Long-term changes in native mussel assemblages following dreissenid mussel invasion

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Abstract

Freshwater mussels (Unionidae) are the most imperiled faunal group in North America, with >70% of species threatened, endangered, or extinct. Unionid mussels on this continent have evolved in the absence of dominant macrofouling organisms; prior to the invasion of the zebra mussel (*Dreissena polymorpha*), no byssally-attached molluscs existed in North American inland waters. Consequently, unionid mussels have no adaptive defenses against zebra mussel fouling and typically suffer substantial mortality or near total extirpation within 4-8 years following invasion of habitats that support dense dreissenid populations. Water chemistry, specifically low calcium concentration, limits the proliferation and impacts of *Dreissena* in invaded waterways. To investigate the long-term effects of *Dreissena* invasion and their context dependence, I surveyed unionid populations and measured fouling intensities in a river with heterogenous calcium concentrations (St. Lawrence River, ~10–30 mg/L Ca^{2+}) and one of its tributaries with a uniformly suboptimal calcium concentration (Richelieu River, ~18 mg/L Ca^{2+}), after 25+ years exposure to *Dreissena*. My results from the St. Lawrence River show that there has been no unionid recovery since the mass mortalities seen in the mid-1990s, although there are now low fouling intensities and *Dreissena* field densities have declined >90% since 1995. In the Richelieu River, my findings show overall unionid population declines and diversity loss comparable to those seen in invaded high-calcium rivers, with some locations providing limited co-existence of unionids and dreissenids at low densities. Collectively, my research contributes to the literature on long-term effects of *Dreissena* invasion and unionid conservation, in addition to emphasizing the importance of monitoring seemingly low-risk environments.

Résumé

Les moules d'eau douce (Unionidés) constituent le groupe faunistique le plus menacé en Amérique du Nord, avec plus de 70 % des espèces menacées, en voie de disparition ou éteintes. Les moules unionidés de cette région ont évolué en l'absence d'organismes macro-salissants dominants; avant l'invasion de la moule zébrée (*Dreissena polymorpha*), il n'existait pas de mollusques fixés par le byssus dans les eaux intérieures de l'Amérique du Nord. Par conséquent, les moules unionidés n'ont aucune défense adaptative contre l'encrassement par la moule zébrée et souffrent souvent d'une mortalité importante ou d'une disparition quasi totale dans les 4 à 8 ans suivant l'invasion. La chimie de l'eau, en particulier une fabile concentration en calcium, limite la prolifération et l'impact des moules zébrées dans les cours d'eau envahis. Pour étudier les effets à long terme de cette invasion et ses dépendances au contexte, j'ai recensé les populations d'unionidés et mesuré l'intensité des salissures dans un fleuve aux concentrations de calcium hétérogènes (fleuve Saint-Laurent, ~10-30 mg/L Ca^{2+}) et dans l'un de ses affluents dont la concentration de calcium est homogène et sous-optimale (rivière Richelieu, ~18 mg/L Ca^{2+}), après plus de 25 ans d'exposition à *Dreissena*. Les résultats obtenus dans le fleuve Saint-Laurent montrent qu'il n'y a pas eu de rétablissement des unionidés depuis les mortalités massives observées au milieu des années 1990, bien que l'intensité de l'encrassement ait été faible et que les densités de champ de *Dreissena* aient diminué de plus de 90 % par rapport à 1995. Dans la rivière Richelieu, mes résultats montrent un déclin global des populations d'unionidés et une perte de diversité comparables à ceux observés dans les rivières envahies par le calcium, certains endroits offrant une coexistence limitée des moules à de faibles densités. Collectivement, ma recherche contribue à la littérature sur les effets à long terme de l'invasion de *Dreissena* et la conservation des unionidés, en plus de souligner l'importance de revisiter des environnements apparemment à faible risque.

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Contribution of Authors

This thesis was completed under the co-supervision of Prof. Anthony Ricciardi and Dr. Zofia Taranu, who will be co-authors on all manuscripts. Prof. Anthony Ricciardi was involved in the conceptualization of each chapter, Dr. Zofia Taranu was involved in the statistical analysis of each chapter, and both provided significant edits to the manuscript. I conducted the field sampling for Chapters 1 and 2 during 2022 and 2023, in addition to gathering and cleaning historical data and writing the manuscript draft. The main body of this thesis (Chapters 1 and 2) was written with the intention of journal submission.

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General Introduction

Dreissenid fouling: a novel interaction in North American freshwater ecosystems

Species invasions are a significant stressor to biodiversity in freshwater lakes and rivers (Dextrase & Mandrak, 2006; Ricciardi & MacIsaac, 2011). Eurasian dreissenid mussels (the zebra mussel *Dreissena polymorpha* and the quagga mussel *Dreissena bugensis*) are considered among the most disruptive freshwater invaders, as they significantly impact native biodiversity, food webs, nutrient and contaminant cycling, and habitat structure; in addition, they reduce the recreational benefits of the waterbodies they invade while incurring large economic costs (Karatayev et al., 1997; Ricciardi et al., 1997; Hecky et al., 2004; Keretz et al., 2021; Haubrock et al., 2022) . The zebra mussel was discovered in the Great Lakes in the late 1980s and was followed soon after by the quagga mussel, both species likely having been introduced through ship ballast water discharge (Hebert et al., 1989; Carlton, 2008). Dreissenids subsequently spread to the remaining Great Lakes and other connected rivers and are now prevalent in most major river systems in North America.

Dreissenid mussels are native to the Ponto-Caspian basins (Black, Caspian and Azov seas) of Eastern Europe, which consist of fresh and brackish waters (Reid & Orlova, 2002; Son, 2007). Ponto-Caspian species (including the round goby, tubenose goby, fishhook water flea, and dreissenid mussels) are highly adapted to a range of environmental conditions (Ricciardi & MacIsaac, 2000; Reid & Orlova, 2002; Pauli & Briski, 2018) and their evolutionary history is thought to have contributed to their successful expansion into non-native water bodies (Soto et al., 2023). Most invasive species discovered newly established in the Great Lakes between 1985 and 2000 originate from the Ponto-Caspian basins (Ricciardi & MacIsaac, 2000). Owing to an evolutionary history in ion-rich waters, zebra and quagga mussels perform best in alkaline environments (Mitchell et al., 1996; Jones & Ricciardi, 2005; Haltiner et al., 2023).

Invaders which use limiting resources more efficiently than native species (i.e. having higher feeding rates, a more generalist diet, etc.) are more likely to disrupt food webs (Vitousek, 1994; Ricciardi & Atkinson, 2004; Ricciardi et al., 2013). Dreissenid mussels possess certain traits of marine bivalves that make them functionally novel in freshwater habitats in North America (Reid & Orlova, 2002). For example, in contrast to native North American freshwater molluscs, dreissenids have planktonic larvae (veligers) produced from external fertilization. Veliger larvae are easily entrained in ship ballast water and survive transoceanic voyages. The larvae develop in the water column for several weeks prior to settling onto bottom substrates as mussels. The second marine-like trait is attachment using proteinaceous (byssal) threads. Repeated settlement events can lead to rapid overgrowth (fouling) of virtually any solid surface, including the shells of native molluscs, notably unionid mussels (Lewandowski, 1976; Ricciardi et al., 1995; Strayer & Smith, 1996). Organisms that have evolved in insular environments lack adaptive traits that allow for coexistence with a broad range of introduced species (Ricciardi et al., 2013). Unionid mussels in North America and in various other regions of the world have evolved in the absence of dominant macrofouling species and are therefore naïve to dreissenid colonization of their shells (Ricciardi et al., 1998).

Fouling as a cause of unionid population mortality

Unionid mussels are among the most threatened groups of animals in North America, with more than 70% of species endangered or already extinct (Ricciardi et al., 1998; Ricciardi & Rasmussen, 1999). After dreissenid mussels became established in North American waterways, they began to decimate multiple populations of unionid mussels (Nalepa et al., 1996; Ricciardi et al., 1996; Schloesser et al., 2006; Strayer & Malcom, 2007). The primary cause of these declines is fouling by attached dreissenids (Ricciardi, 2003; Burlakova et al., 2014). In their normal orientation, unionids partially bury themselves upright in the sediment with their posterior (siphonal) end exposed in the water column for filtration. The exposed shell provides opportunistic substrate for dreissenids during settlement (Mackie, 1991). In environments where there is an abundance of mud and sand, unionid shells are often the only possible solid colonizable surface for dreissenids. Some studies have shown that given choices of substrate, dreissenids prefer to settle on live unionids (Lewandowski, 1976), and that body condition (shell growth, body mass and glycogen content) of zebra mussels is enhanced when attached to unionids rather than inanimate substrates (Pilotto et al., 2016).

There are multiple ways in which dreissenid fouling directly harm individual unionids. Fouling can cause unionid shell deformities, owing to the tension applied by byssal threads pulling at shell matter (Hunter & Bailey, 1992). Dreissenids also benefit from the unionid's siphonal currents, intercepting food particles; larger clusters can obstruct the siphon and thus prevent the unionid from accessing food (Hebert et al., 1991; Schloesser et al., 1996; Hörmann & Maier, 2006). At high fouling intensities, dreissenids will often settle across the valves and suture them shut or, alternatively, will block the gape and prevent normal valve closure (Mackie, 1991; Zwarych, personal observation). Being unable to fully close their valves will render unionids at higher risk of predation and parasitism, whereas being unable to sufficiently open their valves would interfere with siphonal activity needed for normal respiration, excretion, feeding and reproduction; it could also prevent extension of the foot, thereby inhibiting movement and shell orientation (Mackie, 1991; Ricciardi et al., 1996; Schloesser et al., 1996; Burlakova et al., 2000).

Carrying a mass of attached dreissenids can force the unionid to expend high levels of energy to maintain an upright position in the sediment, thereby hindering its movement and burrowing (Gillis & Mackie, 1994; Schloesser & Nalepa, 1994). The loss of energy could result in insufficient energy stores to survive winter in high-latitude regions (Haag et al., 1993; Nalepa, 1994; Schloesser & Nalepa, 1994; Ricciardi et al., 1996). Fouling intensity on individual unionids can grow rapidly through conspecific attraction, creating a large colonizable surface area for further dreissenid settlement (Ricciardi et al., 1995; Dzierżyńska-Białończyk et al., 2018; Zwarych, personal observation). Although unionids face this parasitism, the fouling performance of dreissenid mussels is largely dependent on a suite of environmental variables that can greatly influence its severity.

Context dependencies of fouling impacts

Temperature and water chemistry

Fouling intensity on unionids is influenced by site-specific environmental factors, including temperature and water quality (Jokela & Ricciardi, 2008). One study recorded lower rates and intensities of fouling, as well as higher unionid diversity and abundance, within the thermal plume of a power plant (Bryan et al., 2013), suggesting a warm temperature refuge for unionids. Furthermore, zebra mussels were shown to have lower survival rates during exposure to elevated CO_2 as temperature increases, which did little to no harm to two species of unionids (*Lampsilis cardium* and *Leptodea fragilis*) at any temperature (Waller et al., 2020).

With regards to pH, it has been suggested that the minimum pH level is 8.0 for zebra mussels to reach infestation levels specifically in the Great Lakes (Claudi & Mackie, 1994); however, pH was shown to not be an important predictor variable by itself for zebra mussel growth compared to other parameters (Hincks & Mackie, 1997). Furthermore, when investigating the performance of quagga mussels, their pH tolerance depended heavily on salinity of the water and dissolved calcium concentrations (Seitz et al., 2023). Aside from pH and temperature, arguably the most important water quality variable that effects the distribution of dreissenids is calcium concentration.

As mentioned previously, dreissenid mussels are adapted to ion-rich waters (Reid & Orlova, 2002) and thrive in waters rich in dissolved calcium, which is required for shell growth, osmoregulation, and reproduction (Hincks & Mackie, 1997; McMahon, 1996; Vinogradov et al., 1993). Low calcium concentration has been shown to limit the spread and local abundance of dreissenid mussels (McMahon, 1996; Hincks & Mackie, 1997; Jones & Ricciardi, 2005; Jokela & Ricciardi, 2008). Dreissenid populations rarely occur in waterbodies with minimum calcium concentrations below 25 mg/L (Ramcharan et al., 1992; Mellina & Rasmussen, 1994; Karatayev, 1995; Hincks & Mackie, 1997). Normal ion exchange is disrupted below 15 mg/L (Vinogradov et al., 1993) and shell growth is impaired below 8.5 mg/L (Hincks & Mackie, 1997). Consequently, waterbodies with calcium concentrations below 20 mg/L are considered at low to moderate risk of dreissenid invasion (Therriault et al., 2013; Whittier et al., 2008). In contrast, unionids are much more tolerant to low-calcium conditions (McMahon & Bogan, 2001), with some species in the Great Lakes region (*Elliptio complanata* and *Pyganodon grandis*) having persistent populations in calcium concentrations as low as 2–3 mg/L (Rooke & Mackie, 1984; Strayer et al., 1981). Therefore, waterbodies with low calcium concentrations could serve as a refuge for unionids against severe effects of dreissenid fouling (Jokela & Ricciardi, 2008).

Differences in susceptibility among unionid species

Different species of unionids have varying tolerances of dreissenid fouling, due to morphological, physiological and behavioural differences (Haag et al., 1993; Gillis & Mackie, 1994; Strayer & Smith, 1996; Martel et al., 2001). Some unionids expose a larger amount of shell surface area to the water column, causing them to be more readily fouled (Urbańska et al., 2019). The thickness and mass of a unionid's shell may also affect its tolerance to fouling; individuals with thicker shells may expend less energy keeping themselves upright in the sediment than species with lighter shells subjected to the same mass of attached dreissenids (Haag et al., 1993). Although more research is needed in this area, one study found that the unionid *Unio pictorum* was fouled less than other species, possibly due to its shell surface quality; the chemical composition and micro-topology of some unionid shells might be less favorable for dreissenid attachment, similar to those of marine mussels that have adaptations against severe biofouling (Dzierżyńska-Białończyk et al., 2018).

Some unionids have different burrowing behaviour than others which also affects the severity of fouling they experience (Bowers & Szalay, 2004; Dzierżyńska-Białończyk et al., 2018). For example, *Elliptio complanata* are often found deeply buried in areas with soft sediment, which likely suffocates attached dreissenids or physically dislodges them (Amyot & Downing, 1991; Martel et al., 2001). Furthermore, it has been hypothesized that heavy fouling may trigger a burrowing response in *E. complanata*, in addition to them burrowing for other cues like extreme weather (Martel et al., 2001). Nichols and Wilcox (1997) also observed burrowing in response to dreissenid fouling during lab experiments with two common species of Lake Erie, *Amblema plicata* and *Leptodea fragilis.* Overall, numerous studies confirm that *E. complanata* is less impacted by dreissenid fouling than other unionid species, which may be due to their faster rate of burrowing than other species (Lewis & Riebel, 1984).

Finally, unionids that invest more time and energy into reproduction (e.g. Anodontinae and Lampsilinae) are likely to be more sensitive to fouling than short-term breeders (Haag et al., 1993; Hallac & Marsden, 2000; Nalepa, 1994). Indeed, various studies noted differences in rates of population decline across species (e.g. Ricciardi et al., 1996; Martel et al., 2001). In sexually dimorphic species, females may have lower tolerances to dreissenid fouling than males (Hallac & Marsden, 2000).

Differences between zebra and quagga mussels

Over the past few decades, quagga mussels have become the dominant dreissenid species in various habitats that were first invaded by zebra mussels (Ginn et al., 2018; Marescaux et al., 2015; Matthews et al., 2014; Ricciardi & Whoriskey, 2004). Physiological differnces between these congeneric species can affect their habitat distribution, environmental tolerances, and fouling abilities, and might also contribute to shifts in dominance toward the quagga mussel (Metz et al., 2018). Temperature tolerance of dreissenids is influenced greatly by depth and turbidity (Karatayev et al., 1998), but quagga mussels have been shown to outcompete zebra mussels for food at temperatures $\leq 20^{\circ}$C (Huang et al., 2016). Generally, zebra mussels feed less than quagga mussels, with both species displaying higher filtration rates as temperature increases (Haltiner et al., 2023). In areas of high turbidity, zebra mussels were more prone to mortality and had slower growth than quagga mussels, which were able to acclimate to changing conditions by altering their palp-to-gill area ratio (Ouellette-Plante et al., 2017). Furthermore, quagga mussels are able to colonize greater depths (>200 m) whereas zebra mussels are generally limited to depths of approximately 40 m and shallower (Karatayev et al., 2015). Zebra mussels allocate more energy toward reproduction, whereas quagga mussels grow to larger sizes and have higher survivorship in stable environments (Karatayev et al., 2011; McMahon, 2002). The attachment strength of dreissenid mussels on artificial substrate was found to be positively correlated with size, which therefore benefits quagga mussels more so than zebra mussels (D'Hont et al., 2021). Conversely, the adhesive strength of both zebra mussels and quagga mussels on polyvinyl chloride (PVC) was the same, and zebra mussels displayed greater attachment strength than quagga mussels on more hydrophobic artificial substrate (James et al., 2021). However, quagga mussels do not seem to show the same preference for unionid shells as substrate compared to zebra mussels, although further investigation is needed in this area (Conn & Conn, 1993).

Research objectives

The goal of this research was to determine the long-term impacts of dreissenid (zebra and quagga mussel) invasion on native unionid mussels in river systems in southern Quebec. Unionid densities, fouling intensities, calcium concentrations, and dreissenid field density were measured sporadically over 25+ years in two large water bodies in southern Quebec. Chapter 1 focuses on these dynamics in the upper St. Lawrence River, near the outflow of the Ottawa River and throughout the fluvial Lake St. Louis. Differences in water chemistry between the St. Lawrence and Ottawa rivers creates a natural calcium gradient along the northern shore of Lake St. Louis. Since dreissenids are scarce in low calcium environments, studying this area allows us to separate the effects of dreissenid mussels from other environmental variables that equally affect both rivers. My objectives for this chapter were to measure current unionid densities across this heterogeneous habitat to compare the impacts of dreissenid invasion 30 years after establishment and investigate evidence of any possible recovery.

Chapter 2 focuses on unionid populations in the Richelieu River, which is supplied with zebra mussel larvae from its headwaters, Lake Champlain. The Richelieu River has a narrowly bounded calcium concentration of ~18 mg/L and would be considered of low risk for zebra mussel proliferation. My objectives for this chapter were to investigate if any co-existence between unionids and zebra mussels was occurring and compare long-term densities of unionid populations to those of other invaded, high-calcium rivers.

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Chapter 1: Long-term impacts of invasive dreissenid mussels on native unionids in the upper St. Lawrence River

Abstract

Eurasian dreissenid mussels (the zebra mussel *Dreissena polymorpha* and the quagga mussel *Dreissena bugensis*) invaded the St. Lawrence River in the 1990s. Their negative effects on native North American freshwater mussels (unionids) are well documented, but few studies have investigated their long-term impacts on unionid populations. Using data spanning 30 years, we provide a status update of unionid and dreissenid populations within the upper St. Lawrence River. In 2022-23, we sampled unionids and dreissenids at fifteen sites between the Island of Montreal and the outflow of Lake Ontario, with most sites having been previously sampled multiple times since the early stages of invasion. Combining the results of this survey with historical data, we found that dreissenid population densities and fouling levels (numbers of attached dreissenid mussels) on unionids have both declined by >90%, after attaining peak levels in the mid-1990s. Since 1992, unionid populations at these sites experienced exponential declines such that, on average, they are now at ~1% of their pre-invasion densities. We hypothesize that these declines are primarily caused by the effects of prolonged exposure to dreissenid mussel fouling and competition. At the present time, there is a limited co-existence between unionids and dreissenids in the river, with no evidence of unionid population recovery. Thirty years since dreissenid mussels reached peak abundances and subsequently declined, the legacy of their impacts on native mussels remains.

Introduction

Long-term changes to the impacts of biological invasions are traditionally understudied (Strayer et al., 2006). Thoroughly documenting invasions and their impact history would allow researchers and managers to make more informed conclusions (and even predictions) about invasion risks. This is especially relevant in freshwater environments, where invasions apparently cause greater ecological changes than in continental terrestrial and marine systems (Ricciardi & MacIsaac 2011).

The Great Lakes–St. Lawrence River basin is the most invaded freshwater ecosystem in the world, containing nearly 190 established non-native species (Sturtevant et al., 2019; Ricciardi & MacIsaac, 2022). Of these, Eurasian dreissenid mussels (the zebra mussel *Dreissena polymorpha* and the quagga mussel *Dreissena bugensis*) are considered among the most disruptive invasive species, as they have significantly altered ecosystems and incurred enormous economic costs (Ricciardi et al., 1995, 1996, 1997; Higgins & Vander Zanden, 2010; Haubrock et al., 2022). The St. Lawrence River was the first large river system in North America to be colonized by dreissenid mussels (Griffiths et al., 1991), making it a valuable model system to study the long-term effects of invasion for the purpose of informing risk assessment and predictions for other large rivers.

Some of the most conspicuous effects of dreissenid mussels have been on native freshwater mussels (Order: Unionida, "unionids"), which are already among the most threatened faunal groups in North America (Ricciardi et al., 1998). Native mussels in the St. Lawrence River have experienced many significant changes to their physical environment over the previous century, including intense dredging and major modifications of the river channel during the creation of the modern St. Lawrence Seaway in 1959 (Parham, 2004), as well as other stressors such as organic and heavy metal pollution, urbanization, shoreline development, and warming surface water temperatures (Bartolai et al., 2015; Montiel-León et al., 2019; Foubert et al., 2020). Nevertheless, an assemblage of locally abundant and apparently hardy unionid species have persisted in the river at collective densities as high as 75–120 individuals/m^2 between the mid-1970s and 1992 (Levasseur, 1977; Ricciardi et al., 1995).

Despite the apparent resilience of these populations, they were rapidly decimated in many areas of the upper St. Lawrence River during the 1990s following zebra mussel colonization (Ricciardi et al., 1995, 1996). Dreissenid mussels use collagen-like byssal threads to attach themselves in dense clusters onto virtually any solid surface, including the shells of other molluscs. Unionids were identified as an important substrate early in the invasion of the river, such that zebra mussel occurrence and density were correlated with local unionid abundance (Mellina & Rasmussen, 1994). Dreissenid fouling poses a unique challenge for unionids. Prior to dreissenid invasion, no byssally-attached mussels existed in North American inland waters; consequently, unionids have no adaptive evolutionary experience with such dominant biofouling organisms (Ricciardi et al., 1998). Intense fouling by dreissenids can prevent unionids from fully opening and closing their valves, and can interfere with normal feeding, respiration, excretion, and reproduction (Haag et al., 1993; Tucker, 1994; Schloesser et al., 1996). Furthermore, fouling can add an increasing amount of weight to unionid shells that forces individuals to expend significant amounts of energy to keep themselves upright in the sediment, and their normal movement and burrowing activities are impaired (Schloesser and Kovalak, 1991; Tucker, 1994). Fouling can also reduce the body condition of unionids such that they lack sufficient energy to survive winter in north temperate regions (Haag et al., 1993; Ricciardi et al., 1996). Unionid sublethal effects and mortality are correlated with dreissenid fouling intensity (Ricciardi et al., 1995; Ricciardi, 2003) and severe unionid population declines typically occur within 4–8 years after dreissenid invasion (Ricciardi et al., 1998; Burlakova et al., 2000; Zanatta et al., 2015; Strayer & Malcom, 2018). Dreissenid colonization has accelerated the local extinctions of unionid species by at least a factor of 10 in many areas of the Great Lakes–St. Lawrence River system (Ricciardi et al., 1998). However, it is unknown whether these population declines generally persist through time or are ultimately mitigated such that some level of recovery occurs—and, if so, how much time is required for such recovery.

Dreissenids were first observed colonizing unionids in the St. Lawrence River in 1991 (Conn & Conn, 1993). By the mid-1990s, near total extirpation of populations at several sites in upper section of the river was observed (Ricciardi et al., 1995, 1996). After dreissenid populations reached peak densities of >5000/m^2 in the 1990s, they subsequently declined in abundance (Farrell et al., 2010), which might be expected to reduce fouling levels on unionid (Ricciardi et al., 1996) and thus unionid mortality (Jokela & Ricciardi, 2008). Furthermore, the zebra mussel has been replaced by the quagga mussel as the dominant dreissenid throughout much of the St. Lawrence River (Ricciardi & Whoriskey, 2004), and the quagga mussel has been shown to foul native unionids less intensely (Conn and Conn, 1993; Burlakova et al., 2014). Given that unionid mussels, with few exceptions, depend on a fish host to carry their glochidia larvae until metamorphosis (Bauer & Wächtler, 2001), fish can play a role in mitigating declining populations or recolonizing areas in which they have been extirpated. These considerations lend credence to the possibility that recovery of decimated unionid populations can occur in a large heterogeneous system, given sufficient time.

Unionid species recorded in the St. Lawrence River have a mean life expectancy of ~20–25 years and require 6–10 years to reach reproductive maturity (Magnin & Stanczykowska, 1971). Here, over a period spanning a few generations of unionids, we quantified long-term changes in unionid populations and investigated their possible recovery. We evaluated three scenarios in which unionid populations 1) rebound to the 1992 baseline level prior to massive dreissenid colonization (i.e., complete recovery); 2) reach an intermediate level below their pre-invasion densities (i.e., partial recovery); or 3) remain nearly or completely extirpated with no sign of recovery within the 30-year time frame (Figure 1.1).

Methods

Site Locations

From June to September of 2022 and 2023, respectively, we sampled fifteen sites within the upper St. Lawrence River between Mallorytown, Ontario (~60 km from the outflow of Lake Ontario) and Lac Saint-Pierre in Trois-Rivières, Québec (Figure 1.2). Since unionid populations do not experience significant population fluctuations over a summer season, we were able to sample over four months without having to account for temporal correlations (Bauer & Wächtler, 2001). Sites were selected based on accessibility as well as our knowledge of previously sampled unionid populations (Ricciardi et al., 1995, 1996; Jokela & Ricciardi 2008), to allow spatiotemporal comparisons. Near the Island of Montreal, the St. Lawrence River is joined by the lower Ottawa River, forming a fluvial lake (Lake St. Louis), which contains a conductivity gradient produced by the two contrasting water masses (Magnin, 1970; Kestrup & Ricciardi, 2009). We prioritized sampling sites that were dominated by the ion-rich waters of the St. Lawrence River, since these sites experienced the highest peak abundances of dreissenid mussels (Jones & Ricciardi, 2005) and the most severe declines of unionid populations in the mid-1990s (Ricciardi et al., 1996).

Sampling Techniques

We accessed all sites from shore. At each site, SCUBA divers searched underwater for unionids for a maximum of 60 person-minutes within an approximate area of 1 acre. Divers did not venture deeper than 2 m depths, except at those upstream sites that had maximum depths of ~5–10m (Brockville, Prescott, and Cardinal sites). To estimate density, we haphazardly cast a $1m^2$ polyvinyl chloride (PVC) quadrat onto the bottom substrate and collected all unionids within its boundary (following Ricciardi et al., 1996). We collected all visible unionids, living or dead, and manually probed the upper 10cm of sediment to locate living individuals and empty shells buried immediately beneath the surface. If we failed to locate a living unionid within the sampling period, we recorded a density of 0 individuals/m^2. All specimens were placed in a nylon mesh bag and brought up to the surface and onshore for processing. Once onshore, they were identified to species following Clarke (1981) and McMahon and Bogan (2001). We weighed the individual with any attached dreissenids; if attached dreissenids were present, we manually removed, counted, and identified them, then weighed the cleaned unionid a second time and measured its shell length. All live unionids were returned to the sediment within the area from which they were collected. All dreissenids were placed in plastic bags (one for each unionid specimen), stored in a cooler, and transported to the lab for species identification and enumeration.

Freshly killed unionids were distinguished from older shells by an intact hinge ligament and uneroded nacre (cf. Ricciardi et al., 1996). Where unionid site densities were at least 10 individuals m^{-2}, we sampled five replicated $1m^2$ quadrats per site, as this was previously determined to yield a precision of ±20% (Downing & Downing, 1992). If unionid densities were below 10 individuals m^{-2}, we sampled ten quadrats per site. We also estimated *Dreissena* density at each site via quadrat sampling, in which divers haphazardly tossed a 0.0625m^2 (25 cm × 25 cm) PVC quadrat onto the bottom substrate and collected all dreissenids within its boundary (cf. Ricciardi et al., 1996). We sampled three replicated quadrats per site—except when dreissenid densities were >100 individuals per quadrat (i.e., >1600 m^{-2}), in which case we sampled two quadrats per site. All rocks and other hard substrata within the quadrat were collected, placed in mesh nets to be transported to shore, where attached mussels were removed by hand or by using a small knife. We placed the dreissenids in plastic collection bags in a cooler and transported them back to the lab, where we identified them to species and measured their shell lengths.

We collected water quality data *in situ* using a YSI Pro Quatro multimeter and brought two water samples in separate 1L plastic bottles back to the lab, where we determined the dissolved calcium concentration (Ca^{2+} in mg L^{-1}, converted from $CaCO_3$ in mg L^{-2}) by titration, using a LaMotte chemical test kit. We averaged the two readings to obtain a single estimate of [Ca^{2+}] for each site.

These procedures were identical for all previous data collections (Ricciardi et al., 1995, 1996; Jokela & Ricciardi, 2008; Ricciardi, unpubl. data), thereby permitting direct comparisons over time. All statistics were performed using R Statistical Software (v4.2.1; R Core Team 2023).

Results

Unionid populations in the upper St. Lawrence River declined exponentially since the early 1990s, concomitant with dreissenid mussel population expansion (Figure 1.3a). None of the populations at sites that were sampled previously (Ricciardi et al., 1996) had been found to recover their early-invasion (1992) densities by 2022-23. No living unionids were found at sites at which extirpations had occurred in the mid-1990s. In 2022 and 2023, mean unionid density across thirteen sites was 0.2 m^{-2}, which is approximately 1% of pre-invasion densities (Figure

1.3a). By contrast, unionid densities in the lower Ottawa River have remained stable or declined only slightly over the same time period (Figure 1.3b); but it must be noted that the Ottawa River data are very spatially limited (Jokela & Ricciardi, 2008) and that decline of unionid mussels due to zebra mussel invasion in the Ottawa River watershed has only been studied in detail in one of its tributaries, the Rideau River (Martel et al. 2001). In total, only four live species of unionids were collected across all our sampling sites; *Elliptio complanata* and *Lampsilis radiata* were the most common species, whereas *Pyganodon cataracta* was last encountered alive in 1994 and *Ligumia recta* was encountered alive on only one occasion in 1993, at our sites in the upper St. Lawrence River. Previous exploratory visits to other areas of the St. Lawrence River beyond our sampling sites (Figure 1.2) found *Elliptio cf. crassidens* in 1994 at the Port of Montreal and *Lampsilis cardium* in 2016 in Lake St. Pierre (Ricciardi, unpubl. data).

We found 25 living unionids within the St. Lawrence River in 2022-23, of which nearly half (12 individuals) were fouled by dreissenids. Fouling intensities in the St. Lawrence River peaked in 1994 and then decreased across time to 2022-23, where we recorded the lowest intensities (0 to 4 dreissenids per unionid) across our 30+ year dataset (Figure 1.4). In years where both the St. Lawrence and Ottawa rivers were sampled, the lower Ottawa River unionids were consistently less fouled than those in the St. Lawrence River (Figure 1.4). The composition of attached dreissenids on unionids was dominated by the zebra mussel across all years, but with an increasing proportion of quagga mussels from 2005 to 2022-23 (Table S1). This pattern is mirrored by changes in dreissenid field densities, which peaked in the mid-1990s and subsequently declined by >90% to their lowest observed level in 2022-23, while the proportion of quagga mussels increased (Table S1).

Discussion

Unionid diversity and population declines after dreissenid invasion

Within a decade following dreissenid invasion, unionid populations in the upper St. Lawrence River declined exponentially to the point of extirpation at some sites. The most severe unionid population declines occurred when dreissenid populations reached peak densities ~5 years after colonization began (Ricciardi et al., 1996); a similar time frame has been noted in other invaded systems (Ricciardi et al., 1998; Burlakova et al., 2000; Zanatta et al., 2015). In all our sites in which near total extirpation had previously been recorded, unionid populations remain scarce or absent. In the Soulanges Canal (Pointe-des-Cascades, Quebec), a unionid population that had a density of $21/m^2$ in 1992 was completely wiped out by 1995 (Ricciardi et al., 1996), and no living unionids have since been found at that site in multiple sampling surveys between 2002 and 2022 (Ricciardi, unpubl. data). By contrast, unionid populations in the lower Ottawa River remained more stable and less fouled, likely reflecting low-calcium limitation of dreissenid mussel recruitment in the river (Mellina & Rasmussen, 1994; Jokela & Ricciardi, 2008). In terms of unionid populations, the lower Ottawa River provides a suitable contrast to the St. Lawrence River, owing to its close proximity—including mixed water masses at their confluence at Lake St Louis (Figure 1.2), and historical assemblages that share several species. The major difference in the two rivers in terms of stressors is the proliferation of dreissenid mussels, which we therefore hypothesize to be the primary driver of rapid unionid population declines in the St Lawrence River since the early 1990s.

The composition of unionid assemblages in the St. Lawrence River was dominated by *Elliptio complanata* and *Lampsilis radiata* throughout the 30+ year period. Different species of unionids have varying tolerances of fouling (Haag et al., 1993; Gillis & Mackie, 1994; Dzierżyńska-Białończyk et al., 2018; Urbańska et al., 2019). Both *E. complanata* and *L. radiata* have been found to be more resistant to the impacts of dreissenid mussels (Haag et al., 1993; Hallac & Marsden, 2000) and they also dominate current assemblages in a St. Lawrence tributary, the Richelieu River, which has also been invaded by the zebra mussel (see Chapter 2). Two species previously documented at our sites (*Pyganodon cataracta* and *Ligumia recta*) were not found in our 2022-23 surveys.

Although we have only documented four living species of unionids in the upper St. Lawrence River in 2022-23, rare species may still exist in sites outside our survey or at undetectable densities. Furthermore, stable populations could persist in some habitats that, owing to their physical characteristics, offer refugia against severe effects of dreissenid fouling. Such potential refugia include wetlands (Bowers & Szalay, 2004; Zanatta et al., 2015; Bossenbroek et al., 2018), because dense macrophytes can act as a barrier to dispersal of dreissenid larvae (Bodamer & Bossenbroek, 2008). The most extensive wetlands in the St. Lawrence River occur in Lake St. Pierre, a fluvial lake located ~50km east of Montreal. In 1995, Ricciardi et al. (1996) sampled three sites on the lake and found unionid populations (primarily *Elliptio complanata* and *Lampsilis radiata*) at densities <10 m^{-2}. They noted a spatial north-south gradient of mean fouling intensities of up to 48 zebra mussels per unionid across the three sites, with unionid mortality (freshly killed individuals) increasing along this gradient. In 2013, Genovese and co-workers conducted a biological survey of Lake St. Pierre and reported a unionid assemblage of 5 species, dominated by *E. complanata* and *L. radiata*; the total density averaged 2-8 m^{-2} on both shores, with a maximum local density of 27 m^{-2} (Genovese et al. 2016). Dreissenid mussels were in low abundance (<7 m^{-2}) in the sampling areas, similar to that reported in 1995 (Ricciardi et al., 1996). In the summer of 2016, nearly 25 years after dreissenid invasion of the area, researchers from our lab sampled unionid assemblages at two shallow (<1 m depth) sites on the south shore of the lake at Baie du Febvre, Quebec (Ricciardi, unpubl. data). One site, located near a submerged macrophyte bed, contained a density of 7 m^{-2} and consisted of 4 species, dominated by *E. complanata* (66% of individuals collected) and *L. radiata* (30%); *Lampsilis cardium* (1.8%) and *Pygandodon cataracta* (1.8%) were also collected. Few dreissenids (all zebra mussels) were present on the shells of living unionids; the mean and maximum fouling intensities on were, respectively, 0.14 and 2 zebra mussels per unionid. The second site was in the open water offshore and not located near macrophyte beds. Its unionid assemblage was at very low abundance (0.44 m^{-2}) and consisted exclusively of *E. complanata* (71%) and *L. radiata* (29%). The mean and maximum fouling intensities on these unionids were, respectively, 8.1 and 28 zebra mussels per individual. Although this amount of fouling is considerably lower than the highest levels observed in various areas of the upper St Lawrence River in the 1990s, empirical modeling predicts that a population subjected to a mean fouling intensity of 8 zebra mussels/unionid will experience 30% mortality (Ricciardi et al., 1995). Indeed, the same mean fouling intensity was recorded at a site in Lake St. Louis (Lachine, Quebec) during a major unionid population decline (Ricciardi et al., 1996). Thus, although a few areas of Lake St. Pierre might continue to support multispecies unionid assemblages at moderately high local abundances (Genovese et al. 2016), the damage from long-term exposure to zebra mussel fouling is difficult to estimate but potentially substantial.

The areas of the upper St. Lawrence River that we sampled in 2022-23 might have had historically higher species richness before the 1990s. There is no documented baseline of unionid richness or population density in the upper St. Lawrence River prior to dreissenid invasion, notwithstanding reports from a few sources (e.g., Magnin and Stanczykowska, 1971; Levasseur, 1977). Therefore, we can only define recovery relative to a 1992 baseline and thus might have underestimated the extent of population and diversity declines over a much larger multidecadal time scale.

Dreissenid population trends over 30+ years

Data collected over the course of the dreissenid invasion suggest a >90% reduction in dreissenid field densities from 1995 (peak density) to 2022 and an increase in dominance by the quagga mussel (Table S1), consistent with other published observations (Farrell et al., 2010). An extensive literature review by Strayer et al. (2019) did not find strong evidence of a general temporal pattern of dreissenid population dynamics, apart from rapid post-establishment increases in abundance and subsequent replacement by quagga mussels (see also Ricciardi & Whoriskey, 2004). Dreissenid densities may have decreased in the St. Lawrence River due to multiple factors, including increased predation (Petrie & Knapton, 1999; Miano et al., 2021), competition between zebra and quagga mussels (Haynes et al., 2005; Ricciardi & Whoriskey, 2004), or attenuation of phytoplankton resources after rapid population expansion (Churchill et al., 2016).

Given that dreissenid fouling is often attributed as the main cause of unionid mortality (Ricciardi et al., 1998; Ricciardi, 2003; Burlakova et al., 2014) and that we recorded the lowest fouling levels in 2022-23 (Figure 1.4), one might ask why unionid populations have not shown signs of at least partial recovery thus far? Phytoplankton resources, indicated by chlorophyl-a levels, declined following dreissenid invasion in the 1990s and have remained relatively low since that time (Twiss et al., 2022), which could be limiting the population growth of unionids. Furthermore, unionid mussels rely on specific fish hosts for completing their larval (glochidia) stage (Watters, 1992; McMahon & Bogan 2001). Both *E. complanata* and *L. radiata* are host fish generalists (Bogan, 2002; Kneeland & Rhymer, 2008; Lellis et al., 2013), whereas other species can be more narrowly host-specific and thus sensitive to changes in local fish populations (Wiles, 1975; Watters, 1994). Having long lifespans, slow growth, delayed maturity, and complex reproduction involving host fishes (McMahon & Bogan, 2001), unionids might require decades to recover from a devastating disturbance (e.g. Riccardi et al., 2016).

Unionid and dreissenid co-existence

The severe declines observed in unionid populations during the mid-1990s in the upper St. Lawrence River may require a prolonged and unpredictable time period to re-attain the 1992 baseline. However, limited co-existence (at low densities of both species) is a more likely scenario and has been documented in other waterways; for example, in the Hudson River, a long-term study found that unionid populations stabilized after initial declines following zebra mussel invasion of the river, although unionid body condition remained weaker than in pre-invasion years (Strayer & Malcom, 2007). Partial unionid recovery was also observed in the western basin of Lake Erie (Larson et al., 2016), possibly due to 1) adaptive changes in burrowing behaviours by unionids to rid themselves of attached dreissenids (Nichols & Wilcox, 1997; Nichols & Amberg, 1999), and 2) increasing dominance of quagga mussels, which do not foul unionids as intensely as do zebra mussels (Conn and Conn, 1993; Burlakova et al., 2014). Limited co-existence with dreissenid mussels was also observed in the Richelieu River, likely because of suboptimal calcium concentrations limiting dreissenid proliferation in most areas of the river (Chapter 2).

It is important to recognize that these instances of limited co-existence are not necessarily stable and can change with environmental conditions through time, as observed for unionid assemblages under various other environmental stressors (Hopper et al., 2024). It is difficult to predict if or when unionid populations in the upper St Lawrence will eventually recover, remain in a “loose” (stochastic) equilibrium at low abundance, or continue to slowly erode over time. Regardless, these findings emphasize the value of long-term data collection and its specific importance to the impacts of biological invasions. Without (even fragmented) multi-site, multi-year information on unionid densities during the various stages of dreissenid invasion, erroneous conclusions concerning the effects of dreissenids on unionid abundance and diversity might have been made many years later.

Figures

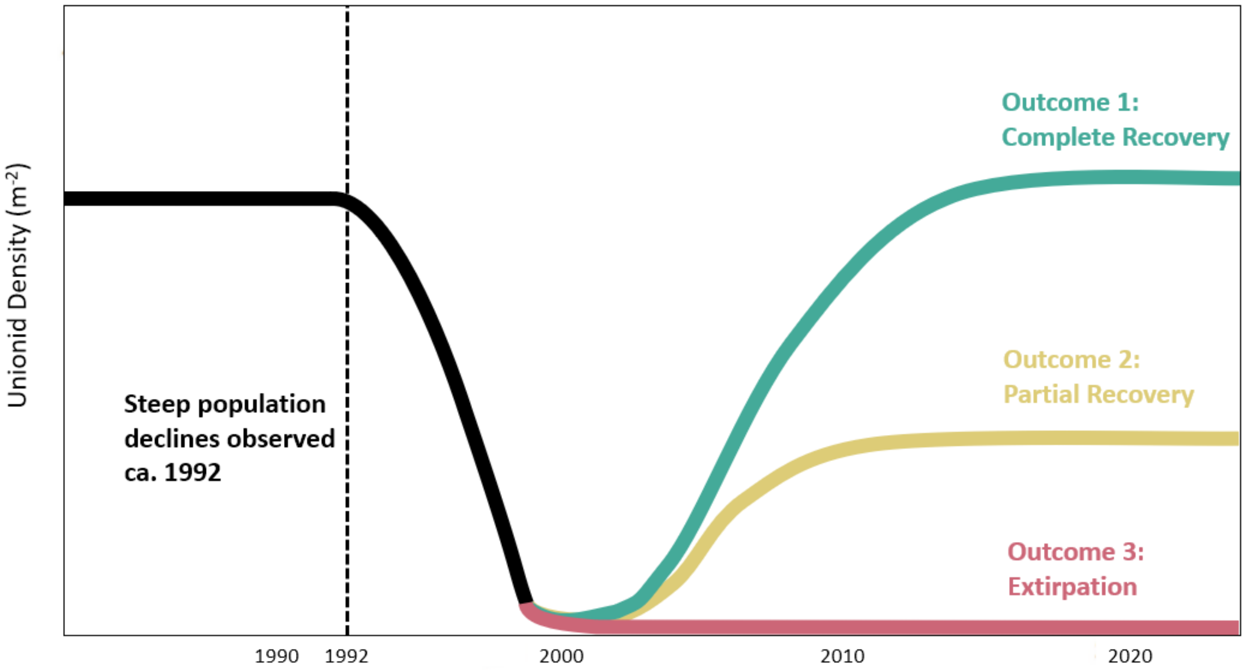

Figure 1.1: Conceptual scenarios of long-term change in unionid populations in the upper St. Lawrence River. The curve to the left of the dotted line represents previous data collected in the St. Lawrence River prior to and including peak dreissenid mussel colonization (Ricciardi et al., 1996).

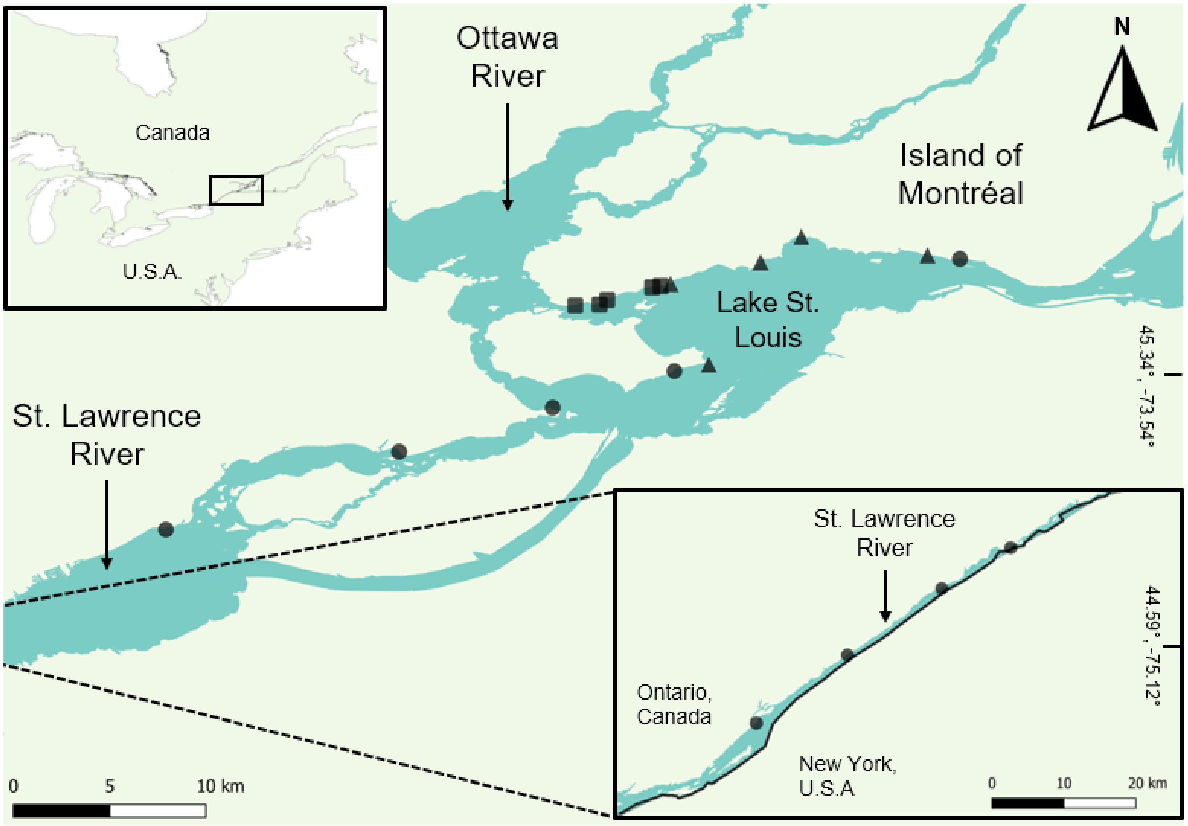

Figure 1.2: Locations sampled in the upper St. Lawrence River. Circles denote St. Lawrence River dominant sites, squares represent Ottawa River dominant sites, and triangles denote sites within the mixing zone.

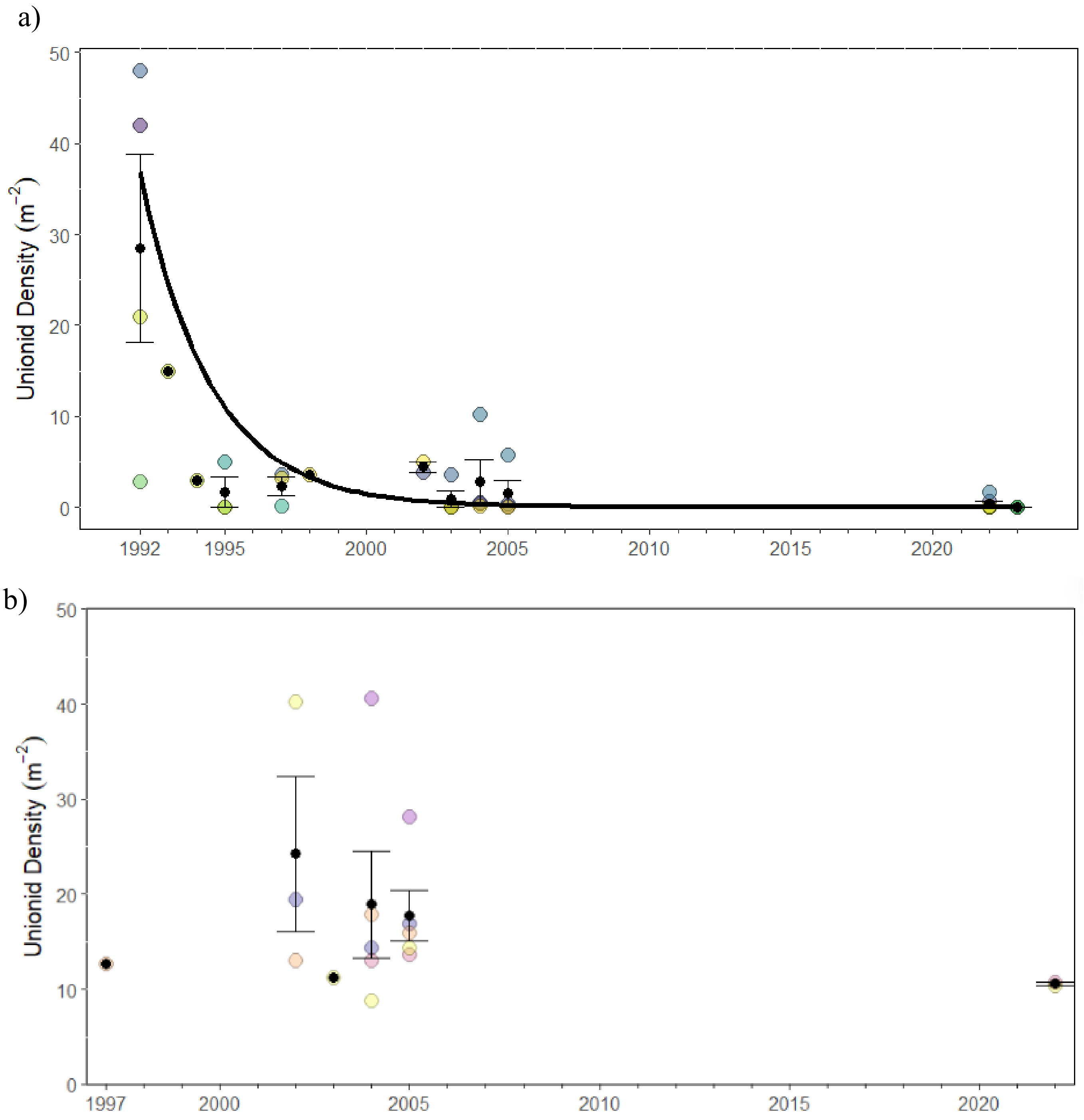

Figure 1.3: a) (Top panel) Mean unionid densities (individuals per m^2) over time in the St. Lawrence River (including Lake St. Louis), fitted with an exponential decay function $y(x) = 36.88e^{-0.402x}$. b) (Bottom panel) Mean unionid densities (individuals per m^2) over time in the Ottawa River. For both plots, black points denote the mean density across all sites for a given year, and coloured points denote mean densities at each location.

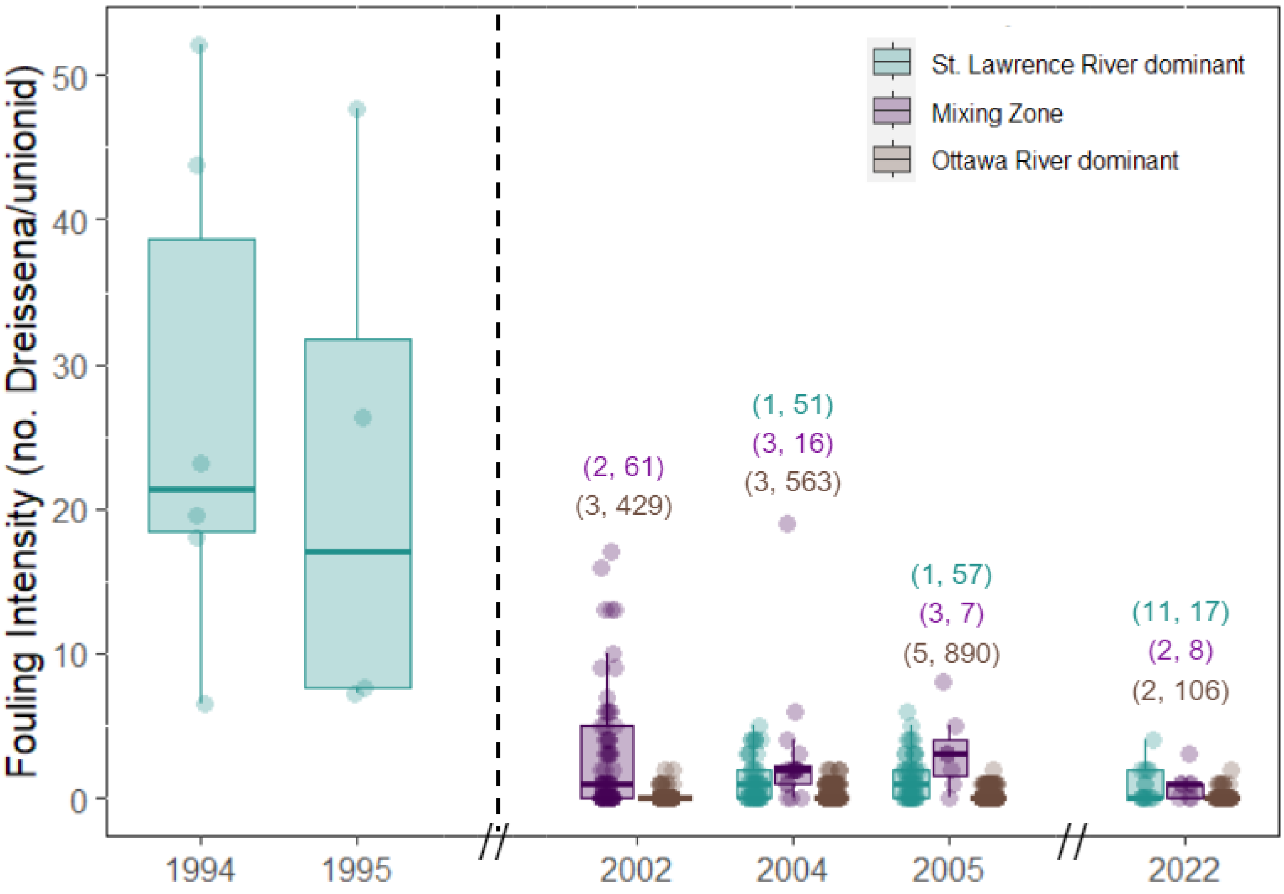

Figure 1.4: Box plots of fouling intensity (number of dreissenid mussels attached to individual unionids); solid vertical lines stretch to the minimum and maximum values, outliers are past the vertical lines, horizontal bars are medians. Data from 1994 and 1995 are the mean fouling intensities at each sampling location. Data from 2002 to 2022 are the fouling intensities of individual unionid found across all locations. The mixing zone is within Lake St. Louis at the confluence of both rivers, where water chemistry values are intermediate between the ion-rich waters of the St. Lawrence River and the ion-poor waters of the lower Ottawa River. St. Lawrence River dominant areas have calcium concentrations >18 mg/L, the mixing zone has calcium concentrations between 12-18 mg/L, and Ottawa River dominant areas have calcium concentrations <12 mg/L. Paired numbers in brackets indicate number of sites sampled (left value) and number of unionids processed (right value).

Tables

Table 1.1: Information on dreissenid composition and abundance at sampling sites within the St. Lawrence River and Lake St. Louis.

Year	Number of sites visited	Dreissenid composition of fouled unionids	Quagga field density	Zebra field density	Average Dreissenid field density
1995	6	NA	NA	NA	5228 m^{-2}
2005	7	99% zebra mussels; 1% quagga mussels (n=133)	NA	NA	NA
2022	11	71% zebra mussels; 29% quagga mussels (n=31)	223 m^{-2} (57%)	167 m^{-2} (43%)	390 m^{-2}

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Linking Statement

Dreissenid invasions typically follow a common pattern: once introduced, their populations grow exponentially within a few years while heavily fouling unionids, then unionid populations decline. In the previous chapter, the St. Lawrence River provides an ideal example of the aforementioned pattern; we recorded exponential decline of unionid populations in the mid 1990s, and showed there has not been any recovery three decades after zebra and quagga mussels invaded. Areas around Lake St. Louis provided us with a natural calcium gradient, and we confirmed that dreissenid proliferation and unionid decimation were most evident in waters with high dissolved calcium. However, dreissenid invasions in suboptimal environments may not follow the general trends that were exemplified in the St. Lawrence River.

The next chapter explores this idea in the Richelieu River, a St. Lawrence River tributary. The river has a uniformly low dissolved calcium concentration (~18 mg/L), which has been shown to limit the survival, body condition and abundance of dreissenid mussels. Despite this homogeneity, parts of Lake Champlain (the source of the Richelieu River) have a higher calcium concentration and support self sustaining zebra mussel populations. We investigated if Lake Champlain provided a source population for zebra mussels in the Richelieu River, and tested if zebra mussel densities and unionid fouling were higher closer to the mouth of the river than its outflow. Also, further downstream of the river lies the Chambly Basin, which could possibly interfere with the downstream flow of zebra mussel larvae if they are only reproducing in Lake Champlain and not within the river. Our lab has access to unionid and zebra mussel data as early as 1998 throughout the Richelieu River, so I was able to analyze zebra mussel impacts on unionids in this unique system over the past 25 years.

Chapter 2: Limited co-existence of native mussels and zebra mussels in a river 25+ years after invasion

Abstract

North American unionid mussels have evolved in the absence of dominant macrofouling organisms. Prior to the invasion of the zebra mussel (*Dreissena polymorpha*), no byssally-attached molluscs existed in North American inland waters; consequently, unionid mussels have no adaptive defense against zebra mussel fouling and often suffer substantial mortality or near total extirpation within several years following invasion. Managers have searched for habitat refugia in which unionid mussel assemblages can avoid lethal levels of fouling and possibly co-exist with zebra mussels. One such potential refuge is the Richelieu River (Quebec), which was invaded by the zebra mussel in the mid-1990s, after having spread from the river's headwaters in Lake Champlain. Risk assessment models suggest that the mean calcium concentration in the river (18 mg/L) is sub-optimal for supporting a dense population of zebra mussels sufficient for exerting lethal levels of fouling on unionids. Using field data collected at various sites throughout the river over a 25-year period, we tested two hypotheses: 1) unionid diversity and abundance would decline over time as zebra mussel fouling intensities increased; and 2) unionid fouling and mortality would decline across sites with distance from the outflow of Lake Champlain, the principal source of zebra mussel larvae. We evaluated whether unionids could co-exist with zebra mussels without suffering the severe population mortality observed in invaded calcium-rich waterbodies. Our results revealed local unionid population declines and diversity loss comparable to those seen in other invaded rivers, despite the suboptimal calcium concentrations in the Richelieu River. We also recorded sustained, low levels of fouling by zebra mussels. Although fouling decreased further downstream, local unionid populations suffered losses and in some cases near total extirpation across sites regardless of the distance from Lake Champlain. We conclude that the Richelieu River is supporting both unionid and zebra mussel

populations in an unstable co-existence in which long-term impacts of zebra mussels appear evident.

Introduction

Biological invasions cause a broad suite of impacts that affect community composition and ecosystem functioning, and they are considered a significant threat to biodiversity (Dextrase & Mandrak, 2006; Ricciardi et al., 2013; Simberloff et al., 2013; Emery-Butcher et al., 2020). The success and impact of invasions are highly context dependent (Melbourne et al., 2007; Ricciardi et al., 2013; Kumschick et al., 2015; Dahal et al., 2023) such that invaders are predicted to have greater impacts in habitat conditions that more closely match physiological optima (Iacarella et al., 2015); however, it is difficult to predict the outcome of invasions in suboptimal environments (Ricciardi et al., 2013; Keretz et al., 2021). In this context, we use the term *suboptimal* to define an environment where a species can establish and persist but have lower survivorship, reduced population growth and weaker performance (e.g., impaired individual growth, feeding efficiency and enemy avoidance) than it would in more physiologically favorable environmental conditions. Species-specific risk assessments do not typically evaluate invasion threats in suboptimal environments, therefore the strength and duration of impacts in these areas may be overlooked or downplayed (Kumschick & Richardson, 2013).

The zebra mussel (*Dreissena polymorpha*), a Ponto-Caspian species, has demonstrated a capacity to substantively alter communities in the lakes and rivers it has invaded (Ricciardi et al., 1995, 1997; Burlakova et al., 2000; Ward & Ricciardi, 2007; Karatayev et al., 2015). Zebra mussels reproduce rapidly and will colonize and overgrow virtually any solid surface (Ackerman et al., 1994; Strayer & Smith, 1996; Barnard et al., 2003). Some of their most prominent impacts have been on native freshwater mussels (Order: Unionida, “unionids”)—the most threatened faunal group in North America (Ricciardi et al., 1998; Ricciardi & Rasmussen, 1999). North

American unionid mussels have evolved in the absence of dominant macrofouling organisms. Prior to the invasion of the zebra mussel, no byssally-attached molluscs existed in North American inland waters; consequently, unionid mussels lack adaptive defenses against zebra mussel fouling. Intense fouling by dreissenids can prevent unionids from opening and closing their valves properly, and obstruct the unionid siphon, thereby interfering with normal feeding, respiration, excretion, and reproduction (Haag et al., 1993; Tucker, 1994; Schloesser et al., 1996). Furthermore, an attached cluster of zebra mussels can add increasing mass to individual unionids such that these individuals expend significant amounts of energy to keep themselves upright in the sediment, while also inhibiting normal movement and burrowing activity (Tucker, 1994; Ricciardi et al., 1995, 1996; Burlakova et al., 2000). Fouling is usually cited as the main cause of unionid mortality in habitats supporting dense zebra mussel populations, though dreissenids can also cause population declines by outcompeting unionids for food (Strayer & Smith, 1996; Ricciardi et al., 1998).

Species tolerate a continuum of habitat conditions with optimal preferences such that there are areas in space or time in which per capita performance and population growth (and thus impacts) are maximized. Water chemistry—specifically calcium concentration—limits the proliferation and impacts of zebra mussels in invaded waterways (Mellina & Rasmussen, 1994; Jokela & Ricciardi, 2008; Whittier et al., 2008; Kirkendall et al., 2021), reflecting physiological constraints linked to having evolved in ion-rich waters in Ponto-Caspian basins in eastern Europe (Reid & Orlova, 2002; Gallardo et al., 2013). Zebra mussels rarely occur in inland waters with calcium concentrations lower than 15 mg/L, and where they do occur under such conditions their population densities are small and body condition is poor (Mellina & Rasmussen, 1994; Jokela & Ricciardi, 2008). In North American inland waters, dreissenid mussel populations tend to expand rapidly, often exponentially, in waters with calcium concentrations of 25 mg/L or higher (Hincks & Mackie, 1997; Jokela & Ricciardi, 2008; Hollandsworth et al., 2011; Kirkendall et al., 2021). Risk assessments consider water bodies with mean calcium concentrations below 20 mg/L to be at low risk (Therriault et al., 2013; Whittier et al., 2008), implying negligible ecological impacts. However, there is a scarcity of zebra mussel impact studies and how they vary over time in such habitats. Moreover, for habitats in general, there are few studies of the long-term impacts of prolonged exposure of unionids to zebra mussels.

The Richelieu River in southern Quebec has a narrowly bounded calcium concentration of ~18 mg/L across its length (de Lafontaine & Comiré, 2004; Jokela & Ricciardi, 2008), which is considered suboptimal for zebra mussels but well above the levels known to be stressful for unionid mussels (Strayer et al., 1981; Rooke & Mackie, 1984). The zebra mussel was discovered in the Richelieu River in 1996 (Cusson and de Lafontaine, 1998), after having spread from the river's headwaters in Lake Champlain, which was invaded circa 1993 (Stickney, 1996). Established populations of zebra mussels present in Lake Champlain apparently exported veliger larvae that resulted in the rapid colonization of the Richelieu River (Cusson and de Lafontaine, 1998; de Lafontaine & Comiré, 2004; Smeltzer et al., 2012). Consistent with this view, an upstream-downstream gradient of mussel colonization in the Richelieu River was observed in the late 1990s. At that time, zebra mussel larval densities were ~90% lower in downstream areas of the river, with Chambly basin (an enlargement of the river located near the middle of its length) apparently interfering with translocation of larvae and thereby resulting in substantively lower recruitment further downstream (Cusson and de Lafontaine, 1998). In September 1997, less than 50% of living unionids were colonized at sites upstream of Chambly basin, and only <1% were colonized below the basin (Cusson and de Lafontaine, 1998).

In waterways that support dense zebra mussel populations, unionids often suffer substantial mortality or near total extirpation within 4 to 8 years following invasion (Ricciardi et al., 1995, 1996, 1998; Martel et al., 2001; Schloesser at al., 2006; Strayer & Malcom, 2007, 2018) . In some habitats, however, unionids have been able to exploit physio-chemical refugia to avoid excessive fouling and co-exist with zebra mussels (Nichols & Amberg, 1999; Zanatta et al., 2002; Bowers & Szalay, 2004; McGoldrick et al., 2009; Keretz et al., 2021). Identifying habitats that support long-term viable unionid populations is a valuable goal for aquatic conservation, as they could serve as target areas for translocation initiatives (Nakamura et al., 2022; Tsakiris et al., 2017). The extent to which invaded suboptimal habitats support a full or limited co-existence with native species remains to be investigated (Peters & Lodge, 2013; Perales et al., 2021) .

Here, we use data collected over 25-year span to quantitatively assess the extent to which unionid populations have persisted in the Richelieu River. We related observed spatiotemporal changes to patterns of zebra mussel fouling and compared these to patterns observed in invaded calcium-rich habitats (Jokela & Ricciardi, 2008; Ricciardi et al., 1998). Specifically, we tested two predictions: 1) unionid diversity and abundance would decline over time as zebra mussel fouling intensities increased, with extirpations expected within the same time frame as in calcium-rich lakes and rivers; and 2) unionid fouling and mortality would decline across sites with distance from the outflow of Lake Champlain, the principal source of zebra mussel larvae.

Methods

Seven locations along the Richelieu River, between Noyan (8 km north of the USA border crossing) and Sorel-Tracy, were irregularly sampled between 1998 and 2023 (Figure 2.1; Table 2.1). In our figures and tables, the sites are numbered upstream to downstream of Lake Champlain, with Sites 1 through 5 upstream of the Chambly basin, and Sites 6 and 7 below the basin (Figure 2.1). Sites were selected based on availability of historical data of previously sampled unionid populations (Jokela, 2006; Jokela & Ricciardi, 2008; Ricciardi, unpubl.), allowing comparisons with newly collected data. Given that unionid populations do not experience significant fluctuations in abundance over a summer season, we were able to compare our data with previous sampling at these sites done between June and October, without having to account for temporal correlations (Bauer & Wächtler, 2001).

Sampling procedures were the same for all previous (pre-2022) data collections (Jokela, 2006; Jokela & Ricciardi, 2008; Ricciardi, unpubl.), thereby permitting direct comparisons over time. We accessed all locations from shore. At each site, SCUBA divers searched underwater for unionids for a maximum of 60 person-minutes in an approximate area of 1 acre. Divers did not venture deeper than 2 m depth. If we failed to locate a living unionid within this period, we recorded a density of 0 individuals/m^2 once time had run out. To estimate density at each site, we cast a 1m^2 polyvinyl chloride (PVC) quadrat haphazardly onto the bottom substrate and collected all unionids within its boundary (following Ricciardi et al., 1996). We first collected all visible unionids, then manually probed the upper 10cm of sediment to locate living and dead unionids buried immediately beneath the surface. At sites where unionid densities were at least 10 individuals m^{-2}, we sampled five replicated 1m^2 quadrats, as this was previously determined to yield a precision of ±20% (Downing & Downing, 1992). At sites where unionid densities were below 10 individuals m^{-2}, we sampled ten quadrats per site. Recently killed specimens were distinguished from older shells by the presence of an intact hinge ligament and uneroded nacre (and some shells still contained decaying tissues); these characteristics were previously shown to be reliable in identifying individuals that had died within 6 months of being collected (Ricciardi et al., 1996; Ricciardi, unpubl. data). Unionids were brought back to the lab for processing, where they were identified to species using characteristic described by Clarke (1981) and McMahon (1991). We measured unionid length and mass (with and without attached zebra mussels) using a digital balance. Where attached zebra mussels were present, they were manually removed, weighed, counted, and measured for their shell length. We removed all living tissue from the unionid and weighed the empty shell and flesh separately. With these data, we calculated the mass ratio (wet weight) of attached zebra mussels and their host unionid, as another measure of fouling intensity (Ricciardi et al., 1996).

We collected water quality data *in situ* using a YSI Pro Quatro multimeter and brought two water samples in 1L plastic bottles back to the lab in coolers within 4 hours of collection. Once there, we determined the dissolved calcium concentration (Ca^{2+} in mg L^{-1}, converted from $CaCO_3$ in mg L^{-2}) using a titration test kit (LaMotte™). We averaged the two readings to obtain a single estimate of [Ca^{2+}] for each site.

All statistical methods were performed using R Statistical Software (v4.2.1; R Core Team 2023). We applied an exponential decay curve to model the decrease in unionid density across time. We also tested for differences in zebra mussel shell length across sites in 2023, but Levene's test returned an insignificant p value. After having tried a logarithmic and square root transformation on the data, and finding that these transformations did not influence the significance of Levene's test, we used non-parametric approach and proceeded with the Kruskal-Wallis and Wilcoxon rank sum tests from the built-in "stats" package.

Results

In total, ten species of unionids were collected alive across our sampling sites at various times from 1998 to 2023 (Table 2.1). *Elliptio complanata* and *Lampsilis radiata* were found at all sites through time, and they were the only living species found at some sites (Table 2.1). Assemblages at sites downstream of the Chambly basin were more diverse than those located upstream; Site 6 (Saint-Antoine) had the highest species richness with all ten species observed (Table 2.1), including specimens whose shell morphology was indistinguishable from those of *Elliptio crassidens*, and are hereafter identified as *Elliptio* cf. *crassidens*.

Unionid populations were at unprecedented low abundances across all sites in 2023, with a mean density of 0.8 m^{-2} (Table 2.1). Populations sharply declined from our earliest collections in 1998 to the mid-2000s and then continued to slowly decrease until 2023, following an exponential decay curve (Figure 2.2). Sites located closer to Lake Champlain had higher unionid densities than the most downstream sites until approximately 2017, when densities became low across all sites (Figure 2.2).

Dreissenids occurring on unionids and throughout the river were exclusively zebra mussels; no quagga mussels (*Dreissena bugensis*) were found. Collectively, across all sites, $\geq$50% of unionids were fouled by zebra mussels in any given year we sampled. In 2023, fouling intensities ranged from 0 to 46 zebra mussels per unionid. Over our 25-year dataset, the number of zebra mussels per live unionid ranged from 0 to 143. Since not all sites were sampled each year, we chose to focus our attention on the three sites sampled most frequently over time, to investigate temporal trends in fouling intensity (Figure 2.3). We found that fouling intensities in 2023 are slightly higher than what they were in 1998, and there were no clear patterns in fouling intensity across time (Figure 2.3b). Mass ratios across all unionids and all sites ranged from 0 to 0.94 (median = 0.91) in 2023, and they were at least as high as those recorded for the three most sampled sites in 1998 (Figure 2.3c). More than half of all unionids at the three most sampled sites were fouled every year they were sampled (Figure 2.3a). There were marked differences in fouling at sites upstream and downstream of the Chambly basin; the average percentage of unionids fouled, the number of attached zebra mussels per unionid, and the mass ratio were lower at downstream sites (Figure S1).

In 2023 we measured the length of zebra mussels attached to unionids at all sites in which there was fouling (Figure S2). Dreissenid shell lengths spanned 4–22 mm across all sites, with those at Site 5 being significantly larger than the remaining sites (Kruskal-Wallis test, $H(3)=10.973$, $p=0.012$).

Discussion

Unionid population trends over 25 years

As predicted, unionid diversity and abundance declined over time. The overall abundance of unionids across sites declined exponentially, although mean densities across sites and mean site densities varied across years (Table 2.1), likely reflecting variance inherent to random quadrat sampling of patchy spatial distributions (Downing et al., 1993; Vaughn & Spooner, 2006; Haag, 2012).

Previous surveys have documented twelve different species of unionids in the Richelieu River, whereas we have documented ten of these; we have never observed *Pyganodon grandis* or *Alasmidonta undulata* (de Lafontaine et al., 2002). It is possible these more rare species are present in areas we did not sample, or they occur in densities too low to be detected and thus our quadrat sampling never captured them, or they were extirpated before our sampling efforts increased in the mid-2000s. Among the species identified in previous surveys (de Lafontaine et al., 2002) is the elephant-ear mussel *Elliptio crassidens*, an eastern North American species primarily distributed in the midwestern and southern United States, where it is considered threatened or endangered in some regions (Cicerello and Schuster, 2003; Sietman, 2003; Hinck et al., 2012). Our specimens match the morphological (conchological) characteristics of the species; however, given its disjunct distribution in North America, and the broad morphological variation of its congener *Elliptio complanata*, the presence of *E. crassidens* cannot be confirmed with certainty without further taxonomical research involving genetic sequencing.

Overall, unionid populations in the Richelieu River have declined over a 25-year period, to near extirpation at some sites, with much of the decline occurring after ten years of exposure to zebra mussels. Severe unionid population decline and near total extirpation have typically occurred within <8 years in invaded rivers and lakes that support dense zebra mussel populations (Ricciardi et al., 1996, 1998; Martel et al., 2001; Schloesser et al., 2006; Strayer & Malcom, 2007, 2018). Differential susceptibility to fouling across unionid species (Haag et al., 1993; Hallac & Marsden, 2000; Dzierżyńska-Białończyk et al., 2018) might reflect differences in burrowing behaviour and access to local refugia in the form of fine sediments (Martel et al., 2001; Nichols & Wilcox, 1997) Furthermore, a potential explanation for rapid population declines in other invaded rivers is the presence of species highly sensitive to fouling; however, the species composition in the Richelieu River (which is dominated by *Elliptio complanata* and *Lampsilis radiata*) is similar to that of the upper St Lawrence River (cf. Ricciardi et al., 1996). Zebra mussels were documented in the Richelieu River in 1996 and were first sampled for this study in 1998. We could not locate data on baseline unionid densities in the river prior to zebra mussel invasion, so our sampling might have underestimated the true magnitude of the population decline.

Variation in unionid fouling intensities across space and time

Supporting our prediction, fouling intensities decreased at sites further downstream from the outflow of Lake Champlain, the main source of zebra mussel larvae. Compared to other invaded rivers, fouling intensities (number of zebra mussels per unionid; mass ratio of attached mussels and their unionid hosts) remained relatively low over time, regardless of the distance from Lake Champlain. There were low fouling levels at sites located <10 km downstream of the lake, which is well within the range that zebra mussel larvae are known to disperse (Horvath et al., 1996; Olson et al., 2018). At sites up to 40 km downstream of Lake Champlain, we recorded zebra mussels less than 17 mm in shell length, which is the high-end estimate of the size of one-year-old mussels (Dorgelo, 1993; Jantz & Neumann, 1992; Neumann et al., 1993; Garton & Johnson, 2000). This suggests three possibilities: zebra mussels are reproducing in the river, adults were translocated by humans or natural mechanisms from upstream sites, or some larvae successfully dispersed downstream through Chambly basin.

The calcium concentration in the Richelieu River might have constrained the ability of zebra mussels to proliferate on unionids (Jokela & Ricciardi, 2008). Zebra mussels require dissolved calcium for growth, osmoregulation, and reproduction (Vinogradov et al., 1993; McMahon, 1996; Hincks & Mackie, 1997), and their calcium requirements far exceed those of North American unionids (McMahon & Bogan, 2001). Persistent zebra mussel populations are rarely found in waterbodies with calcium (Ca^{2+}) concentrations lower than 25–28 mg/L (Ramcharan et al., 1992; Mellina & Rasmussen, 1994; Karatayev, 1995; Hincks & Mackie, 1997). Prolonged survival of settled mussels is possible at calcium concentrations as low as 8.5–12 mg/L (Hincks & Mackie, 1997; Jones & Ricciardi, 2005), depending on the environmental pH, whereas shell growth is impaired below 8.5 mg/L (Hincks & Mackie, 1997). Below 15 mg/L, normal ion exchange is disrupted (Vinogradov et al., 1993). At field sites where $[Ca^{2+}]$ is below 21–25 mg/L, population density is limited (Mellina & Rasmussen, 1994; Jokela & Ricciardi, 2008). Risk assessments have designated habitats of $[Ca^{2+}]$ <20 mg/L as “low risk” of invasion (e.g., Whittier et al., 2008), unless the system is supplied with larvae from a connected lake or stream. The Richelieu River appears to be a sink habitat for zebra mussels, whose populations are sustained by larval supply from Lake Champlain.

Lake Champlain as a source of zebra mussel larvae

Unionid population densities and fouling intensities differed with distance downstream of Lake Champlain. We predicted that sites furthest downstream would have the lowest fouling and therefore more stable unionid populations; but unionid mortality was high at these sites, even at low fouling intensities. Early unionid surveys at sites downstream of the Chambly basin in the early 2000s recorded lower unionid densities compared to locations upstream of the basin; consequently, they reached near-extirpation sooner than sites upstream of the basin. This gradient was also recognized in a previous study that recorded an average of 14 zebra mussels per living unionid at their site closest to Lake Champlain, with other sites downstream having <1 per unionid on average (Cusson & de Lafontaine, 1998). The study concluded that colonization of the river was primarily driven by larval drift from Lake Champlain, and that <50% of living unionids were colonized at sites upstream of Chambly basin while <1% were colonized below Chambly basin (Cusson & deLafontaine, 1998). Furthermore, sampling of veliger larvae in 1996-97 observed a 90% drop in larval abundance between the upper and lower Richelieu River, with Chambly basin apparently interfering with translocation of larvae downstream (de Lafontaine et al., 2002). It should be noted that large, heterogenous rivers often contain slow-moving reaches with lentic qualities that can allow veligers to complete development and thus act as larval sources (cf. Martel & Madill, 2018). If Chambly basin contained a reproducing population of zebra mussels, then it would serve as a source for continued fouling of unionids at downstream sites; instead, it appears to act as a trap for larvae, hindering downstream recruitment.

Zebra mussels as the cause of unionid declines

Native unionid mussels and zebra mussels can have overlapping diets, and unionids are less efficient than zebra mussels at differentiating between nutritious and less nutritious food particles (Baker & Levinton, 2003). These observations, coupled with the high filtration capacity of zebra mussels (Fishman et al., 2010; Higgins & Vander Zanden, 2010), raise the possibility of competition for food as an impact additional to fouling. For example, there is evidence that long-term declines of unionid abundance and diversity in the Hudson River were driven more by competition with zebra mussels for food than by fouling (Strayer & Malcom, 2018). Laboratory experiments found that unionids suffer energetic stress in the presence of zebra mussels; glycogen loss was maximal in unionids fouled by zebra mussels, whereas intermediate losses were measured in unionids that were not fouled but were growing in the presence of zebra mussels of similar biomass to that of the fouling treatment—suggesting the effects of exploitative competition (Beason & Schwalb, 2022). Therefore, a plausible explanation for the decline in unionid populations in the lower Richelieu River where fouling intensities remained low is exploitative competition with upstream zebra mussel populations. Although zebra mussels have been shown to experimentally reduce the biovolume of the phytoplankton community typically found in Lake Champlain (Miller & Watzin, 2007), a long-term dataset on chlorophyll-a concentrations in the northwest basin of the lake (which drains into the upper Richelieu River) does not indicate a major decline of phytoplankton resources between 1996 and 2022 (Vermont Department of Environmental Conservation, 2022), and thus implies no significant loss of particles exported from the lake to the Richelieu River. However, without similar data for the Richelieu River, particularly downstream of Chambly basin, we cannot exclude the scenario of food attenuation via interception of organic particles by zebra mussel populations along the river length.

In conclusion, our results offer evidence that zebra mussel invasion can contribute, at least to some extent, to long-term declines in unionid abundance and diversity, even in a river system whose water chemistry is considered physiologically suboptimal for zebra mussels. We hypothesize that both fouling and exploitative competition are among the drivers of unionid mortality in this system. Consequently, there has been a limited but unstable co-existence between unionids and zebra mussels in the Richelieu River. This knowledge can inform risk assessments by 1) extending the range of habitat conditions in which unionids are negatively affected by zebra mussel invasions, and 2) challenging the assumption that chronic exposure to relatively low fouling intensities poses insignificant risks to unionids.

Figures

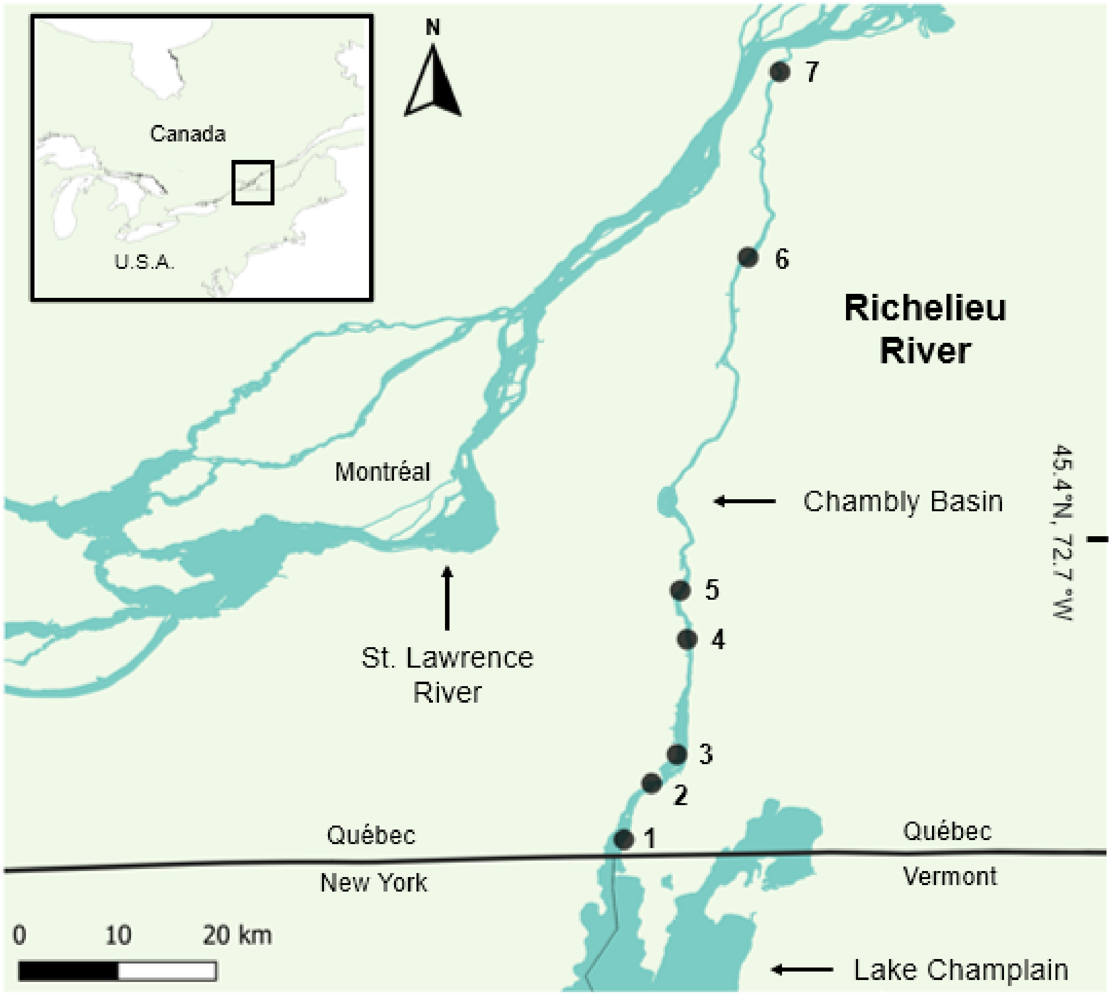

Figure 2.1: Locations sampled in the Richelieu River.

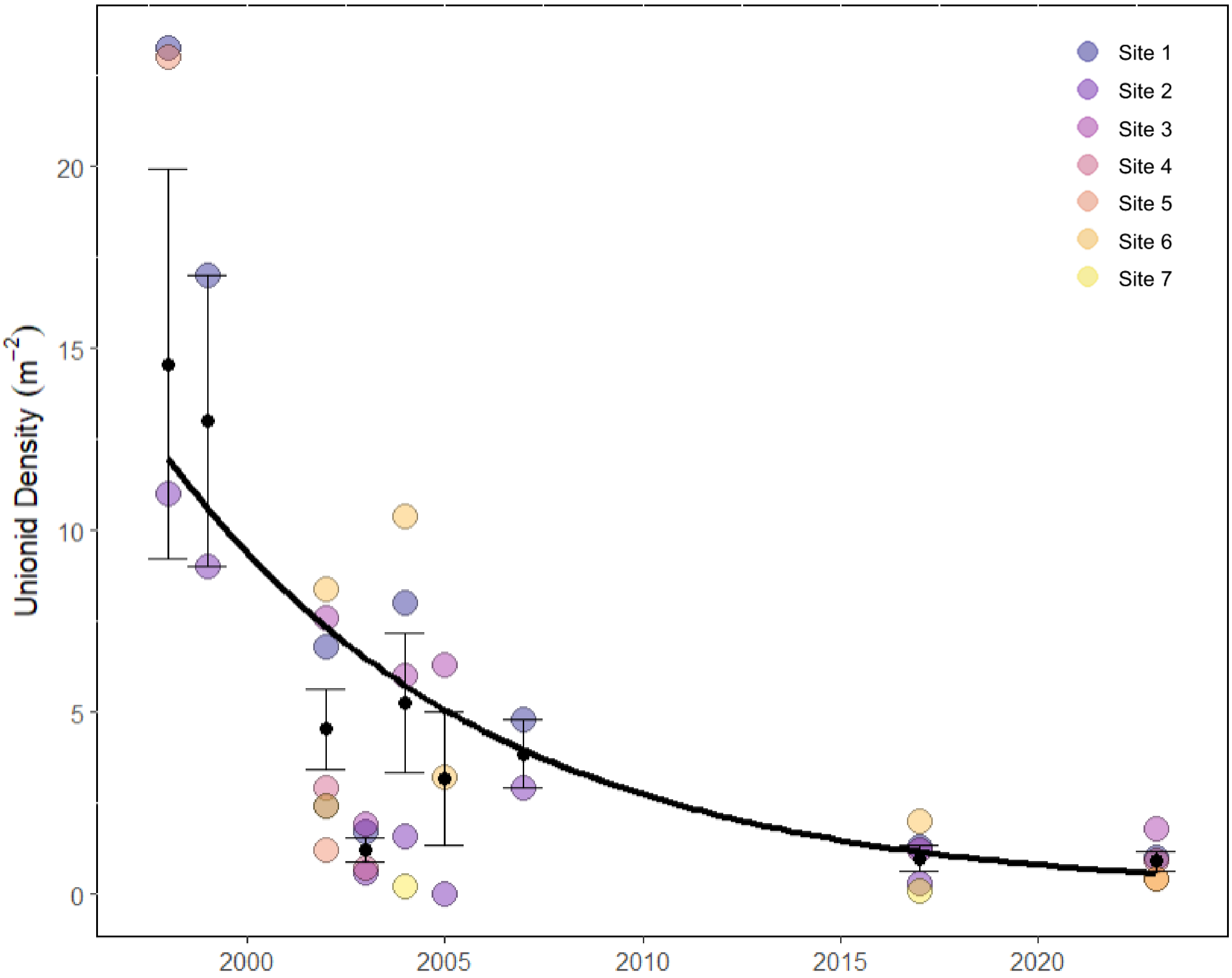

Figure 2.1: Mean unionid densities (individuals per m^2) over time, fitted with an exponential decay function: $y = 11.971e^{-0.123x}$. Black points denote the mean density across all sites for a given year, and coloured points denote mean densities at each location. Cooler (darker) colours are closer to Lake Champlain than warmer colours.

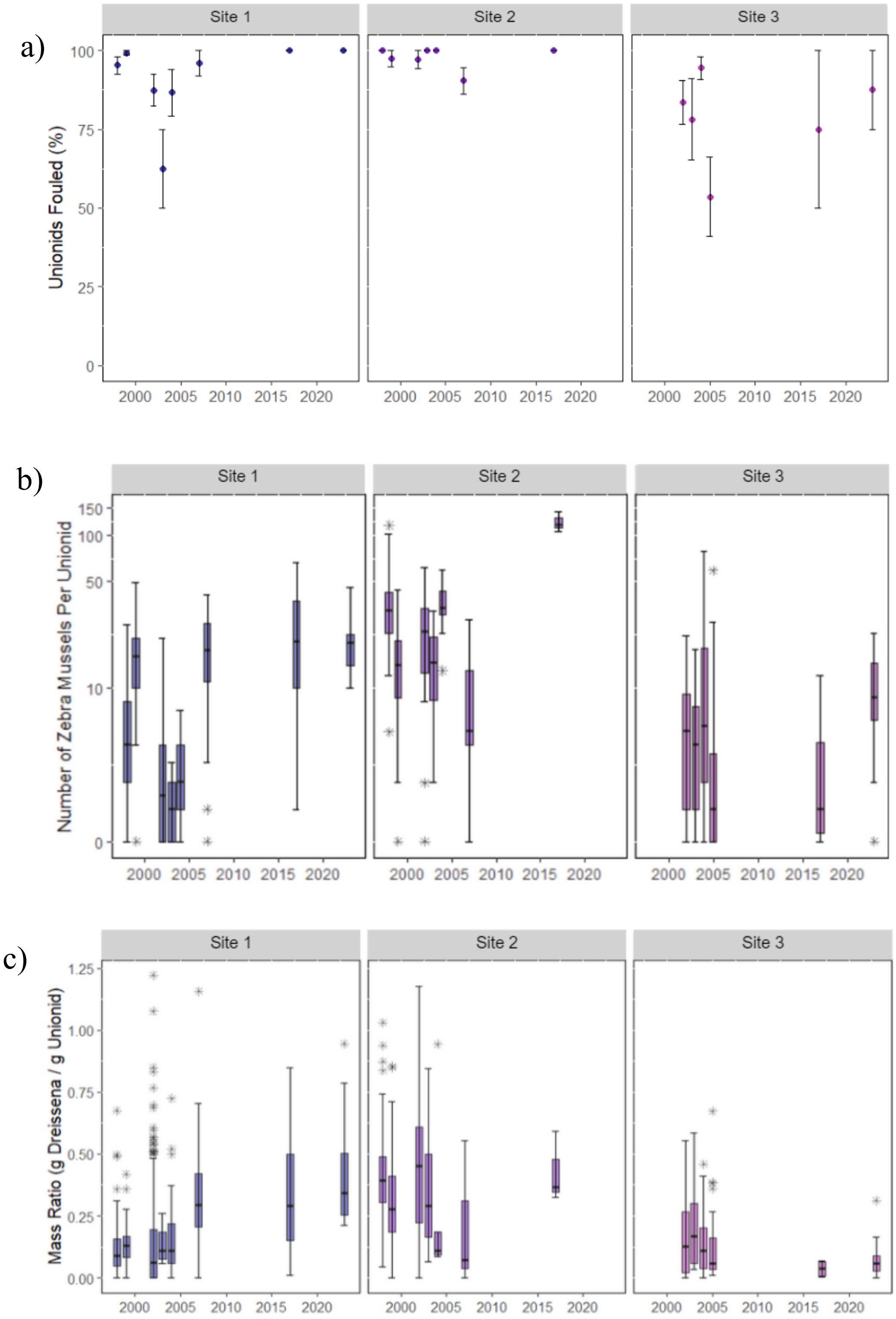

Figure 2.3: Mean fouling intensities on unionid mussels at the three most sampled sites in the Richelieu River. a) Percentage of unionids fouled (i.e. possessing at least one attached dreissenid) at a given site; b) mean number of zebra mussels per unionid; c) mean ratio of the mass of the attached dreissenid mussel cluster to the mass of the host unionid.

Tables

Table 2.1: Mean population densities (individuals per m^2) of unionids over time, separated by species. The standard error is shown in brackets. Gray-filled cells with dashes denote years when sites were not sampled.

Site	Species	1998	1999	2002	2003	2004	2005	2007	2017	2023
1	*Elliptio complanata*	18.8 (6.3)	17.0 (3.7)	23.5 (13.1)	6.4 (2.2)	7.8 (1.5)	-	4.2 (0.7)	1.1 (0.3)	0.4 (0.2)
	Lampsilis radiata	4.5 (1.0)	0.0	1.5 (0.3)	0.4 (0.4)	0.2 (0.2)	-	0.6 (0.2)	0.2 (0.2)	0.5 (0.3)
	Eurynia dilatata	0.0	0.0	0.0	0.0	0.0	-	0.0	0.0	0.1 (0.1)
	Total	***23.3 (6.5)***	***17.0 (3.7)***	***25.0 (13.1)***	***6.8 (2.2)***	***8.0 (1.5)***	***-***	***4.8 (0.5)***	***1.3 (0.4)***	***1.0 (0.4)***
2	*Elliptio complanata*	11.0 (1.4)	8.7 (2.3)	5.2 (1.4)	1.2 (0.6)	1.6 (1.2)	0.0	2.8 (1.0)	0.0	-
	Lampsilis radiata	0.3 (0.3)	0.3 (0.3)	0.8 (0.5)	1.2 (0.6)	0.0	0.0	0.1 (0.1)	0.3 (0.2)	-
	Total	***11.3 (1.7)***	***9.0 (2.3)***	***6.0 (1.8)***	***2.4 (0.7)***	***1.6 (1.2)***	***0.0***	***2.9 (1.0)***	***0.3 (0.2)***	-
3	*Elliptio complanata*	-	-	10.0 (4.2)	5.6 (1.4)	5.8 (1.7)	6.2 (2.0)	-	1.0 (0.3)	1.7 (0.4)
	Lampsilis radiata	-	-	0.2 (0.2)	2.0 (0.9)	0.2 (0.2)	0.1 (0.1)	-	0.2 (0.2)	0.1 (0.1)
	Total	-	-	***10.2 (4.1)***	***7.6 (1.8)***	***6.0 (1.8)***	***6.3 (2.0)***	-	***1.2 (0.4)***	***1.8 (0.4)***
4	*Elliptio complanata*	-	-	5.4 (0.8)	2.3 (1.7)	-	-	-	-	0.4 (0.2)
	Lampsilis radiata	-	-	0.0	0.6 (0.6)	-	-	-	-	0.5 (0.4)
	Total	-	-	***5.4 (0.8)***	***2.9 (2.3)***	-	-	-	-	***0.9 (0.4)***
5	*Elliptio complanata*	-	-	1.0 (0.3)	-	-	-	-	-	0.3 (0.2)
	Lampsilis radiata	-	-	0.2 (0.2)	-	-	-	-	-	0.1 (0.1)
	Total	-	-	***1.2 (0.2)***	-	-	-	-	-	***0.4 (0.2)***
6	*Anodontoides ferrucianus*	-	-	0.0	-	0.2 (0.2)	0.0	-	0.0	0.0
	Elliptio complanata	-	-	6.2 (1.1)	-	8.2 (1.4)	1.8 (0.6)	-	1.0 (0.8)	0.1 (0.1)
	Elliptio cf. crassidens	-	-	0.0	-	0.0	0.2 (0.2)	-	0.0	0.0
	Eurynia dilatata	-	-	0.2 (0.2)	-	0.0	0.2 (0.2)	-	0.0	0.0
	Lampsilis cardium	-	-	0.4 (0.2)	-	0.4 (0.4)	0.0	-	0.2 (0.2)	0.1 (0.1)
	Lampsilis radiata	-	-	0.8 (0.5)	-	1.2 (0.4)	0.7 (0.3)	-	0.6 (0.2)	0.2 (0.1)
	Lasmigona costata	-	-	0.4 (0.4)	-	0.0	0.0	-	0.0	0.0
	Leptodea fragilis	-	-	0.4 (0.4)	-	0.0	0.0	-	0.0	0.0
	Ligumia recta	-	-	0.0	-	0.0	0.2 (0.2)	-	0.0	0.0
	Pyganodon cataracta	-	-	0.0	-	0.2 (0.2)	0.0	-	0.0	0.0
	Total	-	-	***8.4 (0.9)***	-	***10.4 (2.1)***	***3.2 (0.7)***	-	***2.0 (1.0)***	***0.4 (0.2)***
7	*Elliptio complanata*	-	-	1.8 (0.6)	-	0.0	-	-	0.0	0.0
	Lampsilis radiata	-	-	0.4 (0.2)	-	0.2 (0.1)	-	-	0.0	0.0
	Lasmigona costata	-	-	0.0	-	0.0	-	-	0.1 (0.1)	0.0
	Leptodea fragilis	-	-	0.2 (0.2)	-	0.0	-	-	0.0	0.0
	Total	-	-	***2.4 (0.9)***	-	***0.2 (0.1)***	-	-	***0.1 (0.1)***	***0.0***
YEARLY TOTAL		**17.3 (6.0)**	**13.0 (4.0)**	**8.4 (3.0)**	**4.9 (1.3)**	**5.2 (1.9)**	**3.2 (1.8)**	**3.9 (1.0)**	**1.0 (0.3)**	**0.8 (0.3)**

Supplementary Materials

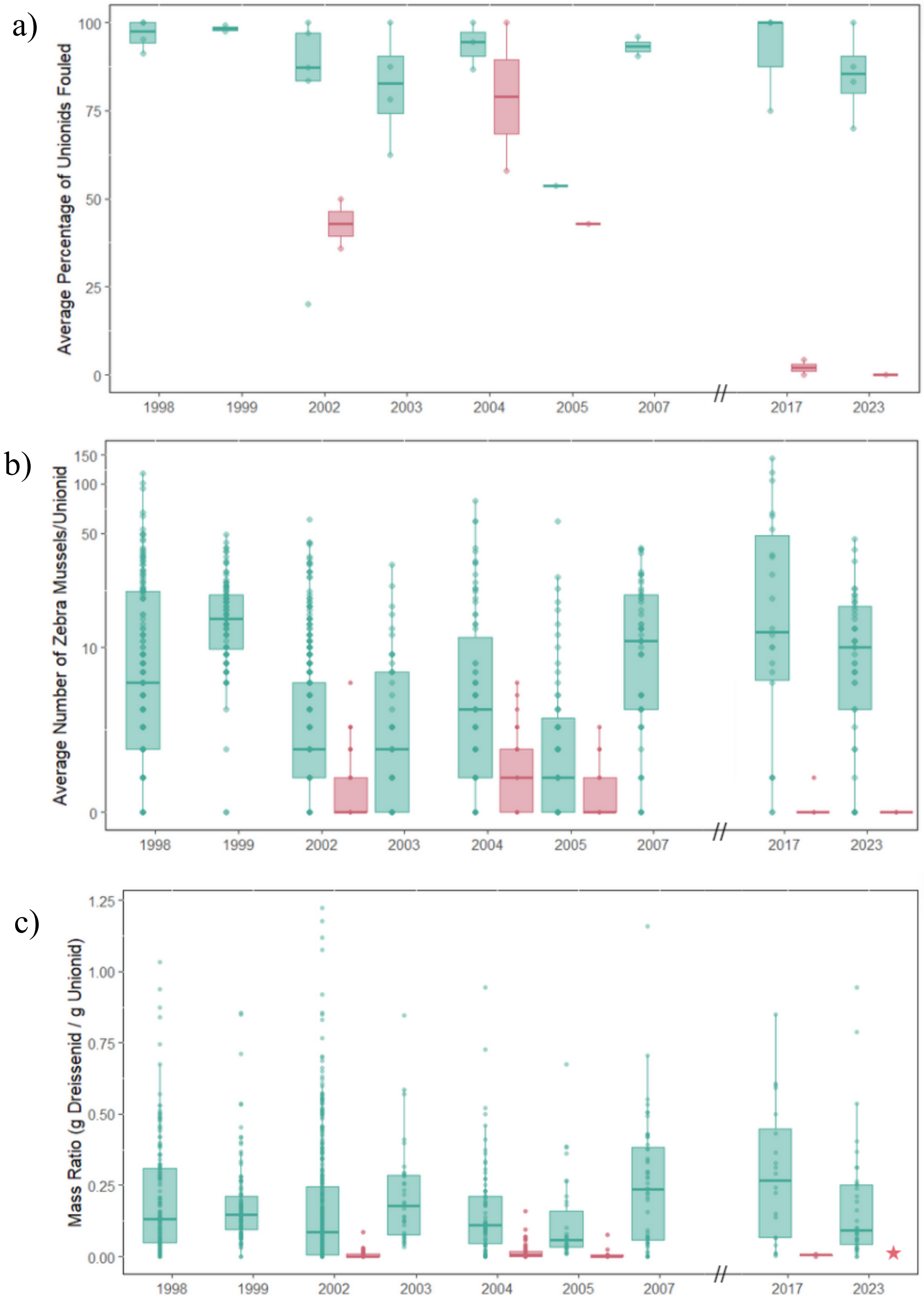

Figure S1: Mean fouling intensities on unionid mussels at sites above (green) and below (red) Chambly basin, in the Richelieu River. a) Percentage of unionids fouled (i.e. possessing at least one attached dreissenid) at a given site; b) Mean number of zebra mussels per unionid; c) Mean ratio of the mass of the attached dreissenid mussel cluster to the mass of the host unionid. The asterisk in 2023 denotes that no dreissenids were present this year below Chambly basin.

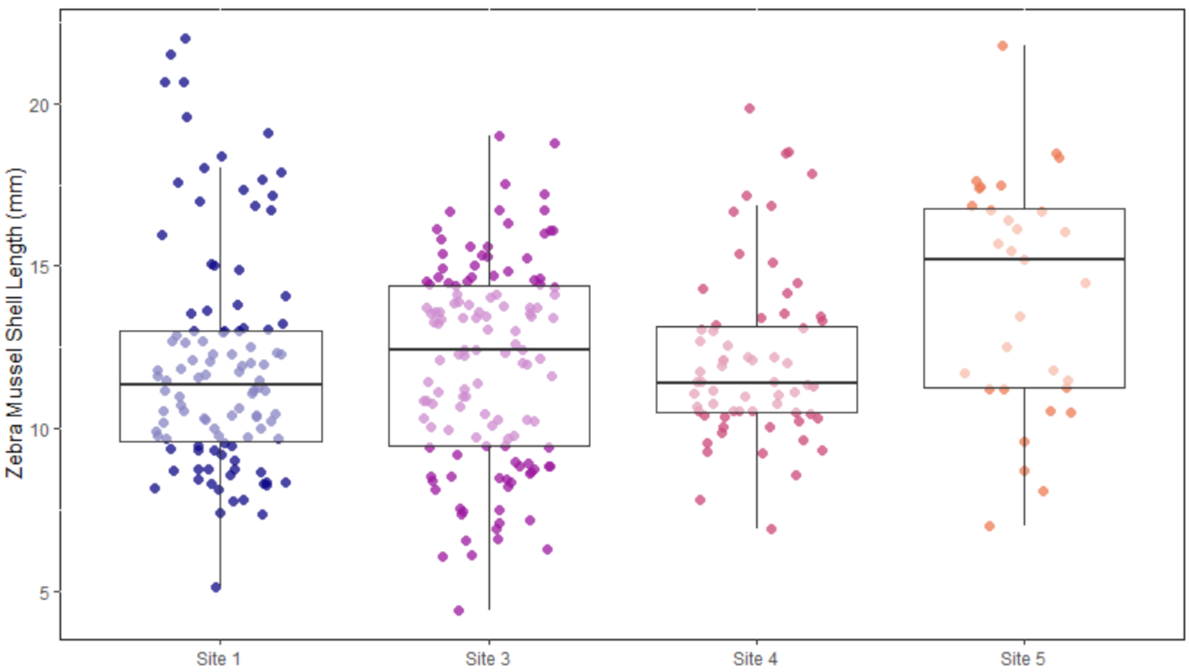

Figure S2: Mean zebra mussel shell lengths at the six sites sampled in 2023 (Site 2 was not sampled, and Sites 6 and 7 had no zebra mussels). Box and whisker plots show median (center horizontal bar) and upper (75%) and lower (25%) quartiles.

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Final Conclusions

Summary and significance of findings

Freshwater (unionid) mussels are North America's most imperiled faunal group (Ricciardi & Rasmussen, 1999), with most species having become endangered or extinct since the early 1900s because of multiple stressors. A serious additional threat that has manifested itself over the past few decades is invasion by dreissenid (zebra and quagga) mussels. Dreissenid mussels have extirpated and replaced unionids in many areas, but they are functionally very distinct from unionids and their presence in North American waterways has substantially changed freshwater communities (Ricciardi et al., 1997; Haynes et al., 1999; Ward & Ricciardi, 2007; Burlakova et al., 2012). The replacement of diverse assemblages of unionid mussels by dreissenid mussels is expected to alter ecosystem dynamics, given the roles bivalves play in inland waters (Howard & Cuffey, 2006; Vaughn & Spooner, 2006; Atkinson et al., 2013) and the differences between unionids and dreissenid activities—including, for example, sediment mixing and aeration.

This thesis aimed to gain a deeper understanding of temporal patterns of dreissenid impacts, so as to inform best practices of conserving freshwater biodiversity. The two chapters presented here explored how the impacts of invasion by dreissenid mussels unfold decades after their introduction, a topic rarely addressed in ecological studies. The findings emphasized the need for long-term investigations of the impacts of invasive species in general, as spatiotemporal variation is often significant and challenges prediction. Long-term studies are particularly relevant when the affected species are long lived, slow growing, and late maturing animals, as exemplified by unionid mussels.

Through multisite sampling of the St. Lawrence River and a major tributary, the Richelieu River, combined with the use of recent historical data from sporadic surveys since the 1990s, we noted 1) a sequence of rapid dreissenid colonization, intense fouling and associated unionid mortality in the early stages of invasion which led to exponential declines in unionid populations within a time period of ~5 years, fitting a general pattern similar to that observed in other waterways that support dense dreissenid populations (e.g. Schloesser et al., 2006; Burlakova et al., 2014; Lucy et al., 2014; Zanatta et al., 2015); and 2) confirmed the lack of recovery in the subsequent two decades that followed (Chapter 1). We found that unionids in the St. Lawrence River have still not recovered to their 1992 densities and appear to be in a limited co-existence with dreissenid mussels. By contrast, over the same time period, unionid populations in the Ottawa River did not experience substantive declines (Chapter 1). This conforms with the proposition that low-calcium environments like the Ottawa River could serve as refugia for unionid populations by constraining dreissenid population densities and associated fouling intensities (cf. Jokela & Ricciardi, 2008). Exploring this idea with the Richelieu River, which has a calcium concentration (18 mg/L) that is suboptimal for dreissenid populations (Whittier et al., 2008), revealed that unionids and dreissenids in the river are currently in an unstable co-existence, with some evidence of biodiversity erosion, perhaps driven over the long-term by continuous dreissenid larval supply from a headwater lake, Lake Champlain (Chapter 2).

Ideally, habitats that allow for stable co-existence between unionids and dreissenids would have conditions that strongly limit fouling intensity, provide sufficient amounts of food for both dreissenid and unionid mussels, support diverse and abundant host fishes, lack significant unionid predators, and contain dreissenid predators (Strayer & Malcom, 2018). Environmental heterogeneity can generate physical gradients that create local refugia (e.g.

Kestrup & Ricciardi, 2009) and therefore can mitigate the most severe impacts of invasive species on native species—as appears to be the case with the Ottawa River. Documented refugia for unionids are typically shallow habitats with fluctuating temperatures, water levels, and currents, all of which are unfavorable conditions for dreissenids (Zanatta et al., 2002; Bowers & Szalay, 2004; McGoldrick et al., 2009).

Although there are focused efforts on identifying unionid refugia in recent decades, there are very few documented cases of unionid populations recovering, partially or fully, after major ecological disturbances. Most of these instances involve management intervention (translocation) and were conducted primarily to test relocation methods, rather than repopulation of areas where unionids experienced a major disturbance (e.g. Carey et al., 2015; Tsakiris et al., 2017; Kamocki et al., 2021). For example, an experiment by Cope et al. (2003) found that translocated unionids in the St. Croix River (Minnesota and Wisconsin, USA) had an overall mean recovery of 95% after 2-3 years. Most cases of unionid recovery involve disturbances unrelated to invasive species. For example, the North Folk Holston River (Virginia, USA) became contaminated with mercury from pollution by a nearby chemical plant, which nearly extirpated the downstream unionid communities (Henley & Neeves, 1999). As stricter environmental protection practices were implemented, unionid richness has increased from 1 to 9 species between 1975 and 1995, and densities increased to a maximum of 2.6 individuals/m^2 (Henley & Neeves, 1999). In another scenario, the Kent River in Australia was experiencing rising salinity levels until action was taken in the 1970s and 1980s; in 2002, these management strategies had begun to take effect, and the river was declining to pre-disturbance salinity levels (Benson et al., 2019). Benson et al. (2019) noticed 17 years later that Australia's only freshwater mussel (*Westralunio carteri*) had begun to recolonize an area of the river near the outflow of another freshwater tributary. In both examples (see also Sietman et al., 2001; Metcalfe-Smith et al., 2000), the onset of unionid recovery was observed approximately two decades after the initial disturbance began to diminish. While dreissenid mussel densities in the St. Lawrence River are at their lowest densities since peak levels in ~1992 (Chapter 1), it is possible that an insufficient amount of time has passed to notice a trend in unionid population recovery.

The importance of long-term studies and implications for risk assessment

Unionids are long lived and slow growing species which allow for multi-year gaps in observation; the value that long-term data bring to the scientific community should not be limited by any hesitancy to publish research with inconsistent sampling efforts. Also, by returning to the Richelieu River in 2023, I was able to gather more specimens of variable forms that allowed me to more confidently distinguish between the congeneric species *Elliptio complanata, E. crassidens*, and *E. dilatata*—of which the latter two species are commonly confused for ecotypes or morphological variants of *E. complanata*. Without distinguishing between ecotypes and congeners, unionid diversity data would have been lost, leading to the underestimation of the number of species that have declined or become locally extirpated from southwestern Quebec.

Advancing our understanding of the temporal impacts of invasions can aid in developing and optimizing intervention strategies. The literature suggests that dreissenid invasion has significantly stronger impacts in habitats with a calcium concentration of >25 mg/L, whereas lower calcium environments are thought to be at low risk (Whittier et al., 2008). Chapter 1 demonstrated that unionid recovery from peak dreissenid mussel fouling is prolonged (if at all achievable) in high-calcium rivers that have supported dense dreissenid populations. The work presented in Chapter 2 suggested that even in a suboptimal habitat, long-term exposure to a dreissenid mussel population (albeit subsidized by a headwater source of larval supply) can reduce unionid abundance and diversity. Collectively, this work indicates that 1) preventing invasions—even in suboptimal environments—is a more prudent approach than assuming that dreissenid impacts will diminish immediately after the population falls to a lower equilibrium density; and 2) improvements to risk assessment require a larger database of long-term studies to identify general patterns of invader impacts.

Future Directions

It would be of significant interest to continue to monitor mussel assemblages at our sampling sites in the St. Lawrence River, to determine if a loose equilibrium has been reached, if declines continue to extirpation at some sites, or if they are recolonized by glochidia transported from the Ottawa River. Similarly, it remains to be determined if the limited co-existence of unionids and dreissenids in the Richelieu River persists. It would be worthwhile to study the role of source-sink dynamics in this context, and specifically the role of Lake Champlain as a continuing source of dreissenid larvae (cf. Horvath et al., 1996) and potentially of glochidia larvae. Further work could also synthesize multi-year data on fouling and survivorship of unionids across invaded sites so as to examine tendencies for certain unionid taxa to be more sensitive to the effects of dreissenids, owing to e.g. their burrowing behaviour, morphology, and reproductive strategies (Haag et al., 1993; Nalepa, 1994; Bowers and Szalay, 2004; Urbańska et al., 2019). Finally, identifying habitat characteristics that dampen the effects of fouling and thus could act as refugia for unionids would direct conservation activities and risk assessment (but see Nichols and Amberg, 1999; Zanatta et al., 2002; McGoldrick et al., 2009). More expansive surveys of environmentally heterogeneous aquatic systems would offer insights into the context-dependencies of invader impacts in general.

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