

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

University of Manitoba

in partial fulfillment of the requirements of the degree of

MASTER OF SCIENCE

Department of Zoology

University of Manitoba

Winnipeg, Manitoba, Canada

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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

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 Shradler-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 longimanus*, 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). Ehippia 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 ehippia, 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