River from Rainy Lake, Ontario, and, ultimately, from Lake Superior. Whether this dispersal was due to human activities or natural dispersal is unknown. Once in Lake of the Woods, *E. coregoni* most likely traveled downstream in the Winnipeg River to Lake Winnipeg. Future studies examining the microfossil record in sediments along the Rainy River and the Winnipeg River may help decipher whether riverine connections are a probable method of dispersal. Further, as rainbow smelt and *E. coregoni* appear in the Lake Winnipeg watershed at similar times, investigating rainbow smelt distribution patterns and gut content analyses will indicate if fish are a possible vector for the transport of *E. coregoni* into these water bodies.

It is important to keep in mind that not all invasions are successful and that a number of inoculations into these water bodies may have taken place before *E. coregoni* began to increase in abundance (Hairston et al. 1999). One way to determine the number of invasion events into these systems is to assess allozymic variation in the *E. coregoni* populations from these lakes (DeMelo and Hebert 1994b). By comparing genetic information from the Lake Superior, Lake of the Woods, and Lake Winnipeg populations, the extent of genetic divergence and levels of genetic variability in all three populations can be determined. Ultimately, this information will indicate the number of clonal lineages that founded the Lake of the Woods and Lake Winnipeg populations, thereby suggesting the number of invasions that may have occurred in order to result in the successful establishment of *E. coregoni* in these water bodies. Similar genetic

variability in all three locations would indicate that a large number of founding individuals colonized Lake Winnipeg. If the Lake Winnipeg population shows low genetic variability compared to the Lake of the Woods and Lake Superior populations, very few individuals would have likely founded the population.

Once the successful introduction of a NIS has taken place, conditions must be suitable for that particular species in order for a population to establish (Kolar and Lodge 2001). In the majority of the Laurentian Great Lakes, *E. coregoni* has become a dominant member of the zooplankton community (Mills et al. 1993). In contrast, the distribution of *E. coregoni* in Lake Superior is restricted to the western region of the lake (Grigorovich et al. 2003). Despite *E. coregoni* having a restricted distribution within Lake Superior, this lake may still have been a source population for Lake of the Woods and Lake Winnipeg. Grigorovich et al. (2003) have suggested a number of reasons why NIS, in general, are scarce in Lake Superior. In terms of establishment, the physical and chemical properties of a water body will be strong factors inhibiting or facilitating the invasion of a NIS. One major contrast between Lake Superior and Lake of the Woods/Lake Winnipeg is that Lake Superior is relatively oligotrophic (Grigorovich et al. 2003). The present study indicates that *E. coregoni* tends to be present in areas of intense cyanobacterial blooms in Lake of the Woods and Lake Winnipeg. Therefore, it is possible that the oligotrophic conditions of Lake Superior prevent the occurrence of cyanobacterial blooms, thereby inhibiting *E. coregoni* populations from establishing throughout the lake. Future studies should consider the limnological characteristics of Lake Superior, Lake of the Woods, and Lake Winnipeg to determine if there are other similarities and/or

differences in these water bodies that facilitate the invasion of *E. coregoni* and other NIS species.

At this time it is not known whether *E. coregoni* will become a dominant member of the cladoceran community in either Lake of the Woods or Lake Winnipeg. Once the factors that favour the establishment of this species are investigated further, the potential effects of *E. coregoni* on the zooplankton community and other trophic levels can be examined. In comparison to other aquatic NIS such as *Dreissena polymorpha* and *Bythotrephes longimanus*, the invasion of *E. coregoni* into Lake of the Woods is relatively non-threatening. It is likely that other aquatic invaders will enter the Lake Winnipeg watershed in the near future. Therefore, the fact that *E. coregoni* is one of the first zooplankton invaders to enter Lake of the Woods and Lake Winnipeg provides a unique opportunity to study the invasion dynamics of NIS before more harmful species arrive in these systems. Precautions should be taken in order to prevent these water bodies from deteriorating to the point that their food webs are dramatically and permanently altered. As both of these water bodies are used extensively for recreational, aesthetic, and commercial (Lake Winnipeg) purposes, studying invasions of NIS in Lake of the Woods and Lake Winnipeg should be a high priority in the coming years.

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